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Washington State University, 1990

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ARCHAEOLOGICAL IMPLICATIONS OF VARIABILITY

IN THE ECONOMIC ANATOMY OF *Bison bison*

By

ALICE MARIE EMERSON

A disseration submitted in partial fulfillment of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

WASHINGTON STATE UNIVERSITY
Department of Anthropology

May 1990

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of Alice M. Emerson find it satisfactory and recommend that it be accepted.

Chair

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materials without which the carcass dissection process would have been much more difficult and labor intensive.

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Subsequent to the completion of the laboratory analyses, an additional analysis of bison liveweight was carried out by examining data made available by several parks and refuges that maintain modern bison herds. Bison liveweight records were provided by Richard Klukas (Wind Cave National Park), Harvey Wickware (Theodore Roosevelt National Park), Jon Malcolm (National Bison Range) and Robert Ellis (Fort Niobrara National Wildlife Refuge). These data provided a means of evaluating the suitability of the TRNP specimens to serve as representatives of bison when the sample size was so small.

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ARCHAEOLOGICAL IMPLICATIONS OF VARIABILITY IN THE ECONOMIC ANATOMY OF *Bison bison*

Abstract

by Alice Marie Emerson, Ph.D.
Washington State University
May 1990

Chair: William D. Lipe

Production and distribution differences in the carcasses of four bison of different age, sex and condition provided by Theodore Roosevelt National Park are examined in order to better understand prehistoric patterns of bison use and archaeological remains. Quantitative differences in carcass yields (based upon weight and caloric value) are compared for individual and grouped products, including meat and protein, skeletal fat (marrow and bone grease), and carcass fat (intramuscular, intermuscular, subcutaneous and cavity depots).

Three phases of hunter selection in bison procurement are considered with respect to quantitative differences in yield: selection of herd types, carcasses, and carcass parts. The analyses indicate that differences in the yield and distribution of products within the carcass may be large enough to affect selection. Models of carcass unit utility, that recognize quantitative differences in yield, are presented and used to analyze archaeological assemblages of bison bone. Three model types--single class, averaged, and mixed class models--are applied under different analytical situations. The mixed class model represents a new development in body part utility modeling, where differences in yields between classes of animals are recognized and incorporated into calculations of carcass unit values.

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Applications of the models to two archaeological assemblages indicate that quantitative differences in yield do affect carcass unit selection, and that axial and appendicular units are abandoned at these two kill sites according to different selection criteria. Appendicular units appear to be abandoned most frequently with respect to the yield of skeletal fat, while axial units are abandoned with respect to the yield of combinations of products (e.g., a combination of fat products or all available carcass products).

A series of preliminary analyses, carried out to assess the representativeness of the bison sample, also provide results of potential importance to archaeologists studying bison procurement. Studies of liveweight records from modern bison herds yield (1) a more detailed picture of differences in male and female bison growth, (2) an indication that bison size may vary significantly between regions, and (3) evidence that substantial mean losses in liveweight may occur in conjunction with changes in weather that affect forage productivity.

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ARCHAEOLOGICAL IMPLICATIONS OF VARIABILITY IN THE ECONOMIC ANATOMY OF *Bison bison*

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LIST OF ABREVIATIONS

Part A. Carcass Units and Anatomical Parts

Unit	Description	Unit	Description
1ST	first phalanges	MAND	mandible
2ND	second phalanges	MTC	metacarpal
3RD	third phalanges	MTT	metatarsal
APHA	anterior phalanges	OTAR	other tarsals (excluding the astragalus
APHS	anterior phalanges with sesamoids		and calcaneus)
AST	astragalus	PATE	patella
ATLAS	atlas	PELV	pelvis
AXIS	axis	PPHA	posterior phalanges
CALC	calcaneus	PPHS	posterior phalanges with sesamoids
CARP	carpals	PFEM	proximal femur
CAUD	caudal vertebrae (excluding the	PHUM	proximal humerus
	first caudal vertebrae)	PMTC	proximal metacarpal
C2C7	cervical vertebrae (second through	PMTT	proximal metatarsal
	the seventh vertebra)	PRAD	proximal radius
C3C7	cervical vertebrae (third through	PRUL	proximal radius-ulna
	the seventh vertebra)	PTIB	proximal tibia
CERV	cervical vertebrae	RAD	radius
DFEM	distal femur	RIBS	ribs
DHUM	distal humerus	RUL	radius-ulna
DMTC	distal metacarpal	RULC	radius-ulna-carpals
DMTT	distal metatarsal	SAC	sacrum
DRAD	distal radius	SAC1	sacrum-first-caudal-vertebra
DRUL	distal radius-ulna	SCAP	scapula
DTIB	distal tibia	SKMAH	skull-mandible-hyoid
FEM	femur	SKWT	skull with tongue
FEMP	femur-patella	SKWOT	skull without tongue
HUM	humerus	SKULL	skull
HYOI	hyoid	SPEL	sacrum-pelvis
KKCF	kidney knob and channel fat	STER	sternebrae
LUMB	lumbar vertebrae	TARS	tarsals

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LIST OF ABREVIATIONS (continued)

Part A. Carcass Units and Anatomical Parts (continued)

Unit	Description	Unit	Description
TARM	tarsals and lateral malleolus	TIB	tibia
THOR	thoracic vertebrae	ULNA	ulna

Part B. Park Abreviations

Park	Description
FNNWR	Fort Niobrara National Wildlife Refuge, Timberlake, Nebraska
NBR	National Bison Range, Moiese, Montana
TRNP	Theodore Roosevelt National Park, Medora, North Dakota
WCNP	Wind Cave National Park, Hotsprings, South Dakota
WMWR	Wichita Mountains Wildlife Refuge, Cache, Oklahoma

Part C. Other Abreviations[a]

Abreviation	Description	Abreviation	Description
DMW	Difference of Mean Weight	MAU	Minimum Animal Units
GWT	Gross Weight Minus Dry Bone Weight	MNI	Minimum Number of Individuals

[a] See Table 8.4 for a list and description of utility model acronyms used in this dissertation.

CHAPTER 1. INTRODUCTION

Variability in the amounts of meat and fat present in the carcasses of bison of different age, sex, and condition, together with herd organizations that group animals into cow/calf, bull, or mixed herds, presented prehistoric and historic hunters with options for selection that were modified somewhat by other factors such as seasonal differences in the nutritional condition of the hunters themselves (Speth 1983) and their capabilities for maneuvering animals to kill areas (Frison 1970, 1978). It is the purpose of this dissertation to examine variability in carcass composition in bison, as represented by four specimens provided for this project by officials at Theodore Roosevelt National Park in North Dakota, and suggest selection priorities for herd types, carcasses, and carcass units in light of the quantitative differences in the yields of meat and/or fat.

This study of variability in the economic anatomy of bison includes investigations of differences in the production of carcass products between animals, as well as differences in the distribution of these products in the bison carcass. It is recognized, however, that the existence of differences in production or distribution may not always result in differences in hunter selection and use of bison of different age, sex, or condition classes. The magnitude of the composition differences are examined to determine whether they affect the rank of animals or body parts when they are ordered by their yield of carcass product(s). Changes in rank are potentially suggestive, though not necessarily indicative of areas that may show selection

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preferences. The importance of substantial differences between animal classes in product yield of a body part is reduced by selection models that average values across animal classes.

A series of body part utility models, similar to those of Binford (1978) and Metcalfe and Jones (1988), are constructed that indicate the relative value of different carcass units based upon their yield of one or more carcass products. These models are applied to two archaeological bison bone assemblages for several purposes. The applications permit the comparison and evaluation of the models constructed using two measurements of productivity: gross weight (Metcalfe and Jones 1988) and caloric yield, as developed in this study. The comparison of these models with the composition of archaeological bison bone assemblages potentially indicates where hunter selection of carcass parts was influenced by factors other than differences in the relative yield of carcass product(s). They also may suggest where one combination of products may have been more relevant to the composition of the resulting assemblage than other product combinations.

This study provides the first detailed account of differences in the economic anatomy of bison. It differs from Binford's (1978) study of the relationship between the economic anatomy of caribou and sheep and their use by Nunamiut hunters, in the recognition (inspired by the work of Speth 1983) that fat is a resource that may be as important as protein in guiding the selection decisions of hunters and gatherers, who like their prey are sometimes subjected to periods when available food is of low quantity and poor quality.

Three types of carcass unit utility models are presented and used in the analysis of archaeological bison bone assemblages. These include (1) single class models based upon carcass composition data from the individual

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bison used in this study, each of which may serve as a representative of a single animal class (e.g., immature males, adult males, adult females, and adult females in poor condition); (2) averaged models based upon the average composition of the bison studied; and (3) mixed class models based upon the composition of at least two animals classes, but which differ from averaged models in the maintenance of class separation. The mixed class model is a new utility model type, capable of dealing with differences in selection that result from differences in productivity between animals. This work also demonstrates that blind applications of utility models, without consideration of pertinent butchering information and data on taphonomic disturbances can lead to misinterpretations of selection and illustrates the need for more detailed information on bone counts as they relate to butchering practices.

History of Research

This project was inspired by the works of John D. Speth and Lewis R. Binford, and has been affected by the recent work of Duncan Metcalfe and Kevin T. Jones. The extensive work of George C. Frison who is perhaps the leading authority on prehistoric bison procurement and butchering patterns has also been important to the evaluation of the models presented in this dissertation. His work has been fundamental to determinations of site seasonality, herd type, age structure, and butchering patterns, and his methods of analysis have become standard practice in this field. In this study, Frison's influence is clearly evident in the derivation of the site data from the Glenrock Jump (Frison 1970), but it is also evident in Speth's (1983) descriptions of the Garnsey Site data. Without his methods of analysis, the differences evident in the bone assemblage compositions of

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these sites would be less clearly understood. A detailed review of the methods Frison uses that yield the assemblage composition data are not necessary to understand the focus of the of the current research. The remainder of this section, therefore, concerns the works of Binford, Speth, and Metcalfe and Jones.

Binford's Study of Economic Anatomy and Bone Assemblage Composition

In an ethnographic study of Nunamiut hunting and butchering practices, Binford (1978) was the first archaeologist to relate the numbers and kinds of bones found in archaeological site assemblages to direct measurements of the economic value of the associated body parts. He found that relative preferrences for particular parts of a caribou or sheep carcass are strongly affected by the quantity and quality of the edible components associated with the body parts. Parts of high economic value are generally most preferred, and parts of low value are least preferred.

Binford included meat, bone marrow and bone grease in his calculations of the economic value of the anatomy of these sheep and caribou. With measures of the yields of these products in different parts of the carcass, he constructed specific and generalized models or indices that express the value of each body part relative to others. The marrow index (MI), the white grease index (WGI), and a model he designated the meat utility index (MUI), but which in actuality includes more than meat, Binford combined into a generalized model, the general utility index (GUI), which expresses the value of a body part as a function of the combined value of its meat, marrow, and white grease resources. He modified the GUI to account for the fact that some limb units are removed from kill sites in higher proportions than would expected from their GUI values. Some units or body parts are

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removed from kill sites in higher proportions than their GUI values would predict, Binford suggests, because their values increase as a function of the average of the values of the surrounding, more highly valued parts. This modification for what Binford calls "riders" yields the modified general utility index (MGUI). Although these are only some of the numerous models Binford presents, these are the models that are relevant to the present study.

After constructing indices of relative body part utility, Binford compared (through graphic means) these values to the corresponding calculations of the percentages of these bones abandoned at Nunamiut sites, relative to the numbers that might possibly have been abandoned (which he expresses as percent minimum number of individuals). In these graphs he found a negative relationship between the frequencies with which bones are abandoned at kill sites and the MGUI model values of the associated body parts. That is, units of high MGUI value were infrequently abandoned at kill sites, but parts of low value were often left behind. He also demonstrated that the composition of bone assemblages from other types of sites, such as processing or habitation sites, differ from those of kill sites, because they represent a different set of decisions and actions with regard to body part utility. For example, the numbers of proximal femora at kill and processing sites differ, with low proportions of these units left behind at kill sites because high proportions are taken to processing sites.

Binford's MGUI model has been used increasingly by archaeologists to determine when the composition of bone assemblages is consistent with the pattern for kill sites as opposed to other site types. The acceptability of this approach, given the fact that caribou models are often applied to other species such as bison, was first expressed by Binford, himself. Binford

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(1978:475) concluded that there is marked correlation in the proportional values of body parts of sheep and caribou and that this similarity suggests that models based upon the economic anatomy of these ungulates could be applied to other ungulates in the absence of data for these species. He then applied his caribou-based models to two bison bone assemblages and noted that although somewhat more "fuzzy" (indicating the points on the plot did not form as tight of a curvilinear pattern as did the model application to caribou assemblages), the applications could help to distinguish between kill and processing site assemblages. Some of the fuzziness, Binford attributed to potential differences in the anatomy of caribou and bison.

Although Binford clearly recognized the potential for the influence of age and sex differences between animals affecting carcass part use, he suggested their importance was minimal in the application of utility models. He suggested that age and sex differences in economic anatomy were largely evident in differences in body size and the corresponding differences in absolute product yields. He apparently did not expect there to be a marked difference in the distributions of meat and fat products in the carcasses of animals of different age, sex, or condition. Standardized models of body part utility (e.g., Binford's MGUI) are constructed to reflect proportional differences in the yield of carcass products in one part compared to another, and therefore, distributional differences in yields within carcasses may be more important than generally considered. Binford felt that resource distribution differences between the carcasses of animals would be small, and that utility models based upon members of one sex or age group would not differ substantially from those of other groups. Binford's position that distribution differences would have minimal effect on the values derived for utility models suggests that he would not attribute the

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plot line fuzziness noted above to differences in hunter treatment of animals carcasses of different age or sex except as they reflect size differences.

Speth's Evaluation of Differences in Carcass Productivity

In a landmark work, Speth (1983) argued that meaningful differences probably do exist in the proportional and absolute yields of carcass products in bison due to differences in age, sex, and animal condition, and that these differences are evident in the archaeological record through selective differences in butchering as seen at the Garnsey Site. Speth's report on the Garnsey Site bison assemblage differed from previous studies of bison kill sites in the detailed analysis of the bone to determine the numbers of male and female elements. With these data, he found that although the majority of animals killed at the site were male (based upon the numbers of skulls and pelves), most of the postcranial bones abandoned at the site were those of females. Speth also found that in examining the major marrow yielding limb bones, that a greater proportion of the unfused than fused bones remained unbroken, suggesting less use of the low-fat marrow of younger animals.

These differences in the use of the same carcass part between classes of animals, Binford (1978) and Metcalfe and Jones (1988) would attribute to differences in animal size. Speth argues, however, that differences in animal condition and in the relative yields of fat could also account for these differences. Speth cites literature from the agricultural sciences and wildlife studies to show that: (1) pregnant and lactating females generally are in poorer condition than non-reproductive cows and bulls during the early spring, and they should provide lower fat yields than

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males, thus accounting for the greater representation of female bones at the site; (2) the female bones that are present at the site in higher proportions than their index values would lead one to expect (e.g., proximal and distal humerus), are bones that mobilize fat during periods of nutritional stress at a faster rate than more distal bones; and (3) a greater percentage of unfused than fused limb elements are complete and this might be attributable to the lower marrow fat content of younger animals. None of these differences in fat yield between members of different animal classes are directly related to body size. This fact demonstrates the need for greater knowledge of differences in carcass composition, and the effect these differences have on modeling selection by hunters.

The influence of fat yield on selective butchering at the Garnsey Site, Speth attributes to the spring seasonality of the site, the condition differences of the animals represented at the kill, and the nutritional requirements of the human population. He notes that for hunters and gatherers, the spring season is a period when potentially diminishing stored food supplies may coincide with the senescence of edible plants, thus reducing the proportion of dietary energy provided by carbohydrate, and potentially reducing total caloric intake. The greater reliance, under these circumstances, on hunted foods leads to an increase in the proportion of dietary energy provided by protein. The lack of carbohydrates in conjunction with reduced caloric intake increases the importance of fat in the diet. The metabolic costs (referred to as specific dynamic action) of ingesting a diet primarily consisting of protein (20-30 percent) are much higher than for fat (four percent) or carbohydrate (six percent). Speth notes that "reliance on fat-depleted meat would have elevated the total energy needed to support a group of hunters" (1983:153).

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The importance of fat during periods when carbohydrates are generally unavailable and caloric intake is low is also related to the fact that humans are limited in the amount of protein they can consume. Speth (1989:330) notes that there is a ceiling of approximately 50 percent (300 gm) to the amount of protein that humans can consume for calories on a sustained basis; the ceiling may in fact be considerably lower for pregnant women (Speth, personal communication). Exceeding this limit for prolonged periods of time can lead to deleterious health effects and sometimes death. Speth (1983:157) suggests that ethnographic accounts of meat gorging may be explained as a short-term measure used to meet caloric needs when carbohydrates are absent and fat limited. He (1989) clearly shows that such a lean meat diet could not be sustained for extended periods of time. He (1983) suggests the need for fat and the need to limit the metabolic costs of eating lean meat may have lead to the selection against poorly conditioned and fat-poor animals at the Garnsey Site.

Speth's work clearly demonstrates the need for greater knowledge of the economic anatomy of the game animals that prehistoric and historic hunters and gatherers exploited. His work also suggests that the model constructions that Binford (1978) presented in his pioneering work relating economic anatomy to archaeological bone assemblage composition are not entirely adequate as constructed to fully deal with the complexities of animal class differences in product yields and composition, and hunter selection.

Metcalfe and Jones's Modifications of Utility Model Construction

Duncan Metcalfe and Kevin T. Jones have collaborated to produce two papers--one concerned with Binford's MGUI index (Metcalfe and Jones 1988)

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and the other with the marrow index, MI (Jones and Metcalfe 1988)--using Binford's caribou and site assemblage data to construct simplified utility models and evaluate their capabilities of predicting body part selection. Their paper (Metcalfe and Jones 1988) on the generalized utility model is of primary importance here.

Metcalfe and Jones (1988) examined Binford's method of constructing the modified general utility index (MGUI) and concluded that it is unnecessarily complex. Binford's MGUI is a model of body part utility that incorporates the values for the production of meat (MUI), marrow (MI) and white bone grease (WGI). Metcalfe and Jones (1988) present a simplified model to substitute for MGUI, which they call the standardized, food utility index, (S)FUI. This model is constructed by subtracting the weight of dry bone from the gross weight of each anatomical part, standardizing the values by expressing these weights as proportions of the weight of the largest part, and modifying these standardized data by applying Binford's averaging routine to the values of the limb elements to account for the effect of riders. This (S)FUI model provides comparable results to Binford's MGUI model when applied to Nunamiut kill site assemblages.

The point of their work, Metcalfe and Jones suggest is that the construction of (S)FUI utility models for other species of animals eliminates the need for the detailed data necessary for construction of the MGUI model, a fact which they hope will encourage new studies of the economic anatomy of other species. Their work also suggests that the lack of fatty acid data for bison originally planned as a part of this study may not be as detrimental as first thought. The exclusion of fatty acid data in the construction of the (S)FUI model did not reduce its usefulness in identifying kill site assemblages at Nunamiut sites (Metcalfe and Jones 1988).

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In light of Speth's analysis of the sexual differentiation of selection and butchering at the Garnsey Site and his discussion of potential age, sex and condition differences in productivity between bison, perhaps one of the more interesting observations made by Metcalfe and Jones (1988:500) is their contention that the FUI model is capable of handling animal class differences in body part yield. Their statement provided the impetus for the construction, in this dissertation, of a series of mixed class models. These models allow investigation of selection between animals of different classes (based upon sex, for example) at sites (unfortunately few in number, to date) where the class distribution of the bone assemblage has been analyzed. Such models are inappropriate at sites where analyses of differences in animal class use have not been done. At bison kill sites such as these, averaged or single class models provide a means of analysis using data derived specifically for this species.

Organization of the Dissertation

The remainder of this chapter is devoted to a brief overview of the organization of this dissertation. Chapters 2 and 3 include discussions concerned with the suitability of using the four Theodore Roosevelt National Park (TRNP) bison as representatives of these animals, in both their modern and prehistoric forms. Chapter 2 includes: descriptions of the four bison; an analysis of bison growth as determined by reports of fall roundup weights for animals of different age and sex classes at five National Parks and Wildlife Refuges; and analyses of the size of the TRNP bison compared with other modern herds based upon this growth data, as well as size analyses based upon comparison of bone measurements from specimens of known sex as

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reported by Speth (1983). Chapter 3 examines the suitability of the TRNP herd as a source of animals to serve as representatives for bison with respect to their general condition. It includes a discussion of the relationship between climatic data, and individual bison weight changes measured on an annual basis at Wind Cave National Park, for the purpose of estimating the general condition of the TRNP herd in the absence of annual, individual liveweight data for this herd.

Chapter 4 presents the procedures and methods used to generate the data for this study of the economic anatomy of bison. This discussion is limited to descriptions of field and laboratory procedures.

Chapters 5, 6, and 7 present the carcass composition data, and discussions of variability in the production and distribution of individual carcass products in bison. Chapter 5 concerns differences in the production and distribution of bone and bone products in the carcasses of the four bison. This includes analyses of marrow and bone grease fat. Chapter 6 concerns variabilty in the production and distribution of meat, protein, and intramuscular fat. Chapter 7 focuses upon other carcass fat depots, including the intermuscular, subcutaneous, and body cavity depots. These discussions of variability include assessments of whether the class differences in productivity are large enough that they produce different orders of body parts when ranked by yield for each resource.

Chapter 8 concerns the three phases of selection that are represented by the bone assemblages at bison kill sites. These include: choosing herd type, determining which carcasses to butcher, and selecting carcass units for removal to processing, camp or habitation sites for later consumption. In this study, these selection phases are all evaluated in terms of the quantitative yield of carcass products for bison of different age, sex, and

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condition classes. The discussion of carcass unit selection turns the focus of this dissertation to models of body part utility. It includes a discussion of how they are constructed, and presents new models for bison based upon both old (as described by Metcalfe and Jones 1988) and new construction procedures.

Three model types are described including single class, averaged, and mixed class models. Single class models of carcass unit utility are based upon the data from one of the four bison studied. These models are meant for application to assemblages that are dominated by bison of the same maturity or sex class as the individual providing the data for model construction. Averaged models are based upon the mean yields from all four bison and are useful for application to assemblages including mixed animal classes, but for which detailed class analysis of the bone has not been done. Mixed class models have more limited application possibilities. They are suitable for site applications to assemblages that have detailed analyses of class distributions of bone, and that represent a single event kill. Models of these three types are presented which include different combinations of carcass products, such as all carcass products, as well as more limited product models that include single resources, such as marrow fat or protein.

In Chapter 9, the models that were developed and presented in Chapter 8 are applied to two archaeological bison bone assemblages--the Glenrock Jump (Frison 1970) and the Garnsey Site (Speth 1983)--both of which represent late prehistoric bison kill sites with limited post-depositional disturbance. The Glenrock Jump includes the remains from a fall season kill, while the Garnsey Site represents a spring season procurement episode. These applications are used to compare the construction of models based upon

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caloric yield, as developed here, and gross weight as represented by Metcalfe and Jones's (S)FUI model. The model-site assemblage applications are also examined for the purpose of evaluating the usefulness of the models for identifying potential priorities of product selection as represented by the composition of the bone assemblages.

The dissertation is concluded with Chapter 10. This chapter includes a summary of the major results, assessments of the usefulness of selection modeling, and suggestions for future research.

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CHAPTER 2. DESCRIPTION OF THE BISON SAMPLE: PART ONE

Four Bison bison were killed to provide the data for this study of bison carcass composition and utility. Additionally, one of the cows was carrying a fetus when killed, which provides a fifth individual for some of the analyses. By all standards, this sample is too small to be statistically representative, but given the lack of composition data available for bison, these animals provide needed baseline information. In this and the next chapter, this bison sample is described and their suitability for use as representatives of bison in general, and as members of their respective age and sex classes is considered. In this chapter, the investigation largely focuses on evaluating the sample specimens with respect to their size, while in Chapter 3, the focus is on the evaluation of herd condition. In both cases, the objective of these studies is to determine how well the sample animals reflect the average state in bison. Such an assessment is necessitated by the goals of this project. It is impossible to understand the meaning of differences in carcass composition between these sample specimens without knowing what the norm is and that the individuals used in the study do not differ from it markedly.

This chapter includes a description of how the animals were selected and a discussion of how that selection affects the current study. Before the sample is evaluated with respect to animal size, each individual is described in terms of its age, sex, and reproductive status. The issue of animal size is examined by consideration of: (1) the size of the individual specimens compared to members of the herd of origin, which is done to

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determine whether they are representative of their herd; (2) the size of the animals of this, the Theodore Roosevelt National Park (TRNP) herd compared with other herds of modern bison, which is done to determine if this herd is representative of bison in general; and (3) the size of the bones of the sample animals compared to those of other modern bison, which is done to determine if weight differences are reflected in bone attribute size differences. Measurements of bone are the primary source of data available to archaeologists interested in the size of historic and prehistoric bison. For this reason, the bone size data are presented in this chapter, despite their inadequacy to address questions of how weight differences are reflected in bone measurements.

Background to Sample Selection

The sample of animals used in this study of variability in Bison bison carcass composition was not selected with the purpose of studying such variability. Instead, this sample and dissertation reflect the results of a change in the source of sample specimens and an associated loss in selective control of the age of those specimens. Originally, a sample composition was chosen which was designed to compare sexual and seasonal differences in bison carcass composition, using sexually mature animals. That project called for the selection of four bison, two adult males and two adult females, all of similar age, which were to be collected at two intervals--once each in the spring and fall--with one male and one female collected during each period.

Prior to collection of the first group, the source for these bison had to be changed from the National Bison Range at Moiese, Montana to Theodore Roosevelt National Park in Medora, North Dakota. Initially, it appeared

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that this change would not adversely affect animal selection, except to decrease the control over the selection of animals of specific ages. This factor became important, however, during the collection of the second, or fall, group of animals, when an immature male, and a significantly older female were chosen by park officials for collection. The animals used in this study, therefore, are not ideal choices given either the original project objectives, or the current focus on variability in carcass composition. To address the originally proposed problem, the animals should have been closer in age to one another and all of adult breeding status. To address the question of the range of variability, it would have been better to collect all the animals in one season to reduce the effects of variability tied to seasonal changes in animal condition, thus focusing on sex and age as factors influencing variability.

Location of the Bison Source

There are numerous parks and wildlife refuges in the United States and Canada that support populations of bison. The four bison used in this study were collected from Theodore Roosevelt National Park (TRNP), Medora, North Dakota. The park is located in southwestern North Dakota, in a part of the mixed-grass prairie known as the Little Missouri River Badlands. The park consists of two units separated by approximately 44 miles (70.8 km). The animals in this study were collected from each of the two park units during two collections periods.

The reliance of the TRNP bison upon the natural vegetation for their subsistence, without supplemental feed, makes this an excellent source for study animals. In some parks, the bison population is given supplemental feed during periods of stress, and their carcass composition might not

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reflect accurately the changes that would occur in the natural state. A discussion of the effects of the local climate and vegetation upon the growth and development of the animals is presented in the next chapter.

Description of the Sample

This section is devoted to a description of the animals collected to study bison carcass composition. It includes a discussion of the sex of the animals, the season they were shot, their reproductive status, and their relative size as individuals representing their age and sex classes.

Seasonal and Sexual Description of the Bison Sample

As previously noted, four Bison bison were killed during two seasons at Theodore Roosevelt National Park (TRNP) for use in this study. An adult male and an adult female were collected April 8, 1985 from the south unit of the park, and an immature male and an adult female were collected October 3, 1985 from the north unit. For ease of discussion, the animals in this study are referred to by acronyms indicating the season of collection (spring or fall), their age class (adult, yearling, or fetus), and their sex (male or female). For example, the spring collected, adult male is designated, SAM, indicating Spring Adult Male. The animals and their acronyms are listed in Table 2.1. It should be noted that the female collected in the spring (SAF) was pregnant, thus producing a fifth individual (SFM, spring fetal male) for the sample.

Age of the Animals

A variety of information was used to determine the ages of the sample individuals. Animals collected from the north unit of the park (FAF and

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Table 2.1. Acronyms for Bison bison Study Specimens Collected from Theodore Roosevelt National Park, 1985

Acronym	Season of Collection	Age Class	Animal Sex
SAM	Spring	Adult	Male
SAF	Spring	Adult	Female
FAF	Fall	Adult	Female
FYM	Fall	Yearling	Male
SFM	Spring	Fetus	Male

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FYM) had eartags that were correlated with park records indicating the years of their births. These records indicate that FAF was 16-1/2 years old and FYM 1-1/2 years old when they were collected October 3, 1985.

Records of age were not available for the animals collected April 8, 1985, from the south unit of the park. Frison's (1982) age classes for spring killed animals, from the Agate Basin Site, which are based on mandibular tooth eruptions and wear, were used to estimate the age of these animals. From these data, it appears that SAM was approximately four years old. The data for SAF indicate she might have been approximately six or seven years old. Descriptions of the dentition of these and the two bison of known age are presented in Table 2.2. The fact that age estimates for the animals of known age, FAF and FYM, using Frison and Reher's (1970) age classes for fall killed animals, correlate well with their age records, offers some assurance that Frison and Reher's methods were applied correctly, and thus, the estimates for SAM and SAF are probably reasonable.

Age of the Bison Fetus (SFM)

Reynolds et al. (1982:979) report that calves generally weigh 14 to 18 kg (30.9 to 39.7 lb) at birth. Meagher (1973:39) cites Park who gives a range of 30 to 70 pounds (13.6 to 31.8 kg) for calves at birth. Approximately two to four weeks prior to the beginning of the calving period, the fetus, SFM, weighed only thirteen pounds (5.9 kg). To estimate the age of the fetus, external characteristics were recorded at the time of sample preparation. Given the lack of information on the external characteristics of bison embryo development, comparisons were made to the development of the cattle embryo. Sorensen (1979a:121) reports the gestation period for bison is 276 days, and in cattle ranges from 278 to 293

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Table 2.2. Descriptions of Mandibular Dental Eruption and Wear in Study Bison

Study Specimen	Age Group	Description of Mandible Dental Eruption and Wear
SAM	Group 4[a] 3.6-3.9 yr	-Teeth present include two permanent incisors (I1, I2), one deciduous incisor (I3), one deciduous canine (C), and all permanent cheek teeth (P2-P4, and M1-M3). -Wear on P4 is slight and tooth is not to full crown height (deciduous P4 was still present over permanent P4 on left side). -M1 in wear, but anterior enamel is not yet impacted by P4. -M2 exostylid just coming into wear; tip shows wear, but dentine is not exposed. -M3 is fully erupted; hypoconulid shows little or no wear; exostylid is well below crown surface; no wear yet on facet VII.
SAF	Group 6[a] 5.6-5.9 yr or Group 7 6.6-6.9 yr	-Teeth present are all permanent dentition. -All incisors are in wear with dentine visible. The canine shows only slight wear. -M1 enamel is not above the level of the alveolus; crown enamel worn at cranial edge by P4. -M2 exostylid is in wear. -M3 hypoconulid is in wear, but the exostylid is not in wear.
FAF	Group VII+[b] 10.5-13.5 yr Known age 16.5 yr	-Left side of mandible is aberrant, which may result in abnormal wear. -Teeth present are all permanent dentition. -I1 and I2 on left side worn to gumline. Other incisors worn to gumline on lingual side; canines nearly to gumline. -All teeth are heavily worn. M1 worn nearly to alveolus on anterior lingual cusp; the prefossette is no longer visible for anterior cusp, but is present on posterior cusp. -M3 exostylid is tear-shaped.
FYM	Group II[b] 1.5 yr Known age 1.5 yr	-Teeth present include deciduous incisors, canines, and premolars, and permanent M1 and M2. -Roots of deciduous premolars P2 and P3 are visible. -M1 is erupted and to the level of the other teeth and shows some wear. -M2 is erupting and shows no evident wear. -M3 can be seen through opening behind M2.

[a] Age class based upon groupings described by Frison (1982:244-247) for spring killed animals.

[b] Age class based upon groupings described by Frison and Reher (1970:46-47) for fall killed animals.

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days (1979b:420), depending upon the particular breed. Burns (c.f., McHugh 1958:31) reports variable gestation periods ranging from 270 to 300 days for bison. Haugen (1974:7) reports that a gestation period of approximately 285 days correlates with the timing of rut-related behavior and the calving period, and argues that a nine month period (270 days) is too short for bison gestation. A gestation period of 285 days is assumed for the purposes of this study.

Assuming comparability in bison and cattle embryo development, the bison fetus was at least 182 days old, but less than 230 days. At 182 days of gestation, the cattle embryo has hair on its tail and horn buds, and at 230 days, the body is fully covered with hair (Sorensen 1979b:369). The carcass of SFM showed the former characteristic, but not the latter. On the head, sparse hair was noted on the muzzle, just above the eyes, in the ears, and at the horn buds. Postcranially, a small amount of hair was present on the hide around the juncture of the hide with the hooves, along the back of the rump, and on the tail. Despite the presence of this hair, the fetal carcass had the appearance of being nearly hairless. When examining the carcass, I failed to note whether or not the eyelids were unsealed. This is a development which occurs by 196 days of gestation (Sorensen 1979b:369). Using a gestation period of 285 days, and again assuming comparability in bison and cattle development, one may estimate the birth of the fetus to have been at least 55 days away, but not more than 103 days. Given the small size of the fetus and the lack of full body hair, one might judge the end of gestation to be closer to 103 than 55 days. This would suggest a calving period for this fetus sometime between June 2 and July 20, but probably closer to the July date. McHugh (1958:30) notes the calving period for bison generally runs from April 15 to May 31 in the Yellowstone region

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herds and similar periods occur at Wind Cave National Park in South Dakota. He also reports that it is not uncommon for a few calves to be born from June through October, and that occasionally, a calf comes between November and March.

Reproductive Status

Excluding the fetal bison, three of the four bison in this study (SAM, SAF, and FAF) were of breeding age; FYM was not. Lott (1974:383) and McHugh (1958:25) report that male bison are sexually mature at three years of age, but generally do not successfully compete for breeding privileges until they are five years old. Shult (c.f., Haugen 1974:3) reports that three of six yearling male bison, five of six two year olds, four of five three year olds, three of three four year olds, and the five year old bull studied at South Dakota and Nebraska ranges were all in breeding condition (i.e., sperm were present in the epididymis of the testes). Haugen (1974:3) notes, however, that it is not probable that a yearling would have the opportunity to breed, because at that age they lack dominance over cows, which he suggests is necessary for successful copulation in cattle. Halloran's (1968:25) work in Oklahoma shows that without competition from older bulls, two year old bulls are capable of siring young. Maher and Byers (1987:95), in a study of age-related changes (ages one through 12) in male bison reproductive behavior, note that under natural conditions participation in the rut started in bulls aged five to six years old, that reproductive effort peaked between eight and eleven years, and slowed again beginning at 12 years.

Females may breed as yearlings, giving birth as two year olds (Halloran 1968:23), but this is rare. Haugen (1974:2), Lott (1974:383), and McHugh

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(1958:30) concur that age two is generally the earliest that bison cows breed, thus first giving birth as three year olds. There seems to be some variability in the reproductive rates of breeding age cows, depending upon both age and animal condition. McHugh (1958:30-31) reports that the pregnancy rate recorded at the National Bison Range between 1950 and 1953 was 87 percent for cows between the ages of two and 12 years, 77 percent between 15 and 18 years, 58 percent between 19 and 24 years, and 21 percent between 25 and 35 years. Green (1986:739) reports a decline in fertility at Wind Cave National Park at 18 years, and cites McHugh and Rutberg, as reporting declines after age 12. Shaw and Carter (1989) found calving rates were lower in cows two years old and older than 13 years than in in cow three to 13 years old at the Wichita Mountains Wildlife Refuge.

In a study of the effects of age and previous year calving on bison productivity, Halloran (1968:24-25) found productivity to be approximately 67 percent for the cows he studied that ranged in age from three to eight years. He suggests that this is higher than the rate for the herd in general, because it excludes cows of older ages and lower fertility. He also found generally reduced productivity for the herd following years of large calf crops, and correlated reduced carcass weights with years following high calf crops. This change in productivity, therefore, could be correlated with a change in animal condition. Lott and Galland (1987:683), in their study of bison at Santa Catalina Island, found only 35 percent of the cows gave birth in a year, and attributed the difference between this and the National Bison Range population to differences in habitat productivity. In a study of bison from the Badlands National Park, Berger and Peacock (1988) concluded that calving in alternate years was not demonstrated for individuals. From these data, one can see that pregnancy

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rates in bison are highly variable, and based upon the work of Halloran (1968) and Lott and Galland (1987), are strongly tied to animal condition.

Reproductive Status of SAM

At the time SAM was killed, he had left the cow/calf herd and was part of a bull group, as is common for males beginning at approximately four years of age, but occurring as early as two years (McHugh 1958:14). Based upon the work of Maher and Byers (1987), it is unlikely that SAM participated in the rut the previous year, at approximately 3-1/2 years. It is also unlikely that he would have participated the following fall, had he not been killed. From their work, one may expect that SAM engaged in some breeding activity behavior, as do typical young males, but the amount of effort expended in these activities would be lower than that expended by older males that are large enough to successfully compete for estrous females. The fat composition of SAM, therefore, should be affected only marginally by activities associated with the rut. The primary factor affecting fat composition in SAM should be related to his nutritional condition, age and sex.

Reproductive Status of SAF

As noted earlier, SAF, at six or seven years of age, was carrying a fetus when she was killed. Given the size and external development of the fetus, it appears that SAF bred relatively late during the rut--possibly as late as the first week of October, most probably after the last week of August, perhaps sometime in late September. It is not known whether SAF calved the previous year. Shaw and Carter (1989:897) report that bison cows do not necessarily calve in alternate years, as noted by Halloran (1968) in

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an earlier study of Oklahoma bison. If SAF did not calve the previous year, then one might expect her to be in relatively good condition compared with a female who did produce a calf the preceeding year. Halloran's (1968:23) work with the Wichita Mountain Wildlife Refuge herd supports this, at the herd level. He found that mean carcass weights for cows following a year of heavy calf crops was lower than for years following lighter calf crops. Shaw and Carter (1989:897) suggest that nutritional stress might also have been a factor. One might expect that the fat composition of SAF should be influenced by her nutritional condition, age, sex, and reproductive status.

Reproductive Status of FAF

The other bison in the sample that was of breeding age was FAF, a 16-1/2 year old female. It is rare to find reports of animals more than 15 to 20 years of age in the herds maintained by state and federal agencies in this country, although Clark and Stromberg (1987:264) report that bison may live to be 41 years of age. This may be attributed, in part, to difficulties related to living in a wild state, but it is sometimes due to policies governing the age at which animals are culled from the herds. Despite the relatively advanced age of FAF, she had calved the previous spring. As noted earlier, cows in the 15 to 18 year age class at the National Bison Range still maintained a high rate of pregnancy in the years 1950 to 1953 (McHugh 1958:31). Shaw and Carter (1989:897) found reduced calving rates (only 45 percent) in cows older than 13 years at the Wichita Mountains Wildlife Refuge. Given the fact that FAF had calved the previous spring, she would not be expected to be in better condition than would be normal for a reproducing female of similar age, killed in the fall. Fat composition in this animal should be largely affected by her reproductive

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status, nutritional condition, sex and age, and may be poorer from other females that skipped calving the previous year.

As noted above, Halloran's (1968) study of calving rates and percent carcass yield showed decreased mean weights following years of high calf crops. This might be attributed to the combined affects of the nutritional condition as affected by the habitat productivity in Oklahoma, and by the increase in energy demands associated with pregnancy and lactation. For example, Schingoethe et al. (1988:425) report that beef cattle maintenance requirements increase 33 percent from the pregnancy to lactating stage, and that dairy cows often lose 90 to 135 kg (198.4 to 297.6 lb) of body weight during early lactation.

In a study of nursing behavior in bison of variable ages, Green (1986) found that older cows nurse their offspring longer, and more frequently allow the calf to terminate the nursing bout. She (1986:741) notes that young cows themselves, are often still in the process of growing during the early stages of lactation. Given Byers and Schelling's (1988a, 1988b) analysis of growth and fat development in cattle, a young cow would be expected to experience higher energy demands than an older cow such as FAF, that had been in a stage of maintenance for many years. Increased frequency and intervals of nursing with older age, therefore, may not be excessively demanding upon these older, fatter cows. Losses in body weight related to nursing are usually regained in cattle (Schingoethe et al. 1988:426), and even in wild ungulates living in harsh environments (e.g., for caribou, Adamczewski et al. 1987), during the following summer and fall. In cattle, Schingoethe et al. (1988:421) found that fertility is profoundly affected by insufficient intake in energy, noting delayed sexual maturity, lower conception rates, and weaker offspring at birth. In very old cows and

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during periods following poor food productivity, one should expect a decline in calf crops.

Reproductive Status of FYM

The yearling male, FYM, would not have been affected by energy demands associated with reproductive behavior, except at a minor level, as would be associated with play activities that mimic future behavior associated with the rut. The major factors, other than age, affecting fat composition in young animals are their nutritional condition and their sex. In comparison with older individuals, a much greater porportion of the energy consumed is targeted for muscle tissue growth, so very little fat is deposited in young animals (Byers and Schelling 1988a:309, 1988b:440-444).

Summary of Effects of Reproductive Status

On the basis of their reproductive status, the females of this sample appear to be representative of the normal breeding population. This may be only partially correct, however, if SAF did not calve the previous year. The males of the sample may be considered to be only minorly affected by their reproductive status, due to their relatively young ages. Of these two, SAM may be expected to have participated in more activities associated with male animals during the rut, but his level of activity would still have been much more constrained than that of bulls aged five years and older.

Other Conditions Affecting Specimen Suitability

The suitability of using the individual FAF as a representative of older female bison must be considered with respect to a dental condition which has the potential to have affected her carcass composition.

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Inspection of the mandibles of FAF shows that she has an abnormal dental wear pattern associated with a deformation of the left mandible. The cause of this abnormality is not known, but it is doubtful that it is a recent development given the extent of dental wear. It is possible that this condition might have affected this female's ability to eat, but the long-term nature of its existence (as suggested by the extent of enamel wear) and the fact that this cow calved the previous year, both suggest that it had not yet developed into a life-threatening condition. It is possible, however, that fat levels in the carcass of this female may be below what is normal for a cow of her age, and consideration must be given to this factor when comparing the composition of this and the other TRNP bison.

Relative Size of the Individuals in the Sample

If modern bison populations were all of similar body sizes, and this similarity extended into prehistory, application of the data resulting from this project would be relatively straight forward. However, there is a clear decrease in bison size through prehistory, although of minor dimensions since the mid-Holocene (Wilson 1974a, 1978, McDonald 1981). The data gathered for this project and those presented by Berger and Peacock (1988) suggest that there are regional variations in bison size as well. Therefore, it is important to discuss the available data concerning relative bison size, and whether or not the animals used in this study may be considered representative individuals of modern bison populations.

Two topics of interest to be considered when discussing the size of the animals used in this study include, first, the actual size of each individual, here measured by liveweight (the weight of the animal including the stomach contents), and second, the size of each animal compared with

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others of its age and sex class. This second topic is important in two respects. First, are each of the animals in this sample good representatives of their age and sex classes, or are they exceptional in terms of where they would be placed in a distribution of liveweight data? Second, are these animals, as members of the TRNP herd, typical of bison liveweight distributions of other herds, or do the TRNP animals tend to be larger or smaller than those in other herds? This question is considered largely in terms of animal liveweights, but is also examined through comparisons of metric attributes of the bones.

Liveweights of Sample Animals

Liveweights were recorded for the two fall collected animals (FAF and FYM) one day prior to their slaughter. The female, FAF, at 16-1/2 years, weighed 1093 lb (495.8 kg), and FYM, at 1-1/2 years, weighed 635 lb (288.0 kg). Liveweights were not available for the spring collected animals (SAM and SAF), but estimates of their weights were determined based upon the ratios for FAF and FYM of the total weight of all the butchered parts to the weight of the live animals. The butchered total weights for all four animals included the combined weights of the carcass quarters, the head, hide, viscera and organs, and the shanks (the metapodials and more distal leg bones). Essentially, it excludes only the weight of the carcass blood lost when the animals were shot and bled. These ratios for FAF and FYM were 98.6 percent and 96.3 percent, respectively (Table 2.3). To estimate the liveweights of SAM and SAF, these ratios were averaged (97.45 percent) and divided into their respective totaled butchered parts weights. The resulting estimates of liveweight for SAM and SAF are 1411 and 1061 lb (640.0 and 481.3 kg), respectively (Table 2.4).

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Table 2.3. Ratio of Carcass Weight to Liveweight: Fall Animals

Component	FAF		FYM	
	lb	kg	lb	kg
Warm Weight[a]	610.00	276.7	356.00	161.5
Hide and Tail Weight	64.75	29.4	39.50	17.9
Head and Shank Weight	87.75	39.8	54.00	24.5
Viscera and Organ Weight	315.00	142.9	162.00	73.5
Total Parts Weight (Carcass Weight)	1077.50	488.7	611.50	277.4
Liveweight	1093.00	495.8	635.00	288.0
Ratio of Total Parts Weight to Liveweight	0.986		0.963	

Average of FAF and FYM ratios of total parts weight to liveweight: 0.9745

[a] Warm weight represents the weight of the standard carcass (carcass without the head, tail, or legs below the tarsals and carpals) after it was skinned and eviscerated, but before it was cooled.

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Table 2.4. Estimating Liveweights of Spring Animals

Component	SAM		SAF	
	lb	kg	lb	kg
Warm Weight[a]	769.0	348.8	565.0	256.3
Hide and Tail Weight	103.5	46.9	65.0	29.5
Head and Shanks Weight	120.5	54.7	71.0	32.2
Viscera and Organ Weight	382.0	173.3	333.0[a]	151.0[b]
Total Parts Weight (Carcass Weight)	1375.0	623.7	1034.0	469.0
Estimates of Liveweight:				
Total Parts Weight / 0.9745	1411	640.0	1061	481.3

[a] Warm weight represents the weight of the standard carcass (carcass without the head, tail, or legs below the tarsals and carpals) after it was skinned and eviscerated, but before it was cooled.

[b] SAF weight includes weight of fetus.

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To evaluate these estimates of liveweight, the ratio of the warm carcass weight (the combined weight of the carcass quarters) to the liveweight (Table 2.5) was compared with those recorded by Halloran (1961) for animals at the Wichita Mountains Wildlife Refuge. He reported that the percent of yield for 510 animals in seventeen yearly age classes varied between 47 and 58 percent, centering around 54 percent (1961:213). Comparing the warm carcass weights for the animals used in the present study with their associated liveweights or estimates of liveweights, the percent yield was determined to range between 53 and 56 percent (Table 2.5). These figures suggest that the estimates of liveweight for SAM and SAF are not unreasonable.

Sample Animals as Representatives of TRNP Herd

The liveweights for the sample animals can also be compared with other animals in their age and sex classes from Theodore Roosevelt National Park to see where they fall within the range of recorded liveweights. Table 2.6 lists the mean, standard deviation, range and sample size for weights recorded for TRNP animals of similar age and sex classes during the 1985 roundup. The female, FAF was the only representative of her age group, so she is compared to a sample of the herd, including all females ten years old or older. The estimates and liveweights for the four TRNP sample animals fall within one standard deviation of the mean weights for their respective age and sex classes. A series of t-tests (Thomas 1976:240) indicates the liveweight for each sample specimen is not significantly different from the mean liveweight of the corresponding age group (Table 2.6). The small sample sizes and large standard deviations might be a factor in this determinations, but in each case the weights are not greatly different from

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Table 2.5. Evaluating Liveweight Estimates Using the Ratio of Standard Warm Carcass Weight to Animal Liveweight

	SAM		SAF		FAF		FYM	
Measurement	lb	kg	lb	kg	lb	kg	lb	kg
Warm Weight[a]	769	348.8	565	256.3	610	276.7	356	161.5
Liveweight	1411[b]	640.0	1061[a]	481.3	1093	495.8	635	288.0
Percent Warm Weight	54.5		53.3		55.8		56.1	

[a] Warm weight represents the weight of the standard carcass (carcass without the head, tail, or legs below the tarsals and carpals) after it was skinned and eviscerated, but before it was cooled.

[b] Liveweight estimates. See Table 2.4 for derivation of these weights.

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Table 2.6. Evaluation of the Study Specimens as Representatives of the Theodore Roosevelt National Park Herd

Sex	Age Class	N	Mean Weight lb	Mean Weight kg	Standard Deviation lb	Standard Deviation kg	Age Class Minimum lb	Age Class Minimum kg	Age Class Maximum lb	Age Class Maximum kg	Animal	Liveweight lb	Liveweight kg	t[a]
Male	4	3	1346.0	610.5	160.0	72.6	1249	566.5	1532	694.9	SAM	1411	640.0	-0.35[b]
Female	7	3	1080.0	489.9	83.4	37.8	984	446.3	1134	514.4	SAF	1061	481.3	+0.20[b]
Male	1	5	596.6	270.6	44.4	20.1	549	249.0	660	299.4	FYM	635	288.0	-0.79[b]
Female	10+	9	1127.8	511.6	82.2	37.3	927	420.5	1264	573.3	FAF	1093	495.8	+0.40[b]

[a] t-test statistic (Thomas 1976:240)

[b] difference between study specimen and age class mean is not significant at $p < .0125$ (one-tailed test)

the mean for the respective age class. All four animals, therefore, appear to be representative of their age and sex classes for animals from TRNP.

Liveweight Comparisons of TRNP and other Park Herds

In the previous section, it was suggested that the four bison used in this study are probably comparable in weight to other bison of their age and sex classes from Theodore Roosevelt National Park. The next step in establishing these animals as good representatives for a study of modern bison in general is to determine how the TRNP bison herd compares with other herds in terms of liveweight sizes for age and sex classes. Data from four other parks are used to answer two questions. First, are the liveweight means for animals of each age and sex class the same or different from samples from other regions? Second, if significant differences occur in the mean liveweights by age and sex class between the parks, then do these differences conform to the pattern of differences predicted for altitudinal, latitudinal, or temperature variations between the sites as suggested by Bergmann's rule? Bergmann's rule states that body size varies inversely with ambient temperature, so that body size increases with latitude or altitude (Geist 1987). This relationship is of interest, because it would be beneficial to understand how liveweight varies and in response to what factors.

The data used to answer these questions were provided by park officials from Theodore Roosevelt National Park (TRNP), Medora, North Dakota; the National Bison Range (NBR), Moiese, Montana; Wind Cave National Park (WCNP), Hot Springs, South Dakota; and the Fort Niobrara National Wildlife Refuge (FNNWR), Timberlake, Nebraska. Also included were data from the Wichita Mountains Wildlife Refuge (WMWR), Cache, Oklahoma (Halloran 1961). Figure 2.1 shows the location of these bison parks. The data primarily came in the

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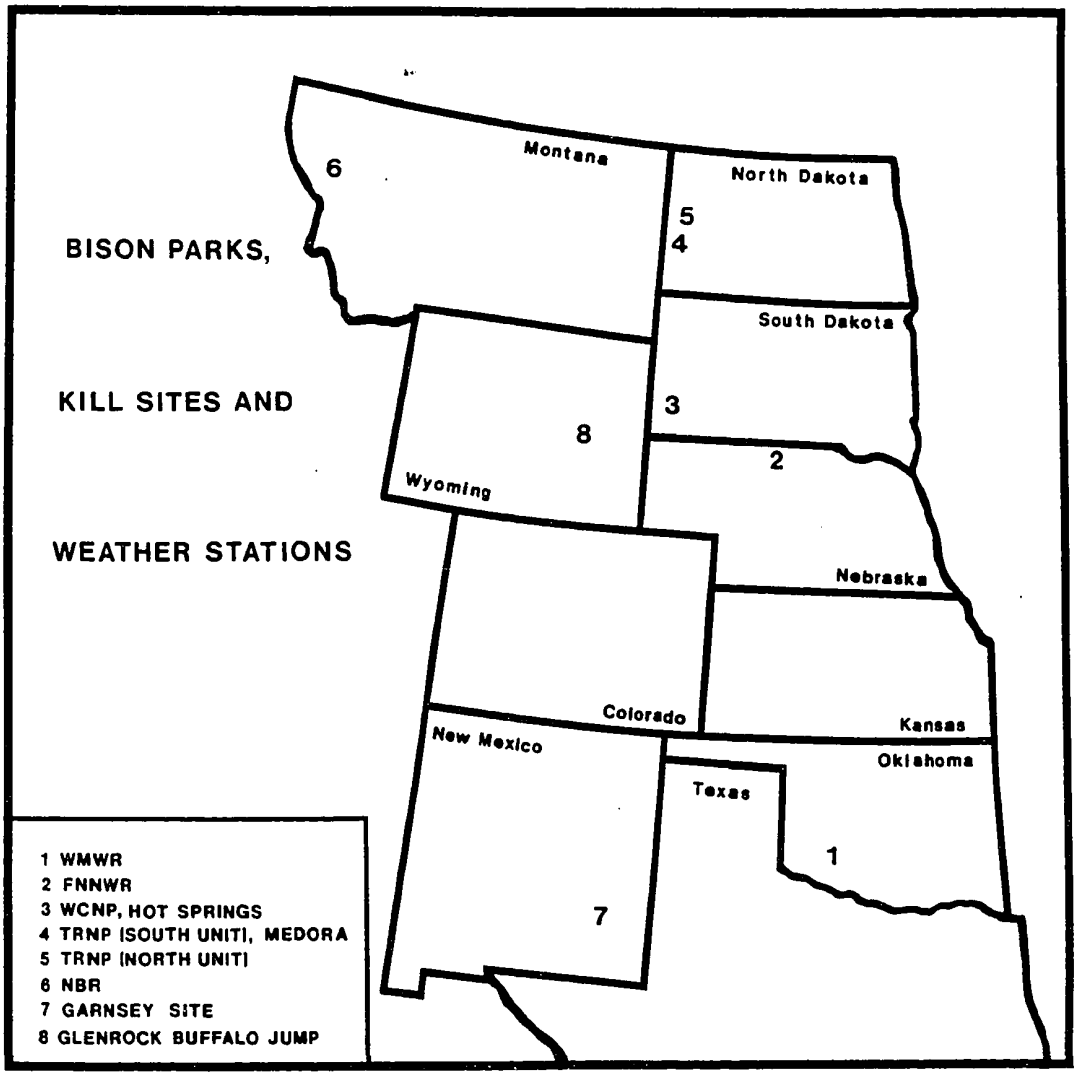

Figure 2.1. Locations of Bison Parks, Kill Sites, and Two Weather Stations.

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form of individual animal liveweights by age and sex classes. The exceptions to this were the Wichita Mountains Wildlife Refuge data, which was published as average liveweights for age and sex classes, and some sets of data for particular years from some of the other parks. Where individual weights are needed to establish the forms of the distributions, the park data that included only averaged liveweights were excluded from consideration. Where standard deviations are not critical to the argument, all the available data for the age and sex classes are considered.

Bison Growth Results from the Parks. Tables 2.7-2.10 list the mean liveweights, sample size, and standard deviation of the distributions where possible, for the females and males from the parks listed above. Figures 2.2 through 2.6 present the growth curves by age class for each park, noting the sample size for each sex, at each age grade. Data from multiple years are combined to determine the liveweight means in these figures. Berger and Peacock (1988) showed that weights plotted by year may vary significantly. Multiple year data are used here to reduce the influence of atypical growth years. Figures 2.2-2.6 show that the sexes differ in their weights for a given age, and have different patterns of long-term growth. In each case, males are larger than females at a given age grade--sometimes by only a small amount as in calves, but generally becoming quite large after the first year. The tables and figures also show that growth (as measured by liveweight) in females slows between two and three years of age, continuing at a slower rate until it reachs a plateau at four or five years. In males, growth continues at a relatively high rate until about three years of age, but continues at a lower rate until five or six years of age when mean liveweight begins to level off. Peterson and Hughes (1980:172-174) conclude that weight gain in bulls tapers off between eight and nine years. The

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Table 2.7. Liveweight Distributions of Bison bison Recorded at Theodore Roosevelt National Park in the Fall, 1966 and 1985

Age Class	Females				Males			
	n	Mean Liveweight kg	Mean Liveweight lb	St. Dev. (lb)	n	Mean Liveweight kg	Mean Liveweight lb	St. Dev. (lb)
Calves	10	148.2	326.8	74.4	9	161.0	354.9	65.3
Yearlings	8	273.3	602.6	51.0	8	308.1	679.3	93.4
2 yr olds	16	397.2	875.7	104.4	9	408.1	899.7	98.5
3 yr olds	7	428.3	944.3	177.5	6	560.1	1234.8	132.6
4 yr olds	5	477.0	1051.6	122.9	7	648.6	1430.0	161.9
5 yr olds	1	636.8	1404.0	----	1	780.2	1720.0	----
6 yr olds	3	493.8	1088.7	120.8	1	835.5	1842.0	----
7 yr olds	4	470.6	1037.5	108.9	1	787.0	1735.0	----
8 yr olds	3	516.0	1137.7	83.0	1	754.8	1664.0	----
9 yr olds	1	467.2	1030.0	----				
10 yr olds	3	479.3	1056.7	120.0				
11 yr olds	2	492.8	1086.5	71.4				
12 yr olds	1	528.0	1164.0	----				
13 yr olds	2	435.4	960.0	106.1				
14 yr olds	3	490.2	1080.7	115.9				
15 yr olds	1	573.3	1264.0	----				
16 yr olds	2	447.5	986.5	150.6				

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Table 2.8, Part A. Liveweight Distributions of Bison bison at the National Bison Range in the Fall, 1984-1987

Age Class	Females			Males		
		Mean Liveweight			Mean Liveweight	
	n	kg	lb	n	kg	lb
Calves	178	139.3	307.1	190	155.4	342.6
Yearlings	93	280.0	617.3	106	326.7	720.3
2 yr olds	72	383.1	844.5	82	472.4	1041.4
3 yr olds	60	422.4	931.2	59	577.1	1272.3
4 yr olds	54	434.0	956.7	38	679.3	1497.6
5 yr olds	43	453.0	998.8	18	742.4	1636.7
6 yr olds	20	455.1	1003.4	17	774.3	1707.0
7 yr olds	25	465.8	1026.9	17	803.3	1770.9
8 yr olds	19	464.3	1023.5	14	786.5	1733.9
9 yr olds	12	477.7	1053.1	11	796.6	1756.1
10 yr olds	12	483.8	1066.5	7	838.7	1849.1
11 yr olds	8	467.2	1030.0	4	867.0	1911.3
12 yr olds	3	498.0	1098.0	4	864.8	1906.5
13 yr olds	4	474.0	1045.0	1	925.3	2040.0
14 yr olds	1	544.3	1200.0			
15 yr olds	2	435.7	960.5			
16 yr olds	1	489.9	1080.0			
17 yr olds	4	491.0	1082.5			
18 yr olds	1	499.0	1100.0			
19 yr olds	2	472.6	1042.0			
20 yr olds	2	474.0	1045.0			
21 yr olds	1	455.4	1004.0			

Note: Mean weights are based upon summarized data from 1984-1986, and weights from individual animals for 1987.

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Table 2.8, Part B. Liveweight Distributions of Bison bison at the National Bison Range in the Fall, 1987

Age Class	Females n	Females Mean Liveweight kg	Females Mean Liveweight lb	Females St. Dev. (lb)	Males n	Males Mean Liveweight kg	Males Mean Liveweight lb	Males St. Dev. (lb)
Calves	50	134.1	295.7	57.1	42	148.0	326.2	66.0
Yearlings	43	273.1	602.0	62.5	52	318.8	702.8	83.5
2 yr olds	34	367.7	810.6	101.1	26	444.6	980.2	107.8
3 yr olds	26	429.0	945.7	80.0	23	566.7	1249.4	101.6
4 yr olds	21	447.7	987.0	82.9	15	683.9	1507.7	115.0
5 yr olds	17	441.6	973.5	53.5	9	756.3	1667.3	92.3
6 yr olds	15	459.3	1012.5	64.2	6	791.4	1744.8	66.1
7 yr olds	13	471.3	1039.1	59.2	6	780.4	1720.5	77.9
8 yr olds	7	473.6	1044.1	71.8	4	817.7	1802.8	118.2
9 yr olds	4	444.7	980.5	33.6	4	805.1	1775.0	160.1
10 yr olds	4	502.4	1107.5	54.7	2	797.2	1757.5	24.7
11 yr olds	3	455.1	1003.3	53.2	1	927.6	2045.0	----
12 yr olds	1	478.1	1054.0	----	1	925.3	2040.0	----
13 yr olds	1	444.5	980.0	----	1	925.3	2040.0	----
14 yr olds								
15 yr olds	1	456.3	1006.0	----				
16 yr olds								
17 yr olds	1	471.7	1040.0	----				
18 yr olds								
19 yr olds	1	455.4	1004.0	----				
20 yr olds	1	453.6	1000.0	----				
21 yr olds	1	455.4	1004.0	----				

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Table 2.9. Liveweight Distributions of Bison bison at Wind Cave National Park in the Fall, 1983-1987

Age Class	Females				Males			
		Mean Liveweight		St. Dev.		Mean Liveweight		St. Dev.
	n	kg	lb	(lb)	n	kg	lb	(lb)
Calves	47	146.2	322.4	52.5	52	154.8	341.3	71.6
Yearlings	123	255.6	563.4	78.0	112	277.2	611.2	95.1
2 yr olds	83	355.6	784.0	92.4	67	407.9	899.2	114.1
3 yr olds	68	378.1	833.5	98.5	27	524.8	1156.9	125.6
4 yr olds	54	403.7	889.9	76.6	9	558.9	1232.2	217.6
5 yr olds	44	420.8	927.6	112.0	2	709.9	1565.0	190.9
6 yr olds	30	420.1	926.2	110.3	2	730.3	1610.0	155.6
7 yr olds	19	419.2	924.2	75.3	2	674.7	1487.5	31.8
8 yr olds	12	416.7	918.6	65.9				
9 yr olds	8	440.0	970.0	112.5	2	723.5	1595.0	77.8
10 yr olds	6	414.7	914.2	102.8	3	734.8	1620.0	115.3
11 yr olds	7	433.9	956.6	79.3				
12 yr olds	5	434.1	957.0	97.8	2	775.6	1710.0	56.6
13 yr olds	2	480.1	1058.5	75.7				
14 yr olds	3	523.1	1153.3	114.1				
15 yr olds	3	449.4	990.7	220.5	2	774.5	1707.5	194.5
16 yr olds	1	467.2	1030.0	----				
17 yr olds	2	495.5	1092.5	166.2				
18 yr olds	2	435.4	960.0	113.1				
19 yr olds	1	430.9	950.0	----				

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Table 2.10. Liveweight Distributions of Bison bison at Fort Niobrara National Wildlife Refuge in the Fall, 1987

Age Class	Females				Males			
	n	Mean Liveweight kg	Mean Liveweight lb	St. Dev. (lb)	n	Mean Liveweight kg	Mean Liveweight lb	St. Dev. (lb)
Calves	16	154.1	339.7	17.2	24	163.2	359.7	16.5
Yearlings	19	321.6	708.9	65.3	12	333.0	734.1	92.4
2 yr olds	11	422.3	931.1	55.8	7	478.0	1053.7	81.5
3 yr olds	8	422.1	930.5	48.6	9	595.7	1313.3	80.4
4 yr olds	9	455.0	1003.1	54.5	8	693.7	1529.3	71.1
5 yr olds	6	476.4	1050.3	44.0	9	772.9	1704.0	93.5
6 yr olds	7	497.1	1096.0	57.6	6	787.0	1735.0	26.0
7 yr olds	7	484.6	1068.4	65.5	4	862.4	1901.3	79.5
8 yr olds	5	477.2	1052.0	106.5	10	845.8	1864.6	106.5
9 yr olds	9	496.7	1095.1	76.0	3	847.4	1868.3	12.6
10 yr olds	3	495.9	1093.3	113.2	5	831.4	1833.0	146.1
11 yr olds	6	495.5	1092.3	84.8	5	820.9	1809.8	118.6
12 yr olds	6	491.4	1083.3	49.9	3	840.6	1853.3	30.1
13 yr olds	4	538.2	1186.5	51.5	5	835.1	1841.0	61.7
14 yr olds	2	451.3	995.0	77.8				
15 yr olds	1	516.2	1138.0	----				

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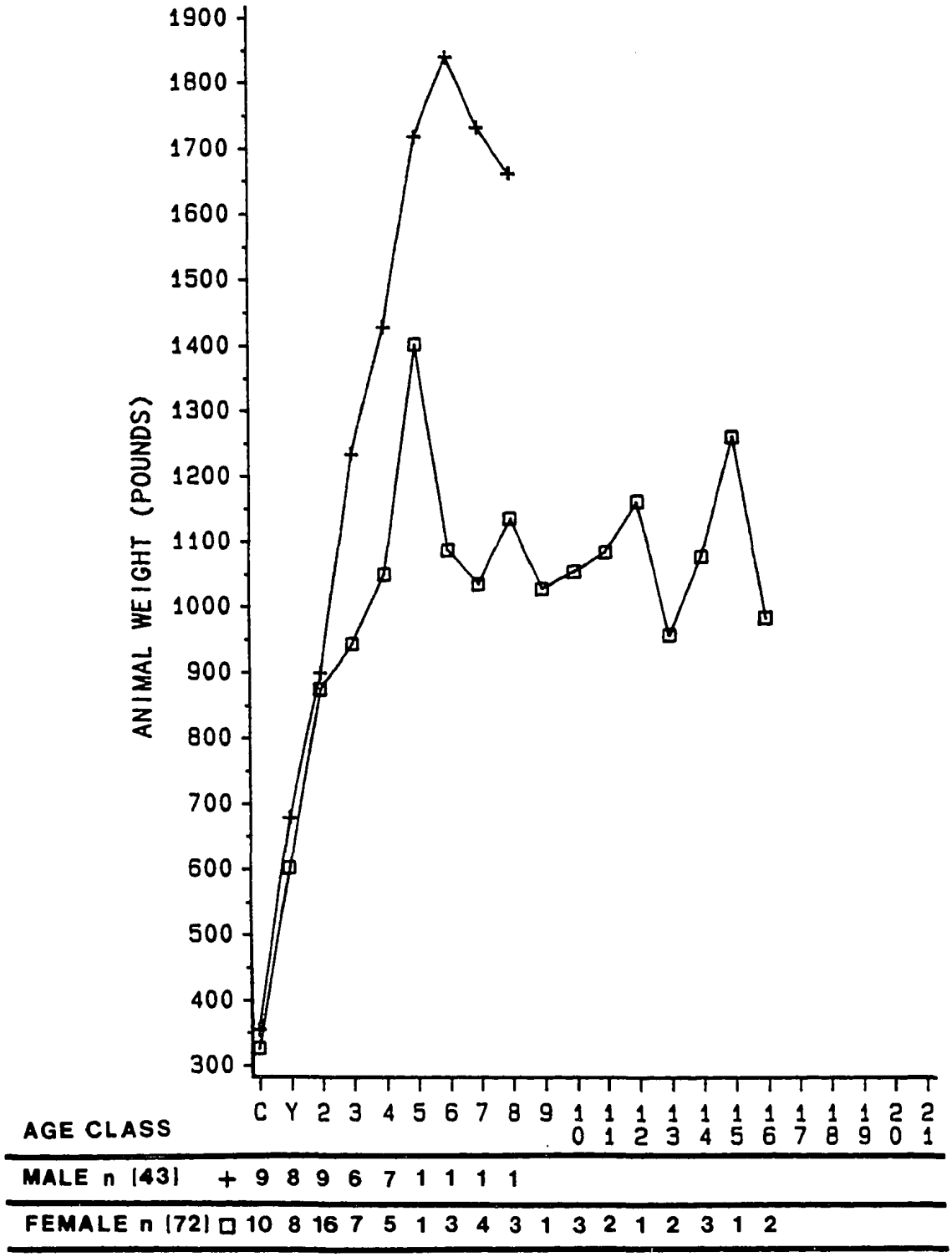

Figure 2.2. Average Male and Female Bison Liveweights, Theodore Roosevelt National Park, 1966 and 1985.

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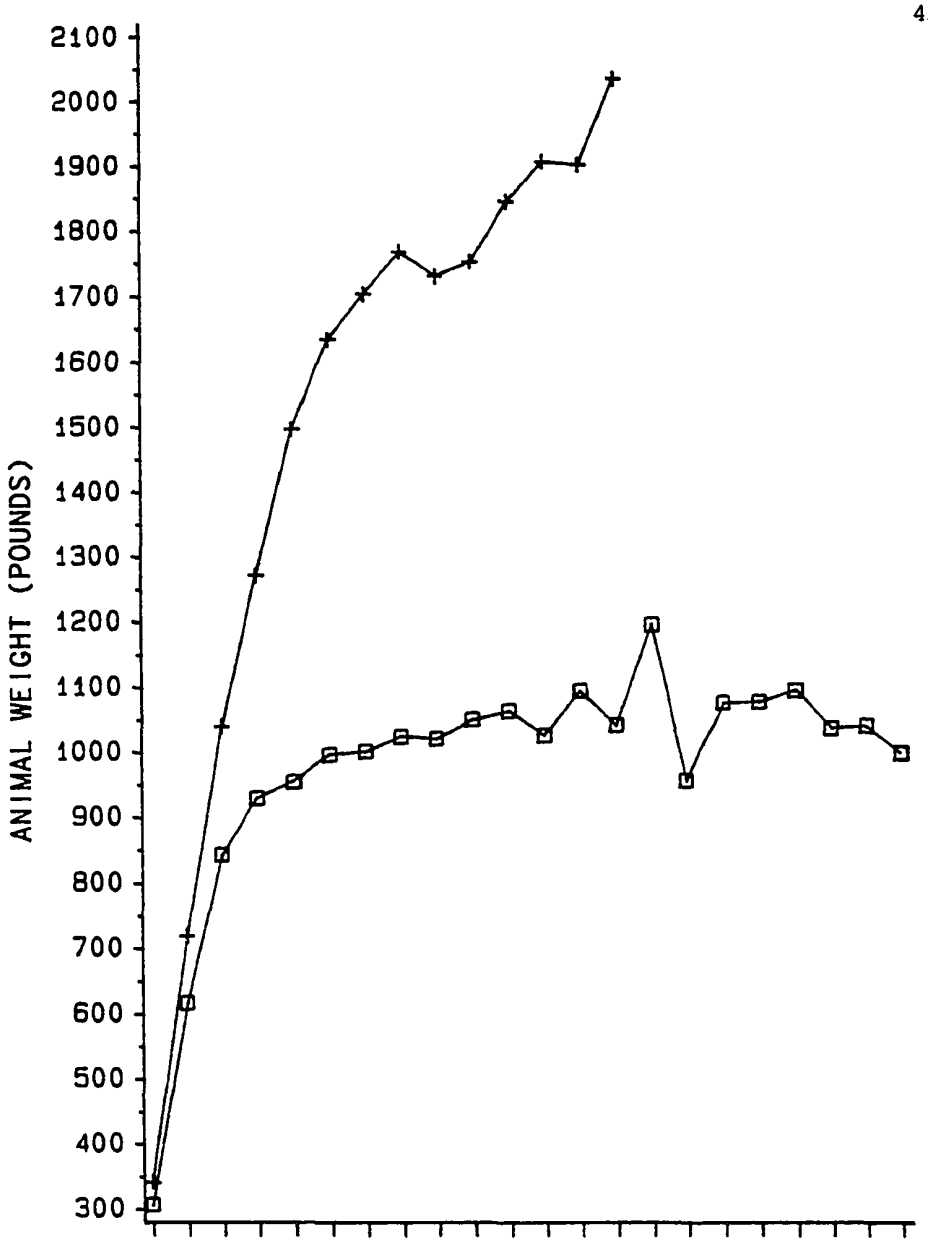

Figure 2.3. Average Male and Female Bison Liveweights, National Bison Range, 1984-1987.

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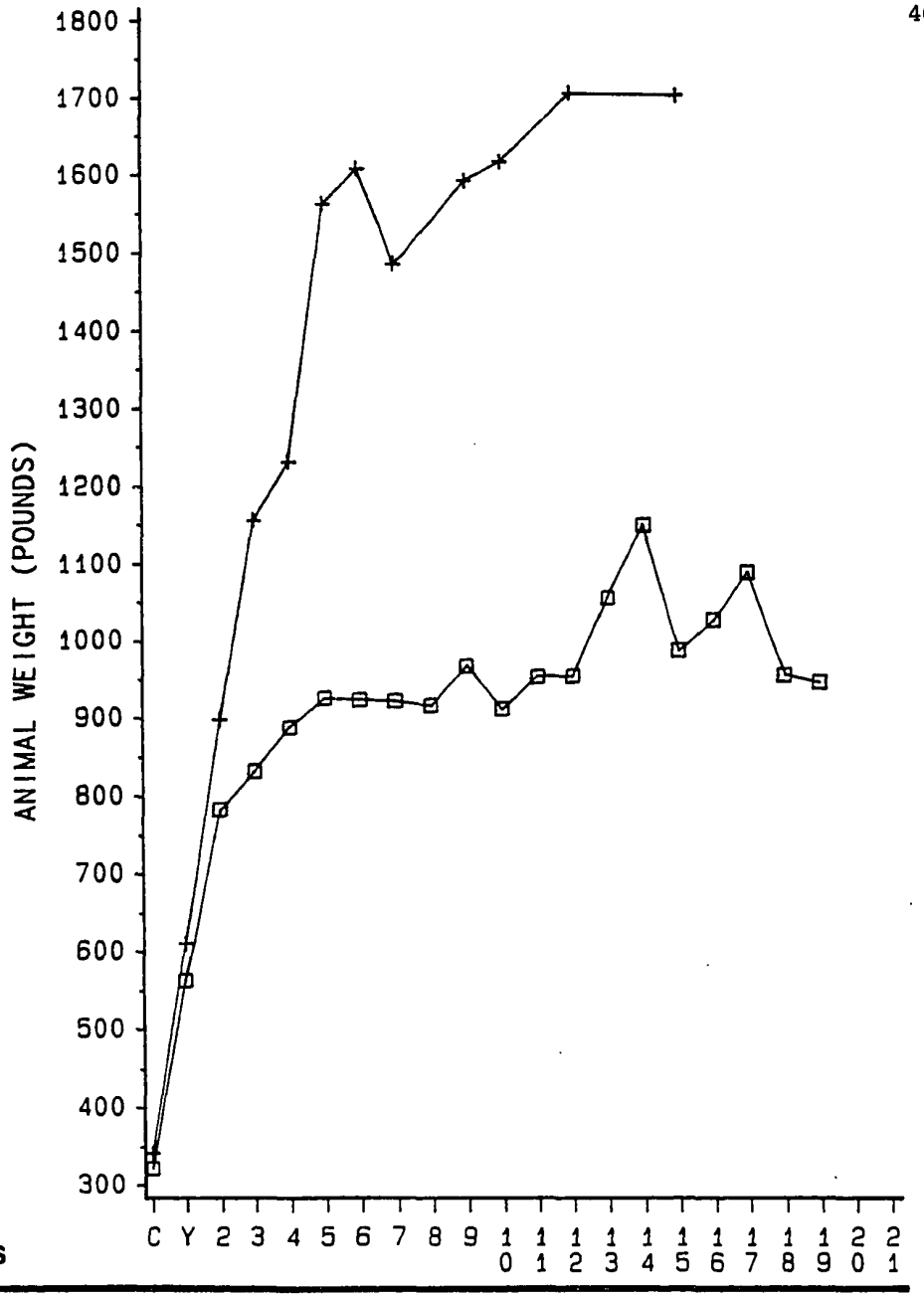

Figure 2.4. Average Male and Female Bison Liveweights, Wind Cave National Park, 1983-1987.

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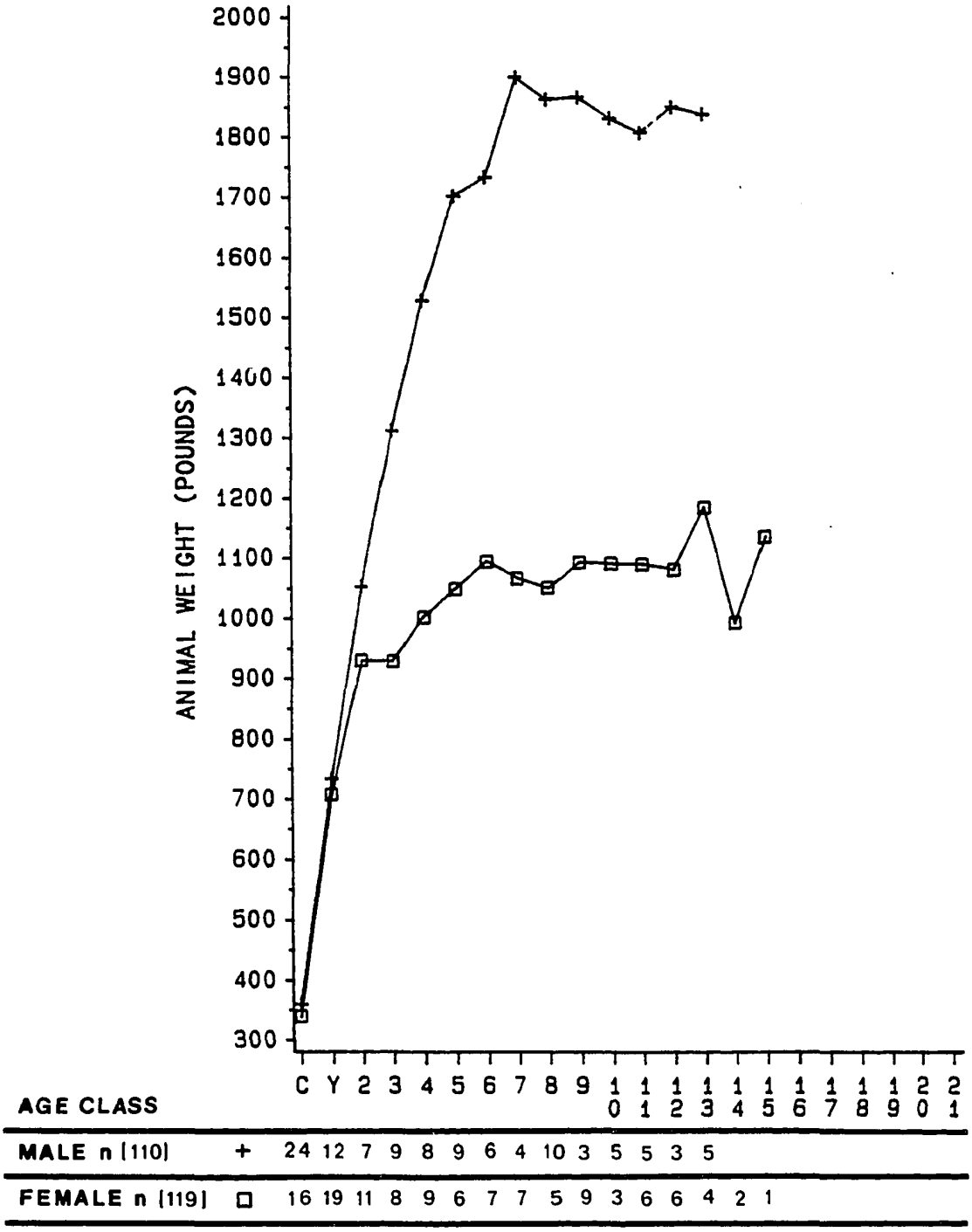

Figure 2.5. Average Male and Female Bison Liveweights, Fort Niobrara National Wildlife Refuge, 1987.

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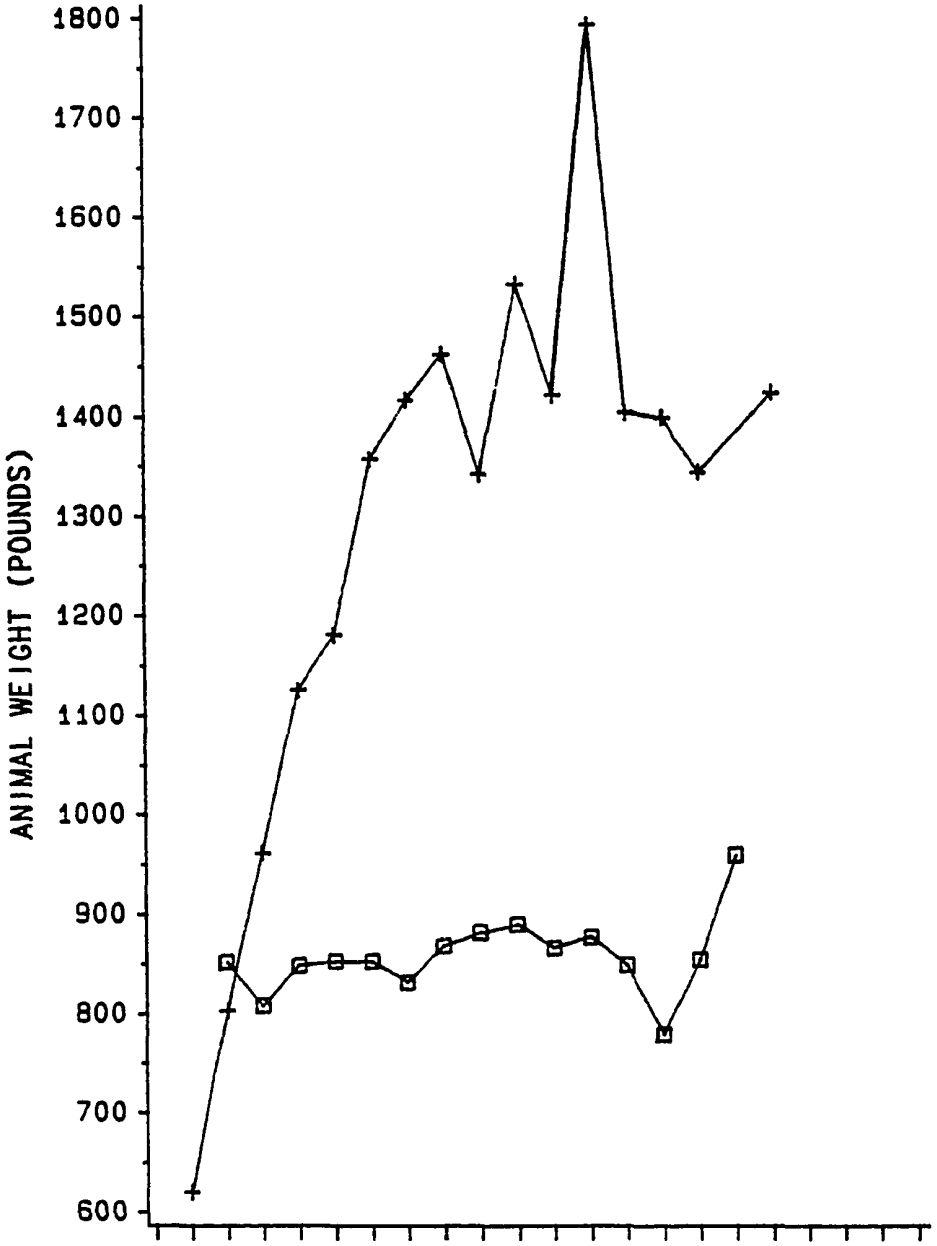

Figure 2.6. Average Male and Female Bison Liveweights, Wichita Mountains Wildlife Refuge, 1953-1960. (Source: Halloran 1961).

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standard deviations of the liveweight distributions for samples of bison from the NBR (1987) and from WCNP (1983-1987) suggest that male weight is more variable than female weight. This conforms to what Berger and Peacock (1988) found for bison and Anderson et al. (1972) found for mule deer (Odocoileus hemionus).

Regional Comparisons of Bison Growth. By combining the growth curves from each park, by sex, it is possible to consider the problem of whether or not bison growth by age and sex class differs significantly between regions. Figure 2.7 presents the growth curves for the female bison and Figure 2.8, the data for the males. Examining these graphs, one is first struck by the comparability in the shape of the curves for each sex. There do appear to be some distinct differences in the mean weights of animals of a given age between parks, however, and the magnitude of these differences vary with animal age.

To compare animal size in these bison populations, the mean liveweights for animals of given age and sex classes were compared between parks. A single mean disregarding age differences was not used for each park because of the evident differences in sample composition. If one park has a larger proportion of older animals, the mean weight might be higher, reflecting this difference rather than a difference related to park location. Age classes were combined after calves and yearlings were examined, because sample sizes decreased substantially. The effect of this combination is to increase the range, and possibly, the standard deviation of the distributions, thus making it more difficult to determine that significant differences occur. For some age classes, the combined samples still have small sample sizes. In future tests, it would be preferable to examine the data by individual, rather than combined age classes.

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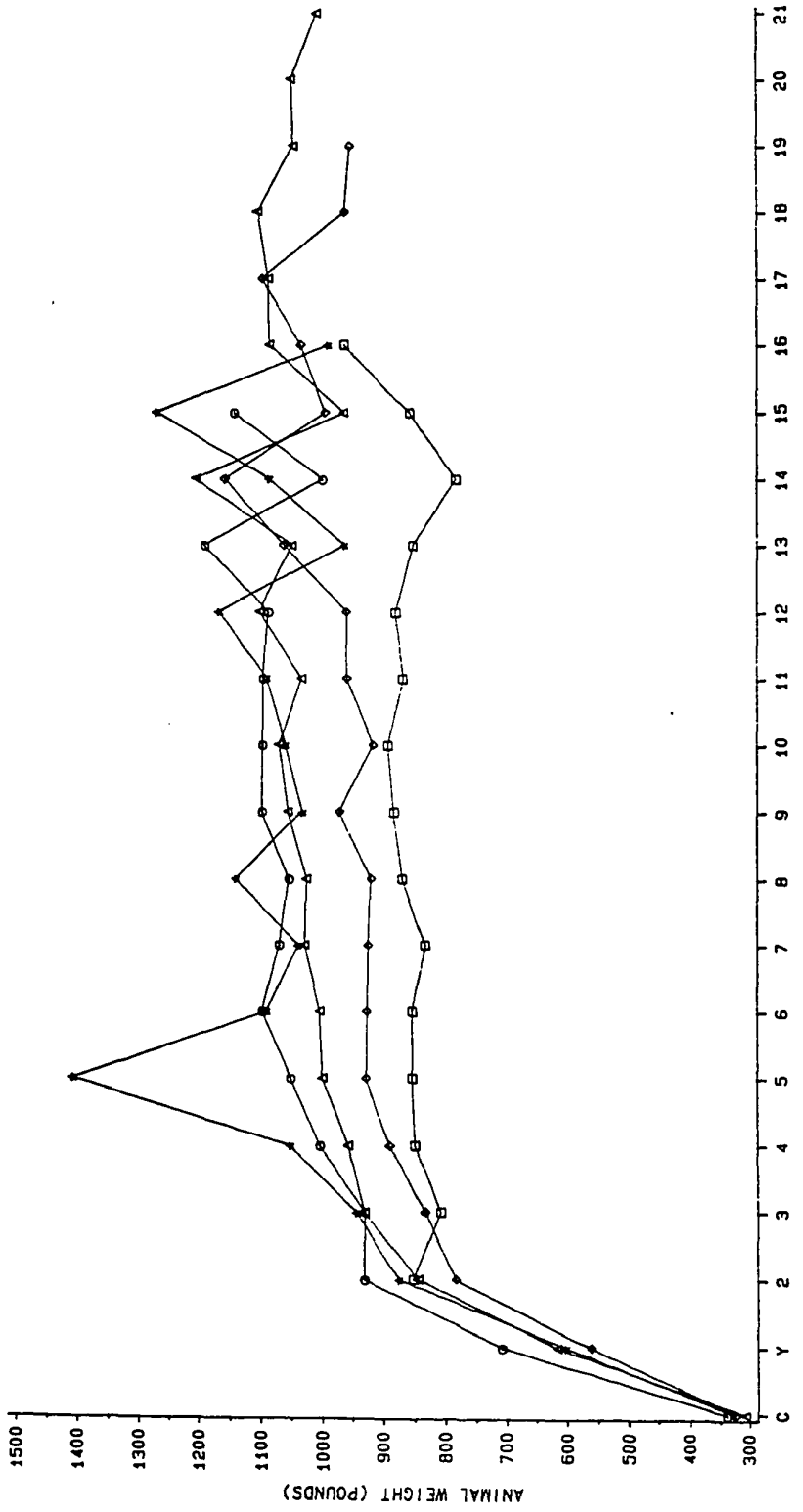

Figure 2.7. Average Female Liveweights by Age Class for Fort Niobrara National Wildlife Refuge (FNNWR), National Bison Range (NBR), Theodore Roosevelt National Park (TRNP), Wind Cave National Park (WCNP), and Wichita Mountains Wildlife Refuge (WMWR, Source: Halloran 1961).

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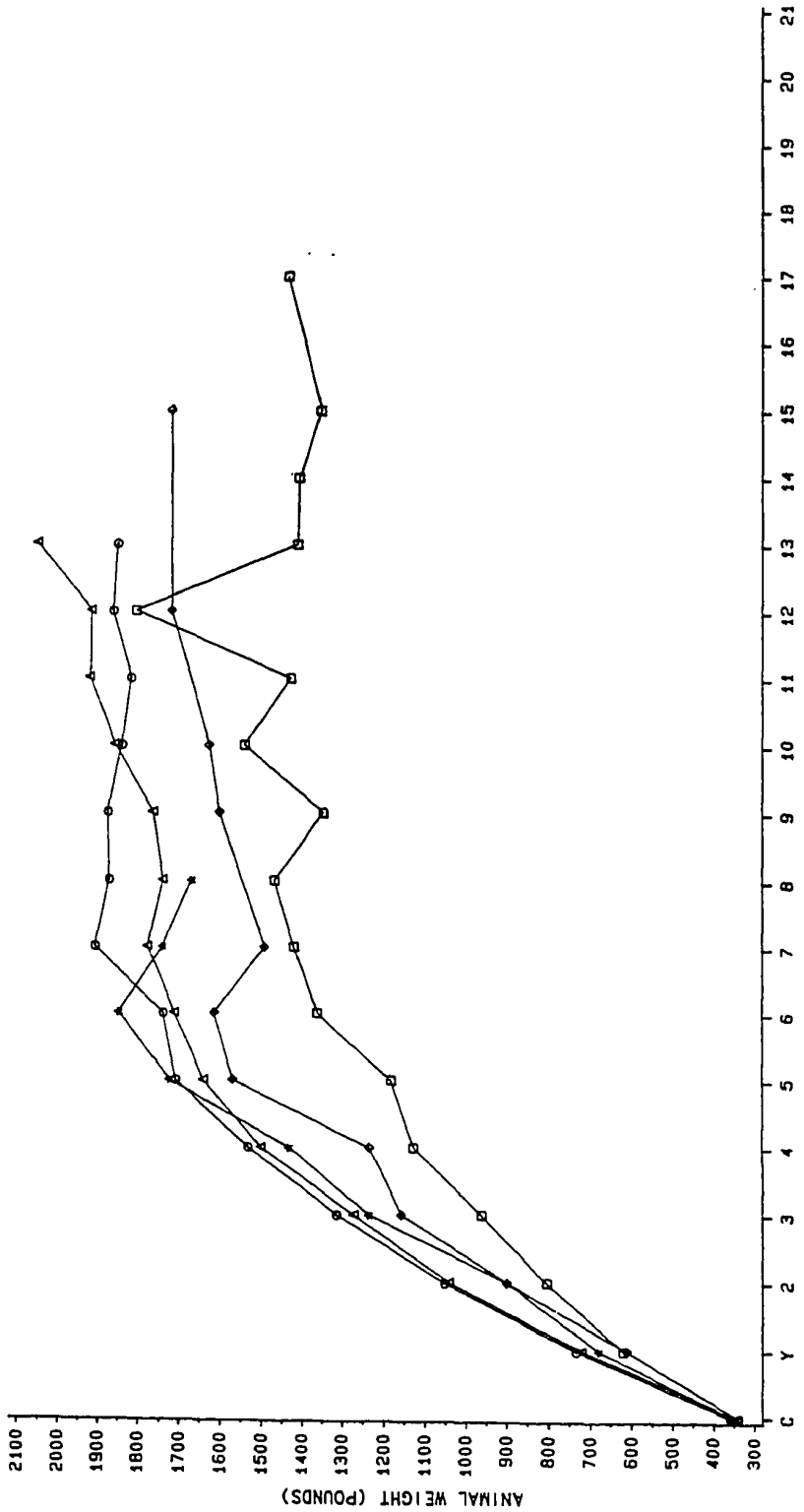

Figure 2.8. Average Male Liveweights by Age Class for Fort Niobrara National Wildlife Refuge (FNNWR), National Bison Range (NBR), Theodore Roosevelt National Park (TRNP), Wind Cave National Park (WCNP), and Wichita Mountains Wildlife Refuge (WMWR, Source: Halloran 1961).

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Tables 2.11 through 2.22 present the combined t-tests for each pairing of parks presented by age classes. A null hypothesis of no significant difference in mean weight is tested. Table 2.23 summarizes the results for females and males, and Table 2.24 summarizes the results with respect to the hypotheses that the northern, higher altitude, or lower average annual temperature park means are larger than the southern, lower altitude, or higher average annual temperature park means when the hypothesis of equal means is rejected. In Table 2.23, pairs in which one of the data sets has a sample size of less than 10 are identified. As noted above, when sample size is small it is more difficult to find the mean weights to be significantly different. Although the null and alternate hypotheses are identified for this analysis, for the sake of brevity significance only is reported in subsequent analyses.

Results of the t-Tests. Inspection of Table 2.23 provides evidence that differences in mean liveweights between park populations (1) are rarely evident in calves of either sex, and (2) are more often statistically significant ($p < .0125$, one-tailed test) between cow than bull populations. Not all age class specific park comparisons of bison size showed the differences to be significant. Significant differences ($p < .0125$, one-tailed test) in mean weights for all age groups older than calves were found for both male and female populations of WCNP bison compared with the NBR and FNNWR bison. Cows differed significantly for all age groups except the 4-5 year group when compared between the NBR and FNNWR, but this could not be demonstrated for the male populations of these parks. The TRNP cow population differed in animal size from the WCNP population in the 2-3 year and older age classes, but the male populations could not be shown to differ significantly in size.

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Table 2.11. t-Test Comparisons of Mean Liveweight Data for Females from Theodore Roosevelt National Park (1985) and Wind Cave National Park (1983-1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	TRNP	9	328.7	78.7	0.3000	54.0	0.7654
	WCNP	47	322.4	52.5			
Yearling	TRNP	5	596.6	44.4	0.9443	126.0	0.3468
	WCNP	123	563.4	78.0			
2-3 yrs	TRNP	15	927.1	136.5	4.3818	164.0	0.0001[a]
	WCNP	151	806.3	98.0			
4-5 yrs	TRNP	3	1112.7	120.9	3.6554	99.0	0.0004[a]
	WCNP	98	906.8	95.5			
6-7 yrs	TRNP	6	1084.3	92.9	3.7894	53.0	0.0004[a]
	WCNP	49	925.4	97.3			
8+ yrs	TRNP	13	1122.5	83.7	4.6241	63.0	0.0001[a]
	WCNP	52	968.9	111.9			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.12. t-Test Comparisons of Mean Liveweight Data for Males from Theodore Roosevelt National Park (1985) and Wind Cave National Park (1983-1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	TRNP	9	354.9	65.3	0.5309	59.0	0.5975
	WCNP	52	341.3	71.6			
Yearlings	TRNP	6	669.0	98.8	1.4474	116.0	0.1505
	WCNP	112	611.2	95.1			
2-3 yrs	TRNP	6	1115.3	255.2	1.9717	98.0	0.0515
	WCNP	94	973.2	165.5			
4-5 yrs	TRNP	3	1346.7	160.6	0.3563	12.0	0.7278
	WCNP	11	1292.7	244.2			
6-7 yrs	TRNP	1	1735.0	---	1.4388	3.0	0.2458
	WCNP	4	1548.8	115.8			
8 + yrs	TRNP	0	---	---	---	---	---
	WCNP	9	1653.9	109.6			

[a] Difference is significant at $p < .0125$ (one-tailed test). None were significant.

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Table 2.13. t-Test Comparisons of Mean Liveweight Data for Females from Wind Cave National Park (1983-1987) and the National Bison Range (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	NBR	50	295.7	57.1	-2.3937	95.0	0.0186
	WCNP	47	322.4	52.5			
Yearlings	NBR	43	602.0	62.5	2.9373	164.0	0.0038[a]
	WCNP	123	563.4	78.0			
2-3 yrs	NBR	60	869.2	114.0	4.0102	209.0	0.0001[a]
	WCNP	151	806.3	98.0			
4-5 yrs	NBR	38	980.9	70.7	4.9452	90.5	0.0001[a]
	WCNP	98	906.8	95.5			
6-7 yrs	NBR	28	1024.9	62.3	5.4562	73.9	0.0001[a]
	WCNP	49	925.4	97.3			
8 + yrs	NBR	25	1030.4	62.0	3.0930	73.4	0.0028[a]
	WCNP	52	968.9	111.9			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.14. t-Test Comparisons of Mean Liveweight Data for Males from Wind Cave National Park (1983-1987) and the National Bison Range (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	NBR	42	326.2	66.0	-1.0552	92.0	0.2941
	WCNP	52	341.3	71.6			
Yearlings	NBR	52	702.8	83.5	5.9545	162.0	0.0001[a]
	WCNP	112	611.2	95.1			
2-3 yrs	NBR	49	1106.6	170.9	4.5224	141.0	0.0001[a]
	WCNP	94	973.2	165.5			
4-5 yrs	NBR	24	1567.5	131.3	3.5065	12.7	0.0040[a]
	WCNP	11	1292.7	244.2			
6-7 yrs	NBR	12	1732.7	70.0	3.8836	14.0	0.0017[a]
	WCNP	4	1548.8	115.8			
8 + yrs	NBR	12	1825.9	146.2	2.9546	19.0	0.0081[a]
	WCNP	9	1653.9	109.6			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.15. t-Test Comparisons of Mean Liveweight Data for Females from Wind Cave National Park (1983-1987) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	16	339.7	17.2	1.9640	61.0	0.0541
	WCNP	47	322.4	52.5			
Yearling	FNNWR	19	708.9	65.3	7.7205	140.0	0.0001[a]
	WCNP	123	563.4	78.0			
2-3 yrs	FNNWR	19	930.8	51.5	8.7425	37.3	0.0001[a]
	WCNP	151	806.3	98.0			
4-5 yrs	FNNWR	15	1022.0	54.4	6.7601	29.4	0.0001[a]
	WCNP	98	906.8	95.5			
6-7 yrs	FNNWR	14	1082.2	61.0	5.6956	61.0	0.0001[a]
	WCNP	49	925.4	97.3			
8+ yrs	FNNWR	36	1092.3	83.6	5.6151	86.0	0.0001[a]
	WCNP	52	968.9	111.9			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.16. t-Test Comparisons of Mean Liveweight Data for Males from Wind Cave National Park (1983-1987) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	24	359.7	16.5	1.7494	61.6	0.0852
	WCNP	52	341.3	71.6			
Yearlings	FNNWR	12	734.1	92.4	4.2636	122.0	0.0001[a]
	WCNP	112	611.2	95.1			
2-3 yrs	FNNWR	16	1199.8	154.3	5.1093	108.0	0.0001[a]
	WCNP	94	973.2	165.5			
4-5 yrs	FNNWR	17	1621.8	121.1	4.1500	13.2	0.0011[a]
	WCNP	11	1292.7	244.2			
6-7 yrs	FNNWR	10	1801.5	99.3	4.1219	12.0	0.0014[a]
	WCNP	4	1548.8	115.8			
8 + yrs	FNNWR	31	1846.1	95.5	5.1465	38.0	0.0001[a]
	WCNP	9	1653.9	109.6			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.17. t-Test Comparisons of Mean Liveweight Data for Females from Theodore Roosevelt National Park (1985) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	16	339.7	17.2	0.4145	8.4	0.6889
	TRNP	9	328.7	78.7			
Yearling	FNNWR	19	708.9	65.3	3.6028	22.0	0.0016[a]
	TRNP	5	596.6	44.4			
2-3 yrs	FNNWR	19	930.8	51.5	0.0998	17.2	0.9217
	TRNP	15	927.1	136.5			
4-5 yrs	FNNWR	15	1022.0	54.4	-1.2731	2.2	0.3247
	TRNP	3	1112.7	120.9			
6-7 yrs	FNNWR	14	1082.2	61.0	-0.0609	18.0	0.9521
	TRNP	6	1084.3	92.9			
8+ yrs	FNNWR	36	1092.3	83.6	-1.1157	47.0	0.2702
	TRNP	13	1122.5	83.7			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.18. t-Test Comparisons of Mean Liveweight Data for Males from Theodore Roosevelt National Park (1985) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	24	359.7	16.5	0.2170	8.4	0.8334
	TRNP	9	354.9	65.3			
Yearlings	FNNWR	12	734.1	92.4	1.3786	16.0	0.1870
	TRNP	6	669.0	98.8			
2-3 yrs	FNNWR	16	1199.8	154.3	0.9545	20.0	0.3512
	TRNP	6	1115.3	255.2			
4-5 yrs	FNNWR	17	1621.8	121.1	3.4833	18.0	0.0027[a]
	TRNP	3	1346.7	160.6			
6-7 yrs	FNNWR	10	1801.5	99.3	0.6387	9.0	0.5389
	TRNP	1	1735.0	---			
8 + yrs	FNNWR	31	1846.1	95.5	---	---	---
	TRNP	0	---	---			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.19. t-Test Comparisons of Mean Liveweight Data for Females from the National Bison Range (1987) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	16	339.7	17.2	4.8060	63.9	0.0001[a]
	NBR	50	295.7	57.1			
Yearling	FNNWR	19	708.9	65.3	6.1212	60.0	0.0001[a]
	NBR	43	602.0	62.5			
2-3 yrs	FNNWR	19	930.8	51.5	3.2686	67.6	0.0017[a]
	NBR	60	869.2	114.0			
4-5 yrs	FNNWR	15	1022.0	54.4	2.0201	51.0	0.0486
	NBR	38	980.9	70.7			
6-7 yrs	FNNWR	14	1082.2	61.0	2.8325	40.0	0.0072[a]
	NBR	28	1024.9	62.3			
8+ yrs	FNNWR	36	1092.3	83.6	3.1491	59.0	0.0026[a]
	NBR	25	1030.4	62.0			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.20. t-Test Comparisons of Mean Liveweight Data for Males from the National Bison Range (1987) and Fort Niobrara National Wildlife Refuge (1987)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	FNNWR	24	359.7	16.5	3.1210	49.4	0.0030[a]
	NBR	42	326.2	66.0			
Yearlings	FNNWR	12	734.1	92.4	1.1481	62.0	0.2553
	NBR	52	702.8	83.5			
2-3 yrs	FNNWR	16	1199.8	154.3	1.9370	63.0	0.0572
	NBR	49	1106.6	170.9			
4-5 yrs	FNNWR	17	1621.8	121.1	1.3442	39.0	0.1866
	NBR	24	1567.5	131.4			
6-7 yrs	FNNWR	10	1801.5	99.3	1.9034	20.0	0.0715
	NBR	12	1732.7	70.0			
8 + yrs	FNNWR	31	1846.1	95.5	0.5336	41.0	0.5965
	NBR	12	1825.9	146.2			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.21. t-Test Comparisons of Mean Liveweight Data for Females from the National Bison Range (1987) and Theodore Roosevelt National Park (1985)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	TRNP	9	328.7	78.7	-1.5019	57.0	0.1386
	NBR	50	295.7	57.1			
Yearling	TRNP	5	596.6	44.4	0.1885	46.0	0.8513
	NBR	43	602.0	62.5			
2-3 yrs	TRNP	15	927.1	136.5	-1.6923	73.0	0.0949
	NBR	60	869.2	114.0			
4-5 yrs	TRNP	3	1112.7	120.9	-2.9626	39.0	0.0052[a]
	NBR	38	980.9	70.7			
6-7 yrs	TRNP	6	1084.3	92.9	-1.9444	32.0	0.0607
	NBR	28	1024.9	62.3			
8+ yrs	TRNP	13	1122.5	83.7	-3.8508	16.0	0.0005[a]
	NBR	25	1030.4	62.0			

[a] Difference is significant at $p < .0125$ (one-tailed test).

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Table 2.22. t-Test Comparisons of Mean Liveweight Data for Males from the National Bison Range (1987) and Theodore Roosevelt National Park (1985)

Age Class	Park	N	Mean Wt (lb)	St. Dev.	t	df	Prob > |t|
Calves	TRNP	9	354.9	65.3	-1.1861	49.0	0.2413
	NBR	42	326.2	66.0			
Yearlings	TRNP	6	669.0	98.8	0.9214	56.0	0.3608
	NBR	52	702.8	83.5			
2-3 yrs	TRNP	6	1115.3	255.2	-0.1125	53.0	0.9109
	NBR	49	1106.6	170.9			
4-5 yrs	TRNP	3	1346.7	160.6	2.6933	25.0	0.0125
	NBR	24	1567.5	131.4			
6-7 yrs	TRNP	1	1735.0	---	-0.0320	11.0	0.9750
	NBR	12	1732.7	70.0			
8 + yrs	TRNP	0	---	---	---	---	---
	NBR	12	1825.9	146.2			

[a] Difference is significant at p < .0125 (one-tailed test). None were significant.

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Table 2.23. Summary Results of t-Test Comparisons of Mean Liveweights Between Paired Parks

Sex	Age Class	Probability > |t|[b]					
		TRNP:FNNWR	TRNP:WCNP	TRNP:NBR	FNNWR:NBR	WCNP:NBR	FNNWR:WCNP
Females	Calves	0.6889[c]	0.7654[c]	0.1386[c]	0.0001[a]	0.0186	0.0541
	Yearlings	0.0016[ac]	0.3468[c]	0.8513[c]	0.0001[a]	0.0038[a]	0.0001[a]
	2-3 yrs	0.9217	0.0001[a]	0.0949	0.0017[a]	0.0001[a]	0.0001[a]
	4-5 yrs	0.3247[c]	0.0004[ac]	0.0052[ac]	0.0486	0.0001[a]	0.0001[a]
	6-7 yrs	0.9521[c]	0.0004[ac]	0.0607[c]	0.0072[a]	0.0001[a]	0.0001[a]
	8 + yrs	0.2702	0.0001[a]	0.0005[a]	0.0026[a]	0.0028[a]	0.0001[a]
Males	Calves	0.8334[c]	0.5975[c]	0.2413[c]	0.0030[a]	0.2941	0.0852
	Yearlings	0.1870[c]	0.1505[c]	0.3608[c]	0.2553	0.0001[a]	0.0001[a]
	2-3 yrs	0.3512[c]	0.0515[c]	0.9109[c]	0.0572	0.0001[a]	0.0001[a]
	4-5 yrs	0.0027[ac]	0.7278[c]	0.0125[c]	0.1866	0.0040[a]	0.0011[a]
	6-7 yrs	0.5389[c]	0.2458[c]	0.9750[c]	0.0715	0.0017[ac]	0.0014[ac]
	8 + yrs	---	---	---	0.5965	0.0081[ac]	0.0001[ac]

[a] Difference is significant at $p < .0125$ (one-tailed test).

[b] See Tables 2.11-2.22 for presentation of each test.

[c] Sample from one park has a small sample size (<10).

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Table 2.24. Comparison of Mean Liveweights and Park Characteristics

Part A. Park Latitude

Sex	Age Class	Northern Location Matches Larger Mean Liveweight					
		TRNP>FNNWR	TRNP>WCNP	NBR>TRNP	NBR>FNNWR	NBR>WCNP	WCNP>FNNWR
Females	Calves	---	---	---	No	---	---
	Yearlings	No	---	---	No	Yes	No
	2-3 yrs	---	Yes	---	No	Yes	No
	4-5 yrs	---	Yes	No	---	Yes	No
	6-7 yrs	---	Yes	---	No	Yes	No
	8 + yrs	---	Yes	No	No	Yes	No
Males	Calves	---	---	---	No	---	---
	Yearlings	---	---	---	---	Yes	No
	2-3 yrs	---	---	---	---	Yes	No
	4-5 yrs	No	---	---	---	Yes	No
	6-7 yrs	---	---	---	---	Yes	No
	8 + yrs	---	---	---	---	Yes	No

Note: --- indicates no significant difference ($p < .0125$, one-tailed test) was found for mean weights.

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Table 2.24. Comparison of Mean Liveweights and Park Characteristics

Part B. Park Altitude

Sex	Age Class	Higher Altitude Matches Larger Mean Liveweight					
		TRNP>FNNWR	WCNP>TRNP	NBR>TRNP	NBR>FNNWR	WCNP>NBR	WCNP>FNNWR
Females	Calves	---	---	---	No	---	---
	Yearlings	No	---	---	No	No	No
	2-3 yrs	---	No	---	No	No	No
	4-5 yrs	---	No	No	---	No	No
	6-7 yrs	---	No	---	No	No	No
	8 + yrs	---	No	No	No	No	No
Males	Calves	---	---	---	No	---	---
	Yearlings	---	---	---	---	No	No
	2-3 yrs	---	---	---	---	No	No
	4-5 yrs	No	---	---	---	No	No
	6-7 yrs	---	---	---	---	No	No
	8 + yrs	---	---	---	---	No	No

Note: --- indicates no significant difference ($p < .0125$, one-tailed test) was found for mean weights.

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Table 2.24. Comparison of Mean Liveweights and Park Characteristics

Part C. Park Mean Annual Temperature

Sex	Age Class	Lower Average Annual Temperature Matches Larger Mean Liveweight					
		TRNP>FNNWR	TRNP>WCNP	TRNP>NBR	NBR>FNNWR	NBR>WCNP	FNNWR>WCNP
Females	Calves	---	---	---	No	---	---
	Yearlings	No	---	---	No	Yes	Yes
	2-3 yrs	---	Yes	---	No	Yes	Yes
	4-5 yrs	---	Yes	Yes	---	Yes	Yes
	6-7 yrs	---	Yes	---	No	Yes	Yes
	8 + yrs	---	Yes	Yes	No	Yes	Yes
Males	Calves	---	---	---	No	---	---
	Yearlings	---	---	---	---	Yes	Yes
	2-3 yrs	---	---	---	---	Yes	Yes
	4-5 yrs	No	---	---	---	Yes	Yes
	6-7 yrs	---	---	---	---	Yes	Yes
	8 + yrs	---	---	---	---	Yes	Yes

Note: --- indicates no significant difference ($p < .0125$, one-tailed test) was found for mean weights.

The lack of significance of the size differnces between many of the pairings of male populations is probably due to a combination of factors including small sample sizes and greater variability in male weights in any given combined age class. The small sample sizes also may be important in some of the comparisons of female populations when the TRNP sample is part of the pairing.

Given that there are significant differences in mean bison liveweight measured by specific age and sex classes between some park populations, the next step of this investigation is to determine whether the differences in mean liveweight are consistent with expectations as suggested by Bergmann's rule. Table 2.24 summarizes three such tests. In each case, only those park pairings which were shown in Table 2.23 to be significantly different in mean liveweight are considered. Table 2.24, Part A examines whether mean liveweight varies as expected with respect to park latitude (i.e., more northern parks are expected to have larger animals than southern parks). Part B examines variability in liveweight with respect to park altitude (i.e., higher altitude is expected to correspond with larger mean weight). Part C examines variability in liveweight with respect to the average annual temperature, where low average annual temperature is expected to correspond with larger mean liveweight. In each case (Table 2.24), the results were not consistent for all park pairings or were contrary to expectations, indicating that if these are adequate measures of Bergmann's rule, then it is not valid.

Other factors which may influence animal size may include genetic variability and/or differences in the productivity of the parks' ranges. The modern herds, managed by state and federal agencies, are all relatively isolated populations of offspring of relatively small populations of bison,

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preserved from extinction in the late 1800's and early 1900's (see Dary 1974). Berger and Peacock (1988) examined bison size at the Badlands National Park, South Dakota, investigating whether differences in weights and body measurements could be attributed to inbreeding in one of the two parent populations. They could not demonstrate that the differences noted were not attributable to other factors, including the residual effects of nutritional differences in the food supplies available to parent populations. It is apparent from the comparison of the park populations above, however, that modern herds with parent populations originating from Oklahoma, Texas, and New Mexico (as part of either the Goodnight or C. J. Jones herds) tend to be smaller than those orginating from more northern herds (e.g., the Allard herd). A genetic-related difference in animal size between herds needs to be more thoroughly examined, but appears at this point to be a possible factor in the observed differences.

As an alternative, Geist (1987) suggests that food productivity probably plays a major role in determining body size. "The hypothesis that body size follows the duration of the annual productivity pulse appears to be valid, and has a sound rationale: body size appears to be a function of how much time growing individuals have unhindered access to food of the highest quality" (Geist 1987:1037). If this is true, then one would expect to see patterns of bison liveweight differences following patterns of grassland productivity.

With the exception of the National Bison Range (NBR), all of the parks used in this study are found in areas of mixed-grass prairie. The NBR is found in what is considered mountain grassland (Sims et al. 1978:253) and elsewhere was classified as Palouse prairie (French 1979a:42). Despite the fact that the parks are nearly all in mixed-grass prairie, there are

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differences in grass species dominance between the parks and in the comparative productivity of these grasslands. Sims et al. (1978:Appendix III) compared biomass quantities for ten grassland study sites in the United States, three of which are located at or near the parks from which the bison liveweight data originate. They call the study site located at the National Bison Range, Bison. The other study sites are Cottonwood in southwestern South Dakota, and Dickinson in west-central North Dakota. These study areas are near the National Bison Range, Wind Cave National Park, and Theodore Roosevelt National Park, respectively. There does not appear to be a site from their study that lies particularly near the Wichita Mountains Wildlife Refuge. Cottonwood is the site that lies closest to FNNWR and may be an appropriate indicator for that area, and possibly more so for that park than for Wind Cave National Park which lies over 300 meters higher in elevation than the study site.

Sims et al. (1978:285) report that the mean live biomass (gm m^2) for grazed study areas (with the corresponding bison park indicated) were as follows: Bison (NBR), 72; Cottonwood (WCNP or FNNWR), 60; and Dickinson (TRNP), 158. Speth (personal communication) suggests that grass condition affects males more than females and calf size more than female size. This is because of differences in maintenance requirements and fat reserves in these animals. It suggests that liveweight differences attributable to differences in range productivity may be evident earlier in younger animals and males than in females if sample sizes are large enough. Comparisons of the biomass data with mean bison liveweight relationships, indicate that factors other than biomass alone are operating to determine bison weight distributions. If available biomass were the only factor influencing size, one would expect the mean liveweights for the TRNP animals to be largest

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followed by the NBR animals and then the FNNWR and WCNP herds. Although the TRNP females are larger than the WCNP females and the NBR animals are larger than the WCNP bison, the NBR animals are smaller than the FNNWR bison, which is contrary to expectation. It is doubtful that range productivity, as measured by biomass alone, is the only factor influencing bison size. Other factors that might be examined to correlate bison liveweight means and park location include characterization of the grasslands and the mixture of species, the proportions of warm and cool season grasses, and grass protein and other nutrient content, as well as environmental factors that may affect energy metabolism in bison or affect their access to the highest quality forage. This appears to be an area that profitably could be explored by those interested in understanding bison variability and the influence such variability might have had upon yields from bison procurement by prehistoric hunters.

Size of the TRNP Herd. Of ultimate interest at this particular point, is the placement of the TRNP herd in relation to the other park herds for comparison of bison liveweight. Referring once again to Table 2.23 and Figures 2.7 and 2.8, it is evident that the differences in mean liveweights were significant for pairings at some ages between parks, but not for others. The TRNP sample did not have large numbers of individuals represented in each age category, so the lack of significance in most of the TRNP pairings may be related to small sample sizes. The lack of significance in the difference of animal size between the TRNP and FNNWR populations might not change with larger sample sizes, however.

The TRNP herd was established in 1956 with a starter herd of 29 animals originating from the FNNWR herd. The fact that significant differences were found for one of the age class comparisons in each of the male and female

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population comparisons is not necessarily important. The male four-five year age class at TRNP was dominated by four year olds, whereas at FNNWR they were more evenly divided between four and five year olds. The larger size of the FNNWR males in this age class, though significant, is probably attributable to this distribution. The difference in female yearlings was significant, however, but the sample size is small. Larger sample sizes are needed to more fully understand the relationship of animal size between the TRNP and FNNWR herds. Significant size differences were found for some age group comparisons of the TRNP bison with other herds. The TRNP mean was larger than the NBR mean for females in the four-five year and eight years and over age classes.

Many more age categories demonstrate significant differences in size between females in the TRNP and WCNP herds. In each case, the TRNP mean was larger than that for the WCNP data. Although distribution data were not available to statistically compare animal sizes between the Wichita Mountains Wildlife Refuge and TRNP, it appears, on the basis of the data presented (Figures 2.7 and 2.8), that a significantly larger mean would probably have been found for the TRNP data.

Metric Attributes of Skeletal Elements as a Measure of Animal Size

As previously noted, in addition to understanding how the TRNP animals compare with other bison herds in terms of liveweight, it is also important to know how this is reflected in the size of the skeletons of the animals. Bones are what remains for archaeologists to examine to determine herd composition, seasonality of the kill, and differences in treatment of the carcasses of the kill with respect to animal age and sex. By studying the metric attributes of skeletal elements, assemblages can be studied for

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differences in herd composition (evident due to the occurrence of sexual dimorphism in bison) and for differences in size between populations of animals. Use of metric attributes for such purposes is relatively recent and has interesting potentials for application.

Speth (1983) studied bones of bison, of known sex, from (1) Harvard University, Museum of Comparative Zoology, (2) the University of Michigan, Museum of Zoology, and (3) the Smithsonian Institution's National Museum of Natural History to show that specific metric attributes could be correlated with bison sex. With this sample, he found that using scatterplots of one measurement plotted against another (e.g., Bedord 1974), some combinations of measurements were better than others for identifying animal sex. The combined attributes, or criteria, were subdivided into three groups based upon their effectiveness in sexing the bones: those providing good, fair, and poor results (Speth 1983:Appendix Table 31). Once he demonstrated the sexual dimorphism of the attributes, Speth subsequently applied these measurements to an archaeological assemblage of bison bone, in order to identify the sex of the animals represented in that collection, and study their differential treatment in the butchering process.

Speth's (1983:Appendix Table 20) original sample of distal humeri of known sex included 28 animals, of which 19 were male and nine were female. When samples from both sides were available, the attribute was measured separately and considered as separate sample values. Unlike many collections, this sample is well represented by males and poorly represented by females. The fact that one animal may be represented by readings for bones from both sides may tighten the clusters of points. One might argue that to compare random animals from populations of unknown origin, as represented in Speth's museum sample, is problematic, in that it represents

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a population that would differ in character from any collected from a single source, probably by demonstrating wider variability. This may be true, but if anything, it enhances the value of his study in that by increasing variability, one might, in effect, also decrease the probability of producing separated groupings of males and females in the scatterplots. One might expect, therefore, that where animal, and therefore, bone sizes, are less variable within a regional population, as compared with a population of mixed regional origin and possibly variable animal size, that there would be less overlapping of sex clusters. If this is true, Speth's work should prove very useful in studies of prehistoric herd composition.

Comparison of TRNP Distal Humeri to Speth Museum Specimens. In this study, the current interest in this method of analysis is in its use for comparing the sizes of the TRNP sample animals to those of bison in general. In doing so, one must recall that the Speth sample bison are varied in their origins and ages beyond their adult status are unknown. It should further be noted that the purpose of Speth's study was not to define specific ranges of measurement for bones with which to determine the sex of animals of unknown sex, but to provide a method which might be applied to a population or assemblage of bones of single origin to identify animal sex. Nevertheless, it should be of interest to add the TRNP sample animals to the mixed population represented by Speth's museum collections, to see whether they lie within the distributions represented, or if they lie outside these distributions.

To make these comparisons, I first selected three attribute combinations for one bone element that Speth noted as providing a good rating for separating the sexes. Just as these attributes vary in how well they separate adult specimens by sex, it should be noted as well, that the

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measurement of skeletal attributes in the TRNP sample specimens indicate that sexual dimorphism is evident in some attributes earlier than in others and in some, appears to be evident as early as 1-1/2 years of age.

Figure 2.9 illustrates the distribution of the attribute measurements (Tables 2.25 and 2.26) from Speth's sample with the TRNP bison measurements indicated by geometric symbols. This figure illustrates that for the distal humerus attributes I, K, M, N and O (Speth 1983), the yearling male, FYM, is larger than the adult females, SAF and FAF. For these measurements, sex determinations may be possible even though the specimen is not from an adult and has not fused. Appendix A, Table 1 lists the measurements of metric attributes for the four study specimens, indicating which attributes are apparently dimorphic by the time bison are 1-1/2 years old. Note that by four years of age (as represented by SAM), male bison appear to larger in their skeletal attribute measurements than females. Figure 2.9 also illustrates that in mature adults, some attributes are more variable than others and their usefulness as determiners of sex vary, as Speth indicated (i.e., those with overlapping distributions are less likely to clearly separate distributions based upon sex).

Figures 2.10 through 2.12 respectively show the scatterplot distributions for the following metric attributes of the distal humerus: I*J, I*M, and J*N. Speth (1983:172) notes that these measurements can be determined with a high degree of replicability and relative ease. From the distributions of the males and females in these illustrations (Figures 2.10 - 2.12) and the locations of the four TRNP sample animals from this study, one can see that there is some variability in how well the TRNP animals fit in their respective sex classes. In all three of these figures, SAM lies intermediate in the distributions of the male measurements, and as expected,

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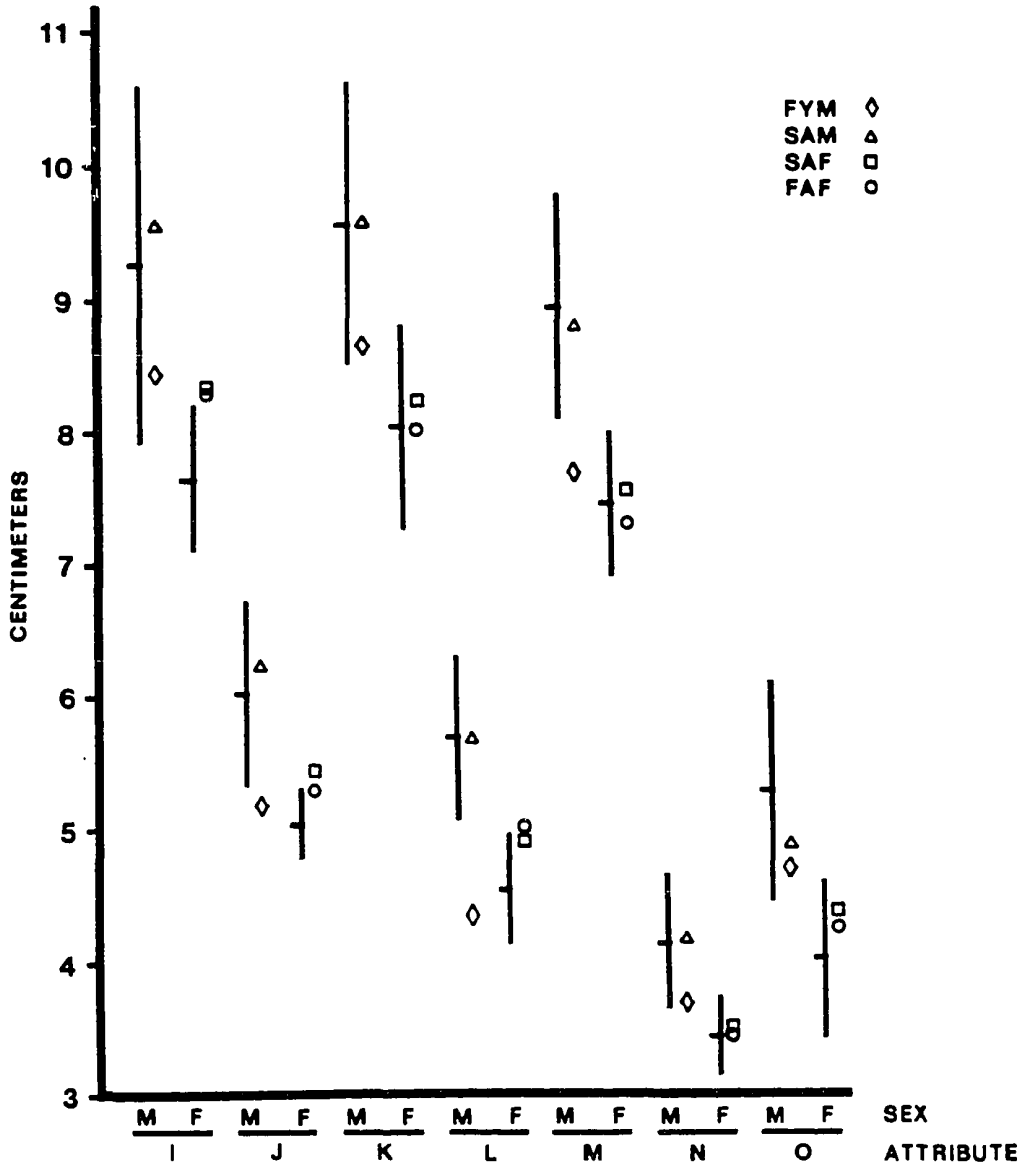

Figure 2.9. Measurement Distributions of Distal Humerus Skeletal Attributes for Males (M) and Females (F) in Speth (1983:Appendix Table 20) Sample with the Corresponding TRNP Bison Specimen Measurements. Mean measurements are indicated by horizontal ticks. Vertical length equals two standard deviations from the mean in each direction.

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Table 2.25. Selected Metric Attributes of the Distal Humeri of the Theodore Roosevelt National Park Study Specimens

Attribute[a]	Attribute Measurement (mm) in Individual Bison			
	FYM	SAF	FAF	SAM
I	84.75	83.40	83.10	95.60
J	51.90	54.50	53.00	62.50
K	86.70	82.60	80.30	96.10
L	43.95	49.45	50.40	57.50
M	77.15	75.90	73.30	88.10
N	37.40	35.70	34.80	42.05
O	47.40	44.05	42.85	49.20

[a] See Speth (1983) for a description of these attributes.

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Table 2.26. Distribution of Metric Attributes of Distal Humeri of Bison from Speth Sample[a]

Attribute	Sex	n	Mean (cm)	Standard Deviation (cm)	Mean (cm)		Mean (cm)	
					- 1 S.D.	+ 1 S.D.	- 2 S.D.	+ 2 S.D.
I	Male	20	9.26	0.67	8.59	9.93	10.60	7.92
	Female	14	7.66	0.28	7.38	7.94	7.10	8.22
J	Male	20	6.03	0.35	5.68	6.38	5.33	6.73
	Female	14	5.06	0.13	4.93	5.19	5.06	5.32
K	Male	20	9.58	0.53	9.05	10.11	8.52	10.64
	Female	14	8.05	0.38	7.67	8.43	7.29	8.81
L	Male	20	5.71	0.31	5.40	6.02	5.09	6.33
	Female	14	4.58	0.21	4.37	4.79	4.16	5.00
M	Male	20	8.96	0.42	8.54	9.38	8.12	9.80
	Female	14	7.49	0.27	7.22	7.76	6.95	8.03
N	Male	20	4.18	0.25	3.93	4.43	3.68	4.68
	Female	14	3.48	0.15	3.33	3.63	3.18	3.78
O	Male	16	5.33	0.42	4.91	5.75	4.49	6.17
	Female	14	4.06	0.30	3.76	4.36	3.46	4.66

[a] Source (Speth 1983:Appendix Table 20).

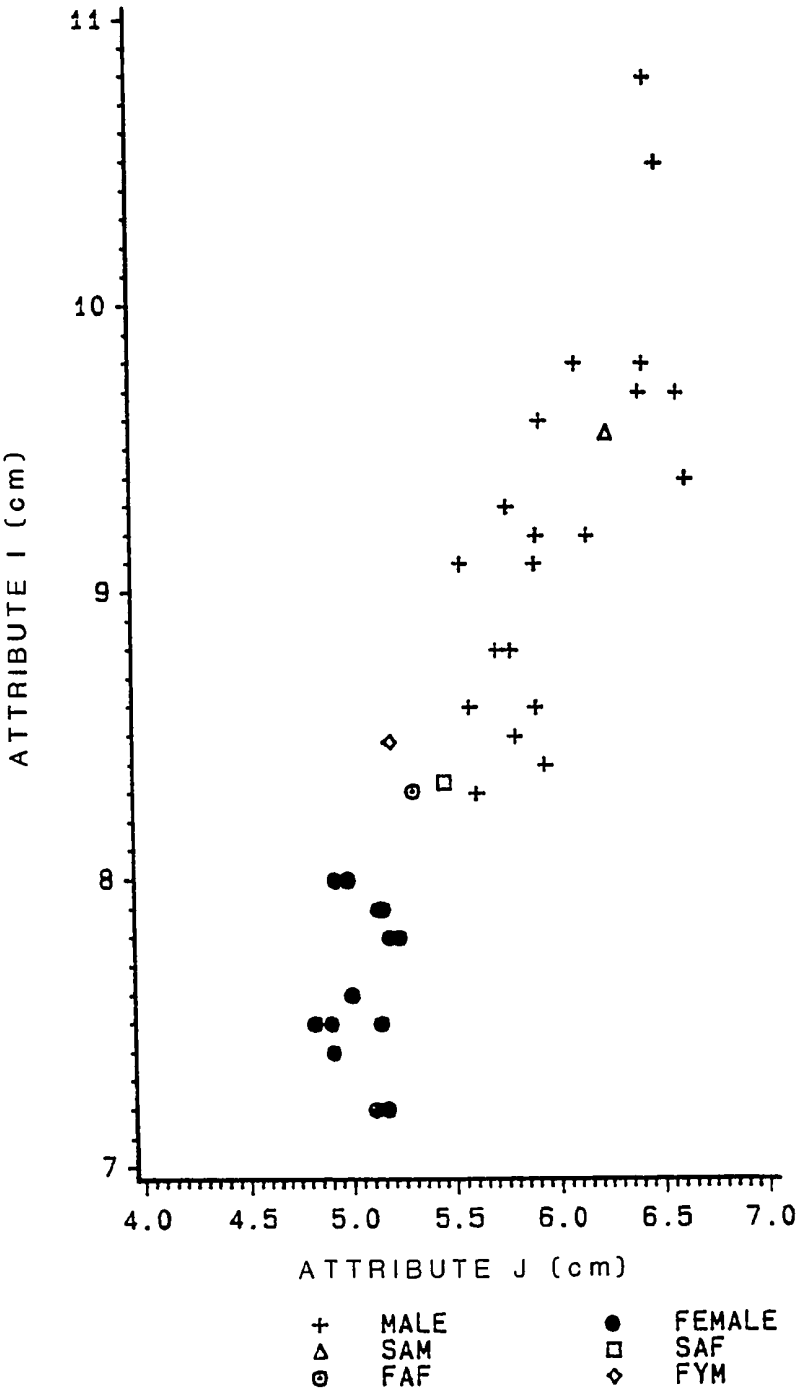

Figure 2.10. Crossplot of Distal Humerus Attributes I and J Size for TRNP Bison Specimens and Speth (1983:Appendix Table 20) Sample.

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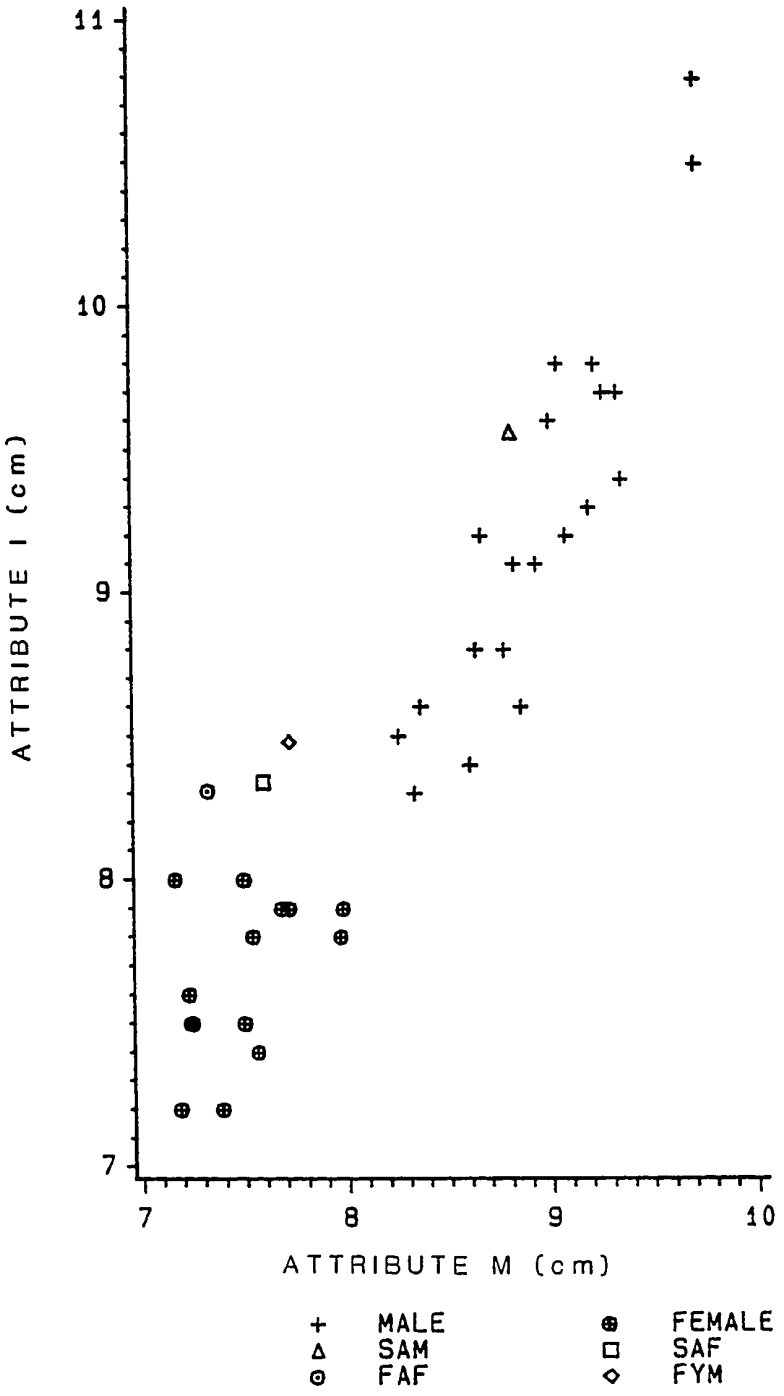

Figure 2.11. Crossplot of Distal Humerus Attributes I and M Size for TRNP Bison Specimens and Speth (1983:Appendix Table 20) Sample.

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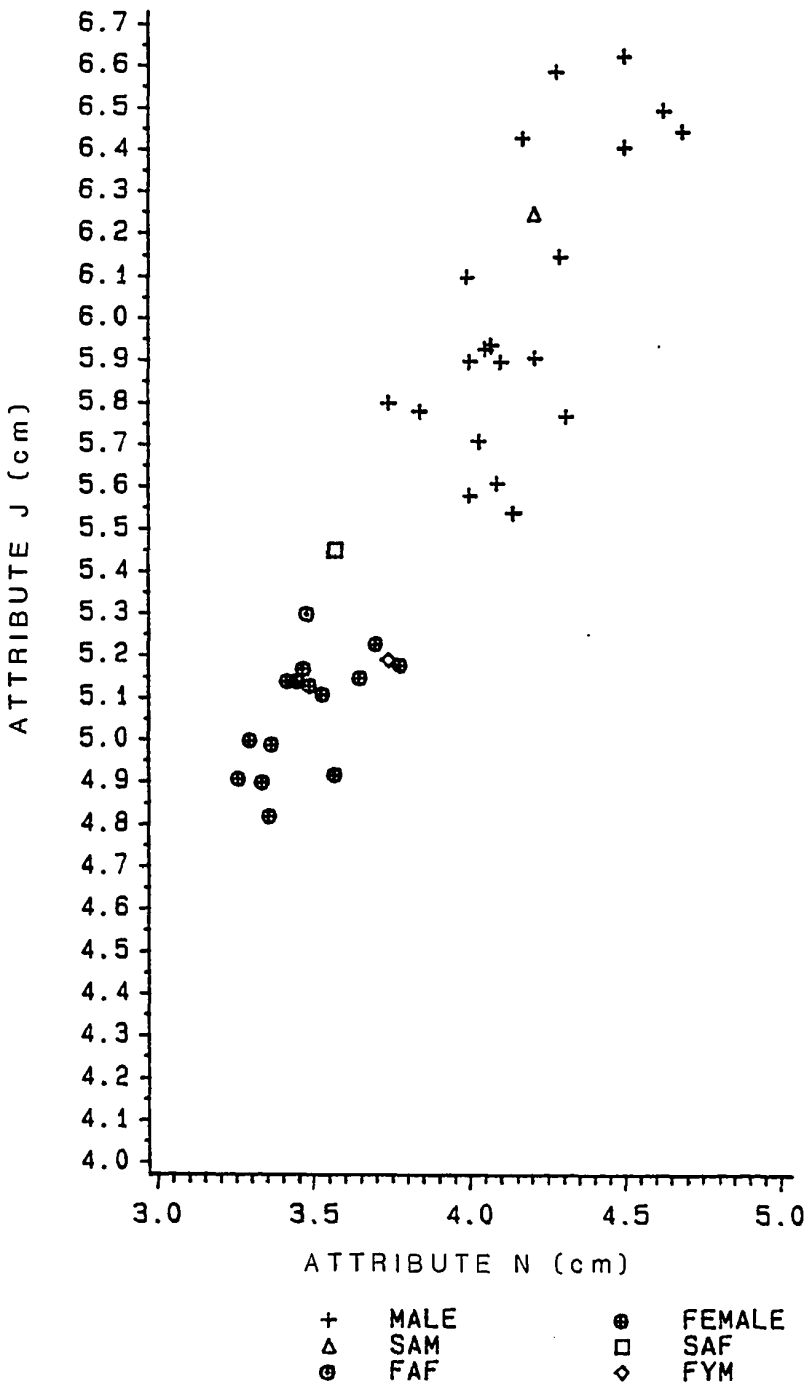

Figure 2.12. Crossplot of Distal Humerus Attributes J and N Size for TRNP Bison Specimens and Speth (1983:Appendix Table 20) Sample.

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FYM, an immature male, lies well below the measurements of these fused elements of more mature males. The females, SAF and FAF, however, show variable position in comparison to the other females, sometimes lying at the lower edge of the male distribution, or intermediate between the sex clusters.

This may indicate that the TRNP female bison are actually larger than the animals in Speth's sample. Their larger size might be attributable to differences in the age distribution of the two samples, or it might be attributable to differences in the place of origin of the samples, assuming the previously described regional size differences are not a recent development. The placement of the TRNP males might be explained by their relatively young ages. Clearly, FYM would not be expected to lie within the adult male measurement distributions. The male, SAM, however, might be larger for his age than the Speth sample specimens, but it would not be possible to so determine if many males older than four years of age are represented in that sample. This is due to the fact that males have an extended period of growth following epiphyseal fusion and appositional bone growth may be quite large (Bedord 1974). As evidence of this, one need only to compare the attribute measurements of the proximal radii of male bison of different ages (Appendix A). The proximal radii in the yearling male, FYM, and in the male SAM were both fused, yet the attribute measurements of the older male are substantially larger. Appositional growth must account for this difference, beyond that which is attributable to individual variability in animal size. The clusters of male measurements in Figure 2.11 may be an indication of age-related differences in bone attribute size as affected by appositional growth. This is something which should be investigated in the future, but is not included in this dissertation. At four years of age, SAM

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is still not at his full adult weight. To determine if the TRNP males are larger than other bison, one should either determine the age structure of the Speth sample or compare skeletal attributes in bones that fuse after full maturity is reached and use an older specimen than SAM.

Alternatively, the difference between the Speth and TRNP samples, illustrated by points on the scatterplots, may be an artifact of differences in individual techniques for measuring the metric attributes. This is not thought to be a serious possibility, however, as it is not expected that the differences in measurement would be large enough to markedly affect the distributions.

In conclusion, it appears that on the basis of the measurement of the distal humerus (which in females is fused at the age at which cows reach full maturity in terms of liveweight), that the TRNP female specimens may be a little larger than many of the individuals in Speth's (1983) sample. The data are inconclusive for males, due to the absence of age data and the effects of appositional bone growth.

Conclusions

In this chapter, the bison sample from Theodore Roosevelt National Park has been described, and the suitability of these animals to serve as representatives of bison in general was assessed with respect to their size. The sample specimens were found to be typical for their age and sex classes at TRNP when compared by liveweight. The analysis of bison liveweight data from several parks presented here, together with published data from Oklahoma (Halloran 1961), are complimentary to those recently published by Berger and Peacock (1988). These park liveweight data, when compared against one another, suggest that animal size differences exist in modern

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bison populations when liveweight means are compared for specific age and sex classes. Bison in the TRNP herd tend to be larger than in many other herds, though due to small sample sizes this could not always be affirmed statistically. Measurements of skeletal attributes of the distal humerus (a bone which fuses near the age when bison cows reach full maturity in liveweight) showed that the female sample specimens from TRNP tended to be larger in the size of some of these attributes as well, suggesting that liveweight differences may also be evident in the skeletons of bison.

These data all suggest that the TRNP animals may be significantly larger than bison of similar age and sex from other locations. The importance of this assessment lies in its implications for use of the carcass composition data to be presented in later chapters. It indicates that meat and fat weights from these TRNP specimens should not be used without giving consideration to the comparability in size of the TRNP specimens to those for which these data are to be applied. This is not a direct adjustment when animals differ in size. It is important to remember that larger sized animals have prolonged growth periods and a delayed onset of the fattening phase relative to smaller sized animals. This is discussed in greater detail in later chapters. The point being made here is that one should consider how differences in size might affect composition when making estimates of available meat and fat from kill site assemblages with animals of appreciably larger or smaller size than the TRNP study specimens.

The descriptions of the study specimens also indicate that the two females may show some differences in condition from animals of their respective ages, killed at the same time of the year. The female, SAF, may or may not have calved the previous year, which might lead her to be in better than normal condition. The female, FAF, demonstrated an abnormal

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dental wear pattern and associated mandible deformation that suggests a long-term problem that might suggest she was in poorer condition when she was killed than females of comparable age. These problems are considered in later chapters when animals are selected for comparisons of carcass composition. The condition of the TRNP herd as a whole is considered in the next chapter.

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CHAPTER 3. DESCRIPTION OF THE BISON SAMPLE: PART TWO

In the previous chapter, the characteristics of the four sample bison were described, and they were found to be adequate representatives of bison from Theodore Roosevelt National Park (TRNP) for their associated age and sex classes. An analysis of liveweights for these and other TRNP bison compared with bison from other parks showed the TRNP herd animals to be significantly larger than animals in many of the other parks. This appears to be the case as well, when the sizes of bone attributes are compared, but the bone study could not be considered conclusive. In this chapter, the principal interest again is related to whether the TRNP animals are good representatives of bison in general, and of animals of similar age and sex classes. However, the focus here is on how one might evaluate whether the TRNP herd animals were in good or poor condition the year the study specimens were shot. By doing so, it may be possible to more clearly understand the results of the data analyses presented in later chapters, under circumstances where the sample size is so limited.

The specific conditions of the TRNP study specimens are discussed in Chapter 5. In this chapter, I use information on changes in temperature and precipitation from 1983 to 1985 as a proxy (in the absence of annual liveweight records) to study the condition of the herd at Theodore Roosevelt National Park. Before making this proxy assessment of the TRNP bison herd condition, it is necessary to demonstrate that such changes in climate may be correlated with changes in bison condition as measured by liveweight. Due to the lack of annual records of individual animal liveweight at TRNP,

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the relationship between individual animal liveweight and changes in climate had to be established at another park--Wind Cave National Park (WCNP)--where such data are available. The bison liveweight data provided by Richard Klukas of Wind Cave National Park offers such an opportunity. Like the TRNP bison, the WCNP herd is range fed and is not given supplemental feed during poor weather, a practice which might distort the natural record of weight gains and losses. The data from this park included eartag numbers for each recorded animal liveweight. With this information, changes in yearly liveweights of individual animals for as many as five years duration is possible. This is important, because grouped means average out differences across multiple years, whereas mean liveweight changes for individuals with multiple year records allow study of fluctuations in animal liveweight. By grouping individual liveweight changes by age and sex classes and comparing them with changes in temperature and precipitation patterns, it should be possible to study WCNP bison responses to major changes in climate. If liveweight changes can be shown to correlate with changes in the climatic record here, then it may be possible to offer an assessment, though tentative, of the condition of the TRNP herd, based upon climatic records for that location, where individual bison liveweights are lacking.

This chapter is divided into five sections. In the first section, Factors in Bison Growth, I discuss bison nutrition, metabolism, and diet. In the second section, Patterns of Bison Growth, I discuss the difference between mean growth and mean individual patterns of growth registered over five years at Wind Cave National Park. In the third section, Bison Growth and Climatic Stress, I discuss the correlation between range productivity and variability in climate, and then discuss the relationship between the climatic data from Hot Springs, South Dakota (which is near WCNP) and the

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changes in liveweight registered for individual bison at Wind Cave National Park. In the fourth section, Evaluating the Condition of the TRNP Herd, I examine the weather data for Medora, North Dakota (which is near the south unit of TRNP) for the years 1983-1985, and discuss the possible implications these data have for changes in range productivity and the subsequent condition of the animals in the bison herd, as might be measured through liveweight changes and through changes in carcass fat composition. Although individual bison liveweight changes are not available for the Theodore Roosevelt National Park herd, demonstration of a correlation between climatic data and individual bison growth at Wind Cave National Park provides a model of the interaction between these elements. The final section of the chapter summarizes the results of the analyses as they relate to the relative condition of the TRNP herd and study specimens.

Factors in Bison Growth

Growth and liveweight gains in bison, as in other organisms, is controlled by whether the animal obtains sufficient energy to meet both its basic requirements for maintaining life, and to permit response to higher energy requirements associated with physical activities and changes in the external environment. Energy requirements are satisfied, following birth, by the ingestion and digestion of food acquired from the environment, or by nursing. Dietary variability occurs due to regional and seasonal variations in forage availability and due to species variability in food preferences. Similarly, energy requirements may vary in seasonal cycles, or in response to conditions that require metabolic adjustment in order to maintain energy balance. These factors--nutrition, metabolism, and growth--are discussed in this section, in addition to a brief review of the general characteristics

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of bison diets, including a short discussion of regional variability in diet.

Animal Nutrition, Metabolism, and Growth

Animal growth in the young and liveweight stability in mature animals is dependent upon intake of energy by the organism adequate to meet maintenance requirements of the body, and to fuel additional energy needs resulting from physical activities, changes in the external environment, and production of hair or milk (Ferrell 1988). Animal liveweight is continuously changing, registering gains and losses through short-term periods of adjustment. The long-term effect, however, generally appears to be one with a positive balance during growth or liveweight gain, and to be more or less at equilibrium, following puberty, once an animal reaches maturity. Periodically, however, the long-term effect may register as a negative balance with liveweight losses during periods of malnourishment. To understand changes in liveweight records for animals over consecutive years, one must first understand how and why energy requirements for animals of different age and sex classes are different, and how deficits in intake are registered.

Two concepts that are important to this discussion and to an understanding of how changes in food availability affect individuals of different age and sex classes are (1) metabolic rate, and (2) maintenance. Basal metabolic rate refers to heat production by an organism and correlates with minimum energy requirements needed to sustain life. It is measured in an environment that requires no metabolic adjustments by the organism under fasting conditions (Blaxter 1962:79-80). Metabolic rate is usually expressed as a given amount of energy per unit of body weight per day.

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Maintenance is equivalent to fasting heat production plus heat production from the food eaten. It represents the portion of metabolizable energy available to the organism that is used "for essential life processes and the efficiency with which the metabolizable energy from food is used to meet those requirements" (Ferrell 1988:258-259). It does not include energy necessary to sustain an animal's production efforts, only the minimum amount of energy needed to keep an organism alive. Maintenance, then, represents a baseline requirement for life, and metabolic rate indicates the relative rate at which heat is produced and therefore required without food, and without stress originating from the environment.

The importance of these concepts lies in their use in explaining differences in how animals respond to the same or similar environmental conditions. Metabolic rates, and thus maintenance requirements, for animals of different ages and sex are different. In addition, metabolic rates may fluctuate in response to changes in the external influences affecting an animal. They respond to changes in the environment that affect them directly, such as high winds coupled with low temperatures, or indirectly, as through changes in the quality or quantity of available forage.

The following section provides a brief discussion of some of the mechanisms that operate to produce differential metabolic rates and maintenance requirements. Following that is a section outlining the implications for liveweight responses in animals of different age and sex classes to periods of food intake that would be above and below maintenance requirements.

Factors Influencing Metabolic Rates and Maintenance Requirements

The metabolic rate of, and maintenance costs for, a given animal are largely affected by its age, sex and body composition. The importance of

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these factors is tied to priorities for energy allocation and differential efficiency of energy utilization by tissues of different types. Although metabolic rates and maintenance requirements are usually determined on non-lactating, non-gestating individuals, the information presented in this section is applicable to reproducing females as well.

Priority and Efficiency of Tissue Growth. In young organisms the priority of tissue growth and thus, the priority with which energy is utilized, varies as the animal increases in age and size. In a review of models of growth, Russell (1969:375) notes that, in the growth of an individual from an embryo to a mature animal, the order of tissue contribution to growth is from the nervous system, to bone and tendon, to muscle, and finally, to fat. Pfander (1969:296) notes that, postnatally, the order of growth of major tissues is from bone, to muscle and fat, and that this period of growth corresponds with a maximum period of protein deposition. A gradient for priority of growth also exists between locations in the body, thus resulting in differential rates of growth for different parts of the body. This was evident in the earlier discussion of metric bone attributes and the differentiation of sex. In some skeletal locations, the yearling male, FYM, was larger than the two females, despite his immature status. In other locations, the measurements for the bones of the yearling male were substantially smaller than those of the adult females. Hammond (c.f., Hafez 1969a:10) found that growth gradients run from the head posteriorly and from the distal ends of the limbs proximally toward the vertebral column.

The amount of growth for different kinds of tissue is affected by these priorities for development, and also by differences in the efficiency of growth for different kinds of tissue. The efficiency of tissue growth is

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tied to its turnover rate, that is, the frequency with which new tissue is deposited (Byers and Schelling 1988a:440). As Ferrel (1988:259) and Byers and Schelling (1988a:439) note, the three metabolic functions of cell maintenance that represent the major costs of maintenance include ion transport, protein synthesis and turnover, and triglycerol (fat) synthesis and turnover. Tissues with high turnover rates are less efficient than those with low turnover rates because they require larger amounts of energy for their production.

Byers and Schelling (1988a:439) identify two primary types of tissue, precursor tissue and user tissue, and note that the former is metabolically very active while the latter is less so. Within the group of user tissues are found other tissue types, including fat and protein, which also show differences in the efficiency of their deposition in the body. Fat tissue, for example, is less metabolically active and turns over less frequently than muscle tissue, and therefore, requires less energy for maintenance. Among fat tissues, as well, there is a hierarchy of metabolically active versus less active tissue types (Byers and Schelling 1988a:439).

As an example of how priority and efficiency work, consider the following. In young animals total energy use is much less efficient because of the priority for growth of tissues with higher turnover rates, and because of the metabolic requirements of maintaining those tissues, once present (Byers and Schelling 1988a:440). With increasing age and growth, maintenance requirements (as a percentage of total energy requirements) decrease due to shifts in the priority for growth toward less metabolically active tissue types, and due to the decrease in the proportions of the more metabolically active tissues (i.e., an increase in the percent of carcass fat relative to carcass muscle) (Byers and Schelling 1988a:440). An

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exception to this is pregnant and lactating cows. The priority for maintenance of precursor tissues and more metabolically active user tissues associated with these reproductive processes accounts for their higher maintenance requirements.

Byers and Schelling (1988a:443) note that differences between individual requirements for energy are also tied to the individual's potential for growth. Specifically, they state that some animals have higher maintenance requirements that are genetically tied to the greater potential for protein growth. This applies to animals who mature to larger sizes because of either sex or breed. The implication of these differences in potential growth and greater energy requirements for larger maturing animals, and therefore, for extended periods of time during which protein tissue growth predominates, is one of decreased availability of excess energy for storage as fat. It should be of no surprise, therefore, that male fat content is smaller than in females (Leat 1976:186).

Both young and small individuals have relatively high metabolic rates, but relatively small net energy consumption requirements. With larger animal size, total energy requirements are greater for tissue maintenance despite a lower metabolic rate. When animals are of similar size and exposed to similar environmental and forage conditions, however, maintenance requirements reflect differences in the composition of the animal, with higher metabolic rates, and thus higher maintenance costs, associated with the larger component of metabolically active tissue.

Role of Cows as Environmental Buffers for their Young. Hafez (1969b:35) notes that, from a nutritional point of view, the fetus is privileged, because it continues to grow despite some degree of maternal malnourishment. During periods of poor nutritional conditions for the cow,

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the energy reserves stored in body fat may be mobilized to provide energy for both the cow and her offspring. This demonstrates again how priority of energy allocation affects tissue growth, but also, how mothers sometimes act as buffers between their young and the environment during periods of high vulnerability. Hafez's assessment of privilege may apply to the unweaned calf as well, because it is still dependent upon its mother for its energy intake, and the adult female may use fat reserves to supply the energy needed for her maintenance and the offspring's food during periods of food stress. The cow's position as buffer for the unweaned calf, however, is limited because of additional energy requirements in the calf over those of the fetus, due to physical activity and exposure to the environment.

In this regard, it is interesting that from the observations of Richard Klukas (personal communication 1988), cows at Wind Cave National Park tend to continue to nurse male offspring longer than female offspring. This is in contrast to Meagher's (Rutberg 1986:90) assessment of bison at Yellowstone National Park where there is no available evidence on differential investment in male and female offspring. Klukas's observation in conjunction with the information concerning maintenance requirements of the young, and the differential requirements associated with differences in potentials for growth, suggest that under conditions of deteriorating climate and range productivity, animals that are able to use the energy production of their mothers by nursing, have an advantage over immature animals that are dependent upon what they can obtain from forage and their own limited fat stores. An extended period of nursing for males, with their higher metabolic rate due to larger potentials for growth than females, in effect, acts to lessen some of the risk of survival.

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Environmental Stress and Metabolic Rates. Metabolic rates change when animals are not in thermoneutral environments. The thermoneutral zone is the range of temperatures at which the organism shows no change in basal metabolic rate and in which this rate is at its minimum (Mount 1979:7). Exposure to cold below a critical temperature can cause an increase in metabolic rate, as the body tries to maintain its core temperature. The same is true in response to temperatures that exceed the thermoneutral zone.

Studies of animal responses to temperature have shown that the range of the thermoneutral zone, and the location of the critical temperatures that mark its upper and lower boundaries, are dependent upon the animal's plane of nutrition (a measure of the amount and quality of food in its diet), its thermal insulation, and its physical activity. In a resting animal, raising the plane of nutrition lowers the lower boundary of the thermoneutral zone, thus increasing cold tolerance (Mount 1979:7, 26-27). Lowering the plane of nutrition has the opposite effect, in that it raises the lower critical temperature. Under conditions of malnourishment, therefore, one would expect to see animals that are more susceptible to cold stress, in part due to their lower plane of nutrition, but also due to the decline in energy available for the production of thermal insulation.

The ability of the animal to respond to heat or cold stress varies with age, species, and breed. Mount (1980:50) notes that the susceptibility of the very young to cold stress, gives way to susceptibility to heat stress in the adult. He (1979:135-136, 209) also comments upon species and breed differences in metabolic responses to thermal changes, and suggests that they are largely dependent upon body size and thermal insulation when they are not attributable to genetically favored tolerances for certain ranges of

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temperature (e.g., differences between European and Indian, or tropical, breeds of cattle).

Christopherson et al. (1979) found the metabolic rates of Hereford cattle to be higher than those of bison, and that these species differed in their responses to changes in temperature. Two bison calves (studied from approximately .5 to 1.5 years of age) showed no evidence of seasonal changes in metabolic rate, but did show susceptibility to heat stress in the winter at 10°C (50°F), and susceptibility to cold stress at -30°C (-22°F) when exposed to winds of 4.7 km per hour (2.9 mph) (Christopherson et al. 1979). Apparently, as the authors note, they exceeded the upper limit of the thermoneutral zone in the winter test at temperatures of 10°C (50°F), but needed the added effects of wind to reach the lower critical temperature in the fall, with exposures to -30°C (-22°F) temperatures. Reynolds et al. (1982:977) suggest the heavy bison pelage offers greater insulation than in cattle and may have some responsibility for these differences in rates.

Implications for Age and Sex Differences in Energy Requirements

From this brief overview of factors affecting metabolic rate, maintenance requirements, and total energy requirements, it is apparent that the issue of nutrition and metabolism is too complex to be dealt with fully here. This review, however, points to several areas in which liveweight responses might be used to monitor long-term changes in animal condition.

From the earlier discussion on turnover rates and metabolic efficiency of different tissue types, it is clear that the proportion of energy consumption that is directed toward maintenance is higher in growing immature animals than in adults that have reached maturity and general liveweight stability. At this point, however, I am uncertain whether the

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difference in size of the animals negates the effect of differing maintenance requirements dictated by sharply different metabolic rates. The combined effects of metabolic rate and size determine the maintenance requirements. In many cases, size may overshadow metabolic rate in comparing total maintenance costs.

The increase in maintenance requirements associated with gestation and lactation noted above have been studied by Schingoethe, Byers and Schelling (1988). These authors (1988:421) note that deficits in energy were much more important than deficiencies in protein in their effects upon fertility, as measured by the length of time it took for heifers to reach maturity, comparative rates of conception, and the size of their offspring at birth. From these data it is apparent that factors that affect the energy available for intake by animals affect not only their growth, but also that of their offspring, and thus the future composition of the breeding population.

If the longer nursing of male than female calves is common, then during periods of poor range productivity one might expect male calves to be in better condition than female calves, and animals older than calves to register liveweight losses or smaller percentage liveweight gains than nursing calves. If the longer nursing period is not enough to offset the larger maintenance requirements expected for males due to their potential for larger growth, then poor periods of range productivity should result in either comparable, or poorer conditions for male than female calves.

In animals older than unweaned calves, the relative condition of the animal is dependent upon the cumulative effects of their maintenance, activity, and production energy requirements, plus the energy requirements incurred from living in an open environment. One may expect that these requirements are relatively small for non-lactating, non-gestating females,

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and higher for all other age and sex classes. The general relationships in the other classes of animals are influenced by the fact that as animals get older, their metabolic rates gradually decrease, and that male maintenance requirements are higher than those of a non-lactating, non-gestating female of the same age, due to both size differences and the larger component of metabolically active tissue in the male.

Summarizing these expectations according to age and sex classes, and whether energy intake is above or below maintenance, suggests the following. From these studies, during periods of climatic conditions that favor the production of high quality forage, one may expect (1) mature animals to meet their energy requirements for maintenance and for non-maintenance activities, and to store excess energy in the form of fat deposits; (2) growing, immature individuals to approach the genetic limits of their potential growth (this has been suggested for prenatal growth (Hafez 1969b:36) and should be true here as well); and (3) fertility rates to be high and offspring large.

During periods of poor climatic conditions and poor forage quality, one may expect liveweight losses for those animals whose maintenance requirements are not met. The following should be evident: (1) mature, non-lactating, non-gestating females should be in the best condition relative to other age and sex classes, because they have the highest proportion of metabolically less active tissue; (2) immature animals, still nursing, should show little evidence of deprivation, unless the duration of the mother's malnourishment is long enough to deplete her fat reserves; (3) weaned immature animals whose metabolic rates are relatively very high, and who have little stored fat, should show slower growth rates, though they probably would not show major liveweight declines, due to their smaller

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total maintenance costs (protein turnover, which accounts for 10-20 percent of maintenance energy expenditures, decreases as an adjustment to lower energy intake when the nutritional plane is lowered (Ferrell 1988:259)); (4) adult, but not fully mature, males should show slower growth rates, and if deprivation is of long duration, they may show liveweight declines; (5) young females may show proportionately less liveweight loss than young males due to the lower potential for growth and earlier pattern of fat accumulation; and (6) lactating or gestating females should show liveweight declines, because they show seasonal declines associated with these activities during periods of optimum conditions; therefore, increased stress during periods of poor climatic conditions should exacerbate these conditions and show a prolonged period of suboptimum condition.

Bison Diet

What bison eat is important because the quantity and quality of that food determines whether nutrient and energy requirements can be satisfied. Although bison tend to be less selective than other ungulates in similar environments (Reynolds et al. 1982:986), as suggested earlier, researchers (Schwartz and Ellis 1981) have identified bison preferences for forage classes. Larson (c.f., Peden et al. 1974) suggested that these animals are primarily grass eaters. The data from several studies of bison diet (Peden et al. 1974, Coppock et al. 1983b, Meagher 1973, Norland 1985) apparently confirm this specialization, although non-grasses are also included. Reynolds et al. (1982:985) cite Meagher and Reynolds in noting that diet is dominated by sedges (*Carex* spp.) at Yellowstone National Park and in northern Canada. Diet, they suggest, is influenced by regional differences in availability. It should also be noted that, bison diet is not regionally

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homogeneous, nor is the quality of the consumed plant material equally nutritious.

Variability in forage quality has been identified for particular species of grasses and contrasted between varieties of warm and cool season species (Peden et al. 1974, Coppock et al. 1983a, 1983b). This is important because, as large animals, bison must consume large amounts of forage in order to satisfy their relatively high energy requirements. Their greater digestive capabilities over many other ungulate species allows them to be less selective under conditions of poor forage quality (Schwartz and Ellis 1981). This does not require nonselective consumption when conditions result in the presence of forage of mixed quality (Schwartz and Ellis 1981, Reynolds et al. 1982:986, Krueger 1986:763).

Meagher (1973), Peden et al. (1974), Reynolds et al. (1982), Coppock et al. (1983b), Hanson (1984), and Krueger (1986) all suggest that bison diets fluctuate, to some extent, depending upon habitat use and forage availability. As Coppock et al. (1983b) illustrated, and as was previously suggested in Chapter 2 by the lack of correlation between regional bison size and relative vegetation biomass, quantity is not always the controlling factor in forage selection. The species that are most abundant, and fall within the classes of preferred forage--grasses and sedges--are most heavily grazed, until periods when less abundant species reach levels of high nutritional quality, and are included in the diet in greater proportions. These less abundant species are heavily used until, with the progression of the growing season, their quality (as measured by nitrogen content and digestibility) drops, and they regain their status as less important components in the diet (Hanson 1984; Schwartz and Ellis 1981).

Given these characteristics, it is evident that seasonal changes in

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species availability and relative quality may lead to changes in bison diet. The appearance of new growth in grasses should be met with greater selectivity for these more nutritious plants. A more generalized grazing pattern should return following the drop in crude protein and digestibility levels associated with continued growth of the plants. It further suggests that during periods of poor forage productivity, selectivity should be less pronounced, and competition between ungulates for the high quality forage more pronounced (Schwartz and Ellis 1981). The fact that some cool season plant species often have higher shoot nitrogen concentrations than many warm season species (Coppock et al. 1983a) suggests that where the ratio of cool to warm season species is higher, animals may be less severely affected by drought conditions. This, of course, largely depends upon the seasonal distribution of precipitation shortages and their effects upon warm and cool season species.

To understand changes in mean individual bison liveweight as influenced by bison diet at Wind Cave National Park and expected changes at Theodore Roosevelt National Park, it is important to know about the seasonal distribution of precipitation, the proportion of warm to cool season species, and the abundance of these species in the diet. Before considering bison diet in different regional locations, however, it may be helpful to review some information concerning warm and cool season species.

Description of Cool and Warm Season Vegetation Classification

Warm and cool season classification refers to the season of primary productivity in plants (Hyder et al. 1975). Cool season species are generally low photosynthetic capacity plants and warm season species are high photosynthetic capacity plants (Sims et al. 1978:257). Black

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(1971:107) correlated photosynthetic pathways with water requirements, noting that plants with high photosynthetic capacity (warm season, C-4 plants) generally have low water requirements, and plants with low photosynthetic capacity (cool season, C-3 plants) have high water requirements. Black further notes that warm season plants are more efficient in water use, as measured by the amount of production for a given amount of water, and that they may be expected to grow more than cool season plants during periods of moisture stress.

Cool season species begin growth early in the growing season and show their primary productivity when air temperatures are relatively cool; warm season species growth is most vigorous during warmer parts of the growing season (Sims et al. 1978:257; Hanson 1984:104-105). Hyder et al. (1975:78) concur, noting vigorous growth in the summer and early fall for warm season species, and in spring and fall for cool season species. Temperature differences between locations appear to control the proportion of warm and cool season species in the mixed-grass prairie (Sims et al. 1978:257). On northern sites (to which category Sims et al. assign both the Dickinson and Cottonwood grassland study sites), with mean annual temperature less than 10°C (50°F), cool season species dominate; on southern sites, with mean annual temperature greater than 10°C, warm season species dominate (Sims et al. 1978:271).

Regional Variability in Bison Diet

Bison diet has been studied in several locations with differing vegetation composition. Publications are available by Peden et al. (1974) and Schwartz and Ellis (1981) for the shortgrass community of eastern Colorado, by Norland (1985) for the mixed grass community of North Dakota,

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by Coppock et al. (1983b) for the mixed grass prairie of South Dakota, and by Meagher (1973) for the mountain grasslands of Yellowstone National Park in northwestern Wyoming. These studies all included identification of diet by analysis of ingested food, or based upon extended periods of observation. Peden et al. (1974) and Schwartz and Ellis (1981) used fistulated bison to study different aspects of bison feeding ecology on a shortgrass range site in northeastern Colorado. Meagher (1973) collected rumen samples from bison shot at different seasons in Yellowstone National Park. Norland (1985) based his assessment of bison diet at Theodore Roosevelt National Park on plant materials recovered from fecal remains collected during both the growing and non-growing season. At Wind Cave National Park, Coppock et al. (1983a, 1983b) based their assessment of bison diet upon repeated observations over a period of six months.

Coppock et al. (1983a), Peden et al. (1974), and Schwartz and Ellis (1981) provide information concerning the quantities of plant species consumed and relate this to habitat availability. The results of the studies indicate that bison diets generally are composed of (1) 85 percent grasses and sedges, primarily warm season species on the shortgrass prairie (Peden et al. 1974:493); (2) over 80 percent grasses and grass-like plants, of mixed warm and cool season varieties, on the mixed-grass prairie of Theodore Roosevelt National Park (Norland 1985:231); (3) primarily cool-season grasses except during summer when bison tend to graze primarily on warm season species on the mixed-grass prairie of Wind Cave National Park (Hanson 1984:102; Coppock et al. 1983a); and (4) over 90 percent grasses and grass-like plants (mostly sedges) on the mountain grasslands of Yellowstone National Park (Meagher 1973:90-94).

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A review of available information on vegetation availability and inclusion in the bison diet shows some interesting relationships. At TRNP, Norland (1985:231) found the diet was dominated by grasses. Table 3.1 includes information from Norland's (1985:231) table, listing contributions to bison diet during the growing and non-growing seasons at Theodore Roosevelt National Park, based upon the mean of twelve sampling periods. The data in Norland's table were used to determine the relative contribution of warm and cool season species to bison diet. Seasonality of species productivity was found in Sims et al. (1978:Appendix I). Sims et al. (1978:271:Table 4) also included data for the mixed-grass prairie, under a grazed treatment, at Dickinson, North Dakota, approximately 30-35 mi (48.3-56.3 km) east of TRNP. One point that should be made before evaluating these data is that Norland's species contribution table lumps perennial grasses, perennial forbs, and trees and shrubs together in separate categories. This means that the abundance of cool and warm season grasses and forbs within these categories cannot be determined, so their contribution to the bison diet is not included in the totals of the warm and cool season categories. This also means that the category "Other" does not correlate directly with the same category in the assessment of Sims et al. (1978), of the contribution of cool and warm seaon species to the above ground standing crop in this mixed-grass prairie.

The totals in Table 3.1 are similar between diet composition and availability for the grazed treatment. Warm season species are approximately eight to ten percent less abundant than cool season species in the bison diet. This is similar to their pattern of availability as determined by Sims et al. (1978), but in their study, while the magnitude of difference is the same, warm and cool season species were 37 and 48 percent of the total, respectively. I expect that, if perennial grasses and forbs

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Table 3.1. Percent Contribution of Warm and Cool Season Species to Bison Diet at Theodore Roosevelt National Park and to Mixed-Grass Prairie at Dickinson, North Dakota

Forage Type	Percent Contribution in Bison Diet[a]		Forage Availability[b]	
	Growing Season	Non-Growing Season	Grazed Areas	Ungrazed Areas
Cool Season Grasses	41.3	43.1	45.0	58.0
Warm Season Grasses	33.1	33.1	27.0	17.0
Cool Season Forbs	----	----	3.0	3.0
Warm Season Forbs	----	----	10.0	22.0
Warm Season Shrubs	----	----	<1.0	<1.0
Cool Season Succulents	----	----	0.0	<1.0
Warm Season Succulents	----	----	<1.0	<1.0
Other (Norland)				
Perennial Grass	13.3	10.8	----	----
Perrenial Forbs	9.6	4.8	----	----
Trees and Shrubs	2.4	8.0	----	----
Total	25.3	23.6	----	----
Other (Sims et al.)	----	----	15.0	<1.0
Total Cool Season Plants	41.3	43.1	48.0	61.0 +
Total Warm Season Plants	33.1	33.1	37.0 +	39.0 +
Total Other	25.3	23.6	15.0	<1.0

[a] Source: Norland (1985:231)

[b] Source: Sims et al., (1978:271)

in the diet of bison were divided between warm and cool season species, then the totals would be closer to those listed for the grazed treatment. These data suggest that, at Theodore Roosevelt National Park, bison diet roughly reflects availability in terms of warm and cool season species, as suggested for bison in general by Hanson (1984).

The season of primary productivity of the dominant species and the dominance of the cool or warm season class in above-ground standing crop may differ. At Theodore Roosevelt National Park, cool season species dominate the above-ground standing crop biomass, and the two most abundant grasses are cool season species as well. This pattern is not evident farther south at the Cottonwood site where the dominant component of the vegetation community is a cool season grass, but where the live, above-ground standing crop plant biomass is dominated by warm season species. The predominance of Agropyron smithii (western wheatgrass), however, is evident in the importance of this species in the diet of bison during most of the year at Wind Cave National Park, another mixed-grass prairie site (Hanson 1984:102). Hanson notes that this species is the primary forage during most of the year, and that warm season grasses increase in importance when bison congregate in areas where these species dominate. In these areas Coppock et al. (1983a) found C-4 (warm season) graminoids (which they define as grasses and grass-like species) more abundant than C-3 (cool season) graminoids, and they also note that that during periods when this habitat type is in use, the proportion of C-4 species in the diet (primarily Bouteloua gracilis, blue grama) increases. From Table 3.2, it is evident that farther east at the Cottonwood Site (Sims et al. 1978) warm season species dominate although Agropyron smithii, a cool season species, it the most abundant species.

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Table 3.2. Percent Contribution of Warm and Cool Season Species on Grazed and Ungrazed Areas of the Mixed-Grass Prairie at Cottonwood, South Dakota (1970-1972) with Temperature and Precipitation Departures from the Annual Norm

	Percent Contribution of Forage Types[a]					
	1970		1971		1972	
Forage Type	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Cool Season Grasses	9	74	22	81	23	80
Warm Season Grasses	88	23	69	17	66	17
Cool Season Forbs	<1	1	7	1	4	1
Warm Season Forbs	<1	2	1	1	2	1
Warm Season Shrubs	<1	<1	<1	<1	0	<1
Cool Season Succulents	2	<1	1	<1	4	1
Warm Seascn Succulents	<1	<1	0	0	0	0
Other	0	<1	1	1	<1	<1
Percent Temperature Departure from Normal[b]	-1.5		-2.1		-2.8	
Percent Precipitation Departure from Normal[b]	-1.4		62.0		-2.4	

[a] Source: Sims et al. (1978:271)

[b] Source: United States Department of Commerce (1970a, 1971, 1972)

The data from Peden et al. (1974) and Schwartz and Ellis (1981) suggest that the previously discussed relationship between selection and forage quality, may be masked to some extent in these data from TRNP and WCNP. Schwartz and Ellis (1981) used the bison diet data from Peden et al. (1974) and correlated it with the availability of warm and cool season species. In their publication, they note the increase of C-3 plant use during the growing season, but suggest it is a minor component in the diet at other times, especially when compared with the warm season grasses (Table 3.3). However, if one compares the percentage that C-3 plants represent of the total diet to their availability in the environment, it appears that bison are using this higher quality forage at a greater rate than might be expected, except perhaps during the month of August. The higher percentage C-3 use in October may be attributed to preference for graminoids over other forage classes, and to periods of new growth in the fall. The high use (approximately three times their availability) of cool season grasses in June and July may indicate selection for these plants, perhaps correlated with their high forage quality relative to many warm season species. Schwartz and Ellis (1981) indicate, however, that bison do not seek out areas with high proportions of C-3 plants, as do cattle, but make use of these species when in grazing locations that support their growth.

Bison movements related to habitat selection apparently are not always directed by selection for areas of high forage quality. Coppock et al. (1983b) note that in Wind Cave National Park in the summer months, prairie dog towns provide areas of high forage quality and high live to dead matter ratios (which increases relative digestibility by reducing the relative amount of high cellulose, but low nitrogen forage). When in areas of the park in which prairie dog towns are located, these habitats become the focus

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Table 3.3. Seasonal Percent Contribution of Warm and Cool Season Species to Bison Diet on the Shortgrass Prairie of Northeastern Colorado

	Percent Contribution in Bison Diet[a]					Availability of Forage in the Shortgrass Prairie[b]			
Forage Type	March	April May	June July	August	October	April May	July	August	October
Cool Season Grasses	28.0	54.0	15.0	7.0	17.0	4.0	5.1	5.3	3.3
Warm Season Grasses	70.0	44.0	78.0	88.0	82.0	60.9	69.5	69.2	68.4
Cool Season Forbs	0.0	1.0	1.0	0.0	0.0	2.4	3.0	1.6	1.2
Warm Season Forbs	0.0	1.0	7.0	5.0	1.0	2.4	7.4	5.1	12.1
Shrubs	0.0	0.0	0.0	0.0	0.0	30.4	15.0	18.8	15.0

[a] Source: Peden et al. (c.f., Schwartz and Ellis 1981:345). The diet is reported as the percent dry matter collected in samples from bison on lightly grazed pasture.

[b] Source: Schwartz and Ellis (1981:345).

of grazing activities. These authors indicate, however, that the bison herds move in and out of this portion of the park, even during periods when the prairie dog town habitat is providing high quality forage. They conclude that "the presence or absence of dog towns did not solely control bison herd movement and habitat use in the park" (Coppock et al. 1983b:12). It appears, therefore, that bison use forage roughly in proportion to its availability, including other species or classes at certain seasons of the year when they have a high nutritive value (Hanson 1984:102), but that herd movements not related to forage selection often carry bison away from areas of high quality forage.

The changes that may affect bison diet, therefore, and cause a decrease in mean individual liveweight, include a decrease in grass productivity, and a decrease in the proportion of the component of the diet including high quality forage. There are very few studies available in which specific changes in grass productivity were measured in response to specific decreases in precipitation. Most of the available data concern increases in productivity or responses to extreme droughts such as those registered in the early 1930's. French (1979b:176) states, however, that in the mixed-grass prairie, seasonal distribution is more important than total annual precipitation for predicting live, above-ground standing crop plant biomass.

Noting changes in individual bison liveweights, and correlating these with climatic change (assuming vegetation responses to changes in the amount and distribution of precipitation) may provide a measure of the magnitude of change required to produce liveweight change at TRNP. These assessments, however, have to be tempered by consideration of the relative difference in the proportions of warm and cool season species in the environment, and the characteristics of bison diet.

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Patterns of Bison Growth

The topic of bison growth was discussed in detail in the previous chapter in terms of comparative regional differences in growth. In this section, bison growth is considered from the perspective of how it reflects changes in bison condition, as measured through liveweight changes. It includes (1) a review of the average pattern of bison growth demonstrated by the WCNP herd, as detailed in the previous chapter; (2) a presentation of the data on individual changes in bison liveweight at WCNP; (3) a discussion of the trends in growth as contrasted between the grouped means of liveweight by age class and yearly changes in mean individual weight by consecutive yearly changes in liveweight; and (4) a presentation of conclusions that may be drawn, first regarding age differences in growth response, and second, regarding yearly assessments of the presence or absense of stressful conditions as demonstrated by changes in individual liveweight.

Review of the General Pattern of Bison Growth at WCNP

In the previous chapter, the pattern of bison growth at Wind Cave National Park, as represented by liveweight records over the years 1983 to 1987, was compared with the patterns found at several other bison parks. Figure 2.4 and Table 2.9 summarize the averages for liveweights recorded by age and sex classes over a five year period. The shape of the growth curves for males and females are characteristic of bison as was seen in Figures 2.7 and 2.8. The females appear to attain full mature weight several years after they reach breeding age (two years), sometime around their fourth or fifth year. Males at WCNP showed a somewhat erratic growth curve that appears to be attributable to small sample sizes in the older age classes.

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Males appear to continue growing through their sixth year, and have been reported elsewhere (e.g., Halloran 1961) to continue growth well after this, into their tenth to twelfth year. Reynolds et al. (1982:980) report that bison producers have observed male growth to continue for as long as 9 years and cow growth for as long as seven years.

The point of interest here, however, is change in liveweight. Table 3.4 presents many of the data from Table 2.9, but includes weight and percent gain between consecutive age classes, as well. These data represent the difference in mean weight (DMW) between one age class and the succeeding age class, and does not represent mean individual weight gain. In essence, this table presents the information illustrated visually in Figure 2.4. These data show that the magnitude of change in mean liveweights between sequential age classes is minimal in females after age five. Sample sizes for bulls are small, but it appears that at least through six years of age, mean weights generally increase.

It is necessary, however, to know the magnitude of yearly change in mean liveweights in order to recognize periods of change. The objectives here are to determine (1) if mean liveweight changes between years for individual animals of given age and sex classes differ from the changes in mean weight gain (DMW) for paired age classes recorded in all years; (2) if differences between age class individual mean weights are consistent for the same age class between paired consecutive years; and (3) if these differences are significant when they do occur. In the next section, I describe the changes in individual liveweight registered at Wind Cave National Park, and address the objectives enumerated above. These analyses are not done on TRNP bison data because sample sizes were too small and yearly records of individual animal weights were not available.

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Table 3.4. Difference of Mean Weights (DMW) Between Consecutive Age Classes by Sex for *Bison bison* at Wind Cave National Park in the Fall, 1983-1987

	Females				Males			
Age Class	n	Mean Wt. (lb)	DMW (lb)	% Increase	n	Mean Wt. (lb)	DMW (lb)	% Increase
Calves	47	322.4	----	----	52	341.3	----	----
Yearlings	123	563.4	241.0	74.8	112	611.2	269.9	79.1
2 yr olds	83	784.0	220.6	39.2	67	899.2	288.0	47.1
3 yr olds	68	833.5	49.5	6.3	27	1156.9	257.7	28.7
4 yr olds	54	889.9	56.4	6.8	9	1232.2	75.3	6.5
5 yr olds	44	927.6	37.7	4.2	2	1565.0	332.8	27.0
6 yr olds	30	926.2	-1.4	-0.2	2	1610.0	110.0	7.0
7 yr olds	19	924.2	-2.0	-0.2	2	1487.5	-122.5	-7.6
8 yr olds	12	918.6	-5.6	-6.1	0	----	----	----
9 yr olds	8	970.0	51.4	5.6	2	1595.0	----	----
10 yr olds	6	914.2	-55.8	-5.8	3	1620.0	25.0	1.6
11 yr olds	7	956.6	42.4	4.6	0	----	----	----
12 yr olds	5	957.0	0.4	0.0	2	1710.0	----	----
13 yr olds	2	1058.5	101.5	10.6	0	----	----	----
14 yr olds	3	1153.3	94.8	9.0	0	----	----	----
15 yr olds	3	990.7	-162.6	-14.1	2	1707.5	----	----
16 yr olds	1	1030.0	39.3	4.0	0	----	----	----
17 yr olds	2	1092.5	62.5	6.1	0	----	----	----
18 yr olds	2	960.0	-132.5	-12.1	0	----	----	----
19 yr olds	1	950.0	-10.0	-1.0	0	----	----	----

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Changes in Individual Bison Liveweight at WCNP

The liveweight data from Wind Cave National Park (WCNP) recorded in the fall months of the years 1983 through 1987 included 541 female records and 291 male records. Eartag numbers were different for each individual bison and were used to compare liveweight records across multiple years. A total of 199 individuals had more than one year of record. Of these, 138 were female and 61 were male. A portion of these do not appear in the summaries of individual weight changes because they had only two liveweight records and these did not occur in consecutive years. The total number of individuals with weights recorded in at least two consecutive years was 193, including 135 females and 58 males. Records for each age class (e.g., calves to yearlings, etc.) were separated into groups by paired consecutive years in order to identify periods when mean liveweight changes varied from other years.

Table 3.5 lists the frequencies of animals of given age classes that registered liveweight losses for paired consecutive years. These data indicate that for males, between the calf to five year old age class, only one individual lost weight over the period 1983-1987. This is sharply different from the pattern of liveweight loss registered by females. Females show both age and year of record differences in the frequency of individuals registering liveweight losses. Animals younger than two years of age do not frequently register liveweight losses for the period of study. After age two, cows show varied frequencies of liveweight loss by age and year of record. Given that males are expected to continue substantial weight gains throughout the period for which the records are available, and that females show substantial weight gains with age, only into their third year, the pattern of loss frequency is not surprising. In growing animals,

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Table 3.5. Frequency of Individual Bison Registering Liveweight Losses at the Fall Roundup at Wind Cave National Park, 1983-1987

Age Class	Statistic	Females				Males			
		1983-1984	1984-1985	1985-1986	1986-1987	1983-1984	1984-1985	1985-1986	1986-1987
C-Y	Frequency	0	0	----	----	0	0	----	----
	Sample Size	14	16			12	25		
Y-2	Frequency	0	1	0	0	0	0	----	0
	Sample Size	16	8	8	24	10	8		2
2-3	Frequency	----	5	5	0	0	0	0	0
	Sample Size		18	9	10	2	6	2	1
3-4	Frequency	----	8	7	0	----	1	0	0
	Sample Size		16	13	10		3	2	2
4-5	Frequency	----	3	5	0	----	----	----	----
	Sample Size		9	10	11				
5-6	Frequency	----	3	3	1	----	----	----	----
	Sample Size		3	7	8				
6-7	Frequency	----	2	2	3	----	----	----	----
	Sample Size		5	3	4				
7-8	Frequency	----	----	4	0	----	----	----	----
	Sample Size			5	3				
8-9	Frequency	----	1	----	0	----	----	----	----
	Sample Size		1		4				

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Table 3.5. (continued)

Age Class	Statistic	Females				Males			
		1983-1984	1984-1985	1985-1986	1986-1987	1983-1984	1984-1985	1985-1986	1986-1987
9-10	Frequency	----	----	1	----	----	----	----	----
	Sample Size			1					
10-11	Frequency	----	1	1	0	----	----	----	----
	Sample Size		1	2	1				
11-12	Frequency	----	1	----	1	----	----	----	----
	Sample Size		2		2				
12-13	Frequency	----	----	1	----	----	----	----	----
	Sample Size			1					
13-14	Frequency	----	----	----	0	----	----	----	----
	Sample Size				1				
14-15	Frequency	----	2	----	----	----	----	----	----
	Sample Size		2						
15-16	Frequency	----	0	----	----	----	----	----	----
	Sample Size		1						
16-17	Frequency	----	----	----	----	----	----	----	----
	Sample Size								
17-18	Frequency	----	----	0	----	----	----	----	----
	Sample Size			1					

a record of weight loss indicates that the normal weight gain did not occur. Until full maturity has been reached, smaller than expected individual weight gains (rather than weight losses) are adequate to establish that forage conditions may not be sufficient to meet maintenance requirements. In fully mature animals where growth and weight has stablized, an extended period of poor forage conditions should show larger numbers of animals with losses between years. From Table 3.5, it is apparent that 1986-1987 included very few animals with losses in liveweight. The years 1984-1985 and 1985-1986, however, both show frequent liveweight losses. It is not clear from this table, however, whether these represent large or small losses in liveweight. To determine this, records of change for animals of the same age category are averaged and compared between years of record.

Table 3.6 presents the mean individual liveweight changes, the standard deviation and sample size for each age class category by paired years for females and males. The data for males in most cases suffer from small sample sizes. The data for the females include many more age classes and generally have larger sample sizes. To understand the changes in mean liveweight gains and losses, one must first have some expectation of the magnitude of difference expected. This is explored in greater detail in the next section. At this point, the changes in mean liveweight are noted and marked for further investigation.

Mean liveweight gain for the years 1985-1986 was negative for females aging from two to three years (Table 3.6). During this same year, females aging from three to four years, showed only a minor increase in their mean liveweight. The plateau in mean liveweight gain in females five years old and older, corresponds with widely varied changes in mean individual liveweight gain in Table 3.6. The pattern by year, however, seems to be

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Table 3.6. Summary of Mean Individual Weight Changes Between Paired Years by Age and Sex Classes

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
C-Y	mean (lb)	304.4	262.1	---	---	366.8	266.4	---	---
	n	14	16	---	---	12	25	---	---
	st. dev.	69.6	54.7	---	---	117.2	53.5	---	---
Y-2	mean (lb)	320.0	184.6	165.6	262.3	414.0	238.6	---	317.5
	n	16	8	8	24	10	8	---	2
	st. dev.	96.1	88.9	26.2	55.3	67.2	48.9	---	74.2
2-3	mean (lb)	---	44.3	-14.4	91.0	312.5	205.3	171.5	310.0
	n	---	18	9	10	2	6	2	1
	st. dev.	---	85.2	87.8	46.6	88.4	73.3	30.4	---
3-4	mean (lb)	---	26.8	0.5	121.0	---	-18.3	137.5	315.0
	n	---	16	13	10	---	3	2	2
	st. dev.	---	108.6	70.9	58.0	---	315.4	10.6	7.1
4-5	mean (lb)	---	30.0	65.8	71.8	---	---	---	---
	n	---	9	10	11	---	---	---	---
	st. dev.	---	59.1	186.0	71.0	---	---	---	---
5-6	mean (lb)	---	-35.7	-19.0	43.1	---	---	---	---
	n	---	3	7	8	---	---	---	---
	st. dev.	---	43.3	143.6	60.1	---	---	---	---
6-7	mean (lb)	---	10.0	-16.7	16.3	---	---	---	---
	n	---	5	3	4	---	---	---	---
	st. dev.	---	30.5	62.6	59.5	---	---	---	---

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Table 3.6. (continued)

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
7-8	mean (lb)	---	---	-44.0	81.7	---	---	---	---
	n	---	---	5	3	---	---	---	---
	st. dev.	---	---	41.9	62.9	---	---	---	---
8-9	mean (lb)	---	-23.0	---	45.0	---	---	---	---
	n	---	1	---	4	---	---	---	---
	st. dev.	---	---	---	21.2	---	---	---	---
9-10	mean (lb)	---	---	-60.0	---	---	---	---	---
	n	---	---	1	---	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---
10-11	mean (lb)	---	-20.0	10.0	120.0	---	---	---	---
	n	---	1	2	1	---	---	---	---
	st. dev.	---	---	141.4	---	---	---	---	---
11-12	mean (lb)	---	-50.0	---	12.5	---	---	---	---
	n	---	2	---	2	---	---	---	---
	st. dev.	---	120.2	---	67.2	---	---	---	---
12-13	mean (lb)	---	---	-5.0	---	---	---	---	---
	n	---	---	1	---	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---
13-14	mean (lb)	---	---	---	25.0	---	---	---	---
	n	---	---	---	1	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---

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Table 3.6. (continued)

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
14-15	mean (lb)	---	-241.5	---	---	---	---	---	---
	n	---	2	---	---	---	---	---	---
	st. dev.	---	252.4	---	---	---	---	---	---
15-16	mean (lb)	---	5.0	---	---	---	---	---	---
	n	---	1	---	---	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---
16-17	mean (lb)	---	---	---	---	---	---	---	---
	n	---	---	---	---	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---
17-18	mean (lb)	---	---	65.0	---	---	---	---	---
	n	---	---	1	---	---	---	---	---
	st. dev.	---	---	---	---	---	---	---	---

one of positive mean liveweight gain from 1983-1984, mixed mean gains from 1984-1985, negative mean gain in older females from 1985 to 1986, and positive mean gains once again in 1986-1987. Calves and yearlings showed positive mean liveweight gains in all available years of record.

Reviewing Table 3.6 for changes in male mean liveweight gains, there is one example of negative mean liveweight gain. Young bulls aging from three to four years in 1984-1985 registered a negative mean gain. This negative value, however, may be attributed to the weight loss registered by one individual. The other two animals in this small sample both registered positive liveweight gains. The striking feature of the male portion of Table 3.6 is the difference in magnitude in mean liveweight gains for animals of the same age across different years of record. This is suggestive of markedly different conditions between years and is examined in more detail later in this chapter.

Individual Versus Group Means in Liveweight Changes

The next step in investigating the pattern of mean liveweight changes is to determine how these mean individual liveweight gains compare with the differences in age class mean weights (DMW) for all records from 1983 to 1987. The DMW values indicate what the normal pattern of weight difference between two age classes should be for the years 1983 to 1987. Based upon the pattern of growth reviewed in the previous section, one would expect under normal conditions that the mean individual liveweight gains in Table 3.6 should be relatively large for the first two records (calves to yearlings, and yearlings to two year olds) for both females and males. After this, mean individual liveweight gains should decrease in magnitude in females, but continue to register positive growth until liveweight gain

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stablizes at approximately age five. The record for males does not extend to the period of liveweight stability, so one would expect that large gains in liveweight would be registered for all of the individuals.

Figures 3.1 and 3.2 illustrate the difference between female mean individual weight gains for age classes for the years 1983-1984 and 1984-1985, and for 1985-1986 and 1986-1987, and the change in means (DMW) of the age classes for all data from 1983 to 1987. Figures 3.3 and 3.4 illustrate similar data for males. When mean individual liveweight gains are larger than differences in mean liveweights (DMW) for the pertinent age classes, then animal growth between paired years may be considered above the average for the five years of the study. Conversely, lower mean individual liveweight gains than the difference in mean liveweight for the age classes compared, indicate slower growth than the norm for the period 1983 to 1987. If the mean for individual weight changes falls below zero, this indicates that liveweight losses occurred between consecutive years. These figures also demonstrate that poor conditions may be indicated by lower than expected gains without actually registering liveweight losses. Table 3.7 presents the data for males and females for years in which liveweight gains are expected (years with positive DMW values) with percent departures from these norms.

Table 3.7 and Figures 3.1a, 3.2b, 3.3a, and 3.4b show that in the years 1983-1984 and 1986-1987, males and females had higher mean individual liveweight gains than the difference of the mean liveweights (DMW) for the same age classes for almost every age category comparison. During the period 1984-1985 (Figure 3.1b, Table 3.7) the mean individual female liveweight change is usually less than the difference of the mean weights (DMW) for the same age categories for all recorded data. The individual

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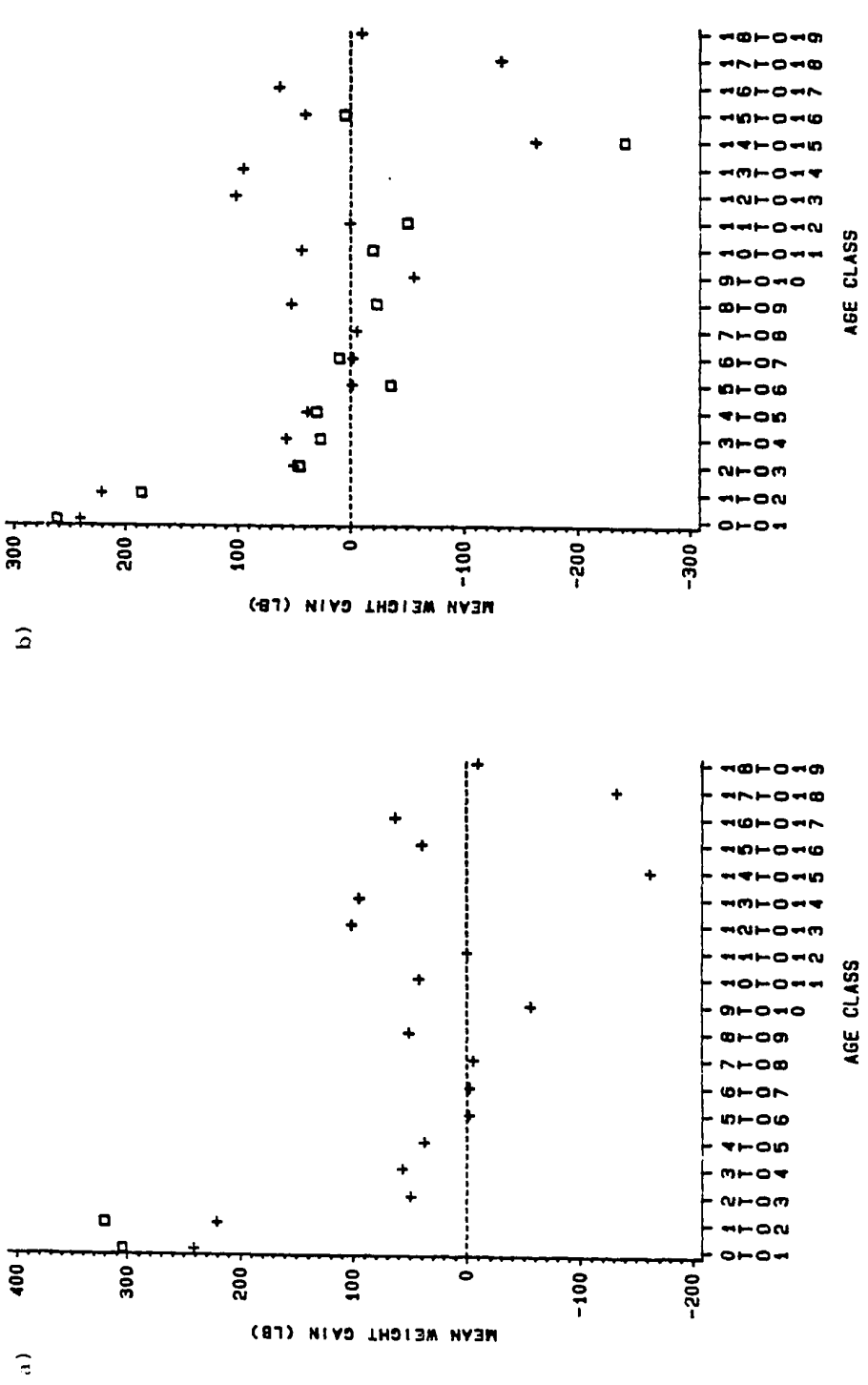

Figure 3.1. Mean Individual Weight Changes Compared with Difference of Mean Weights Between Consecutive Age Classes (DMW) for Females at WCNP, (a) 1983-1984, (b) 1984-1985.

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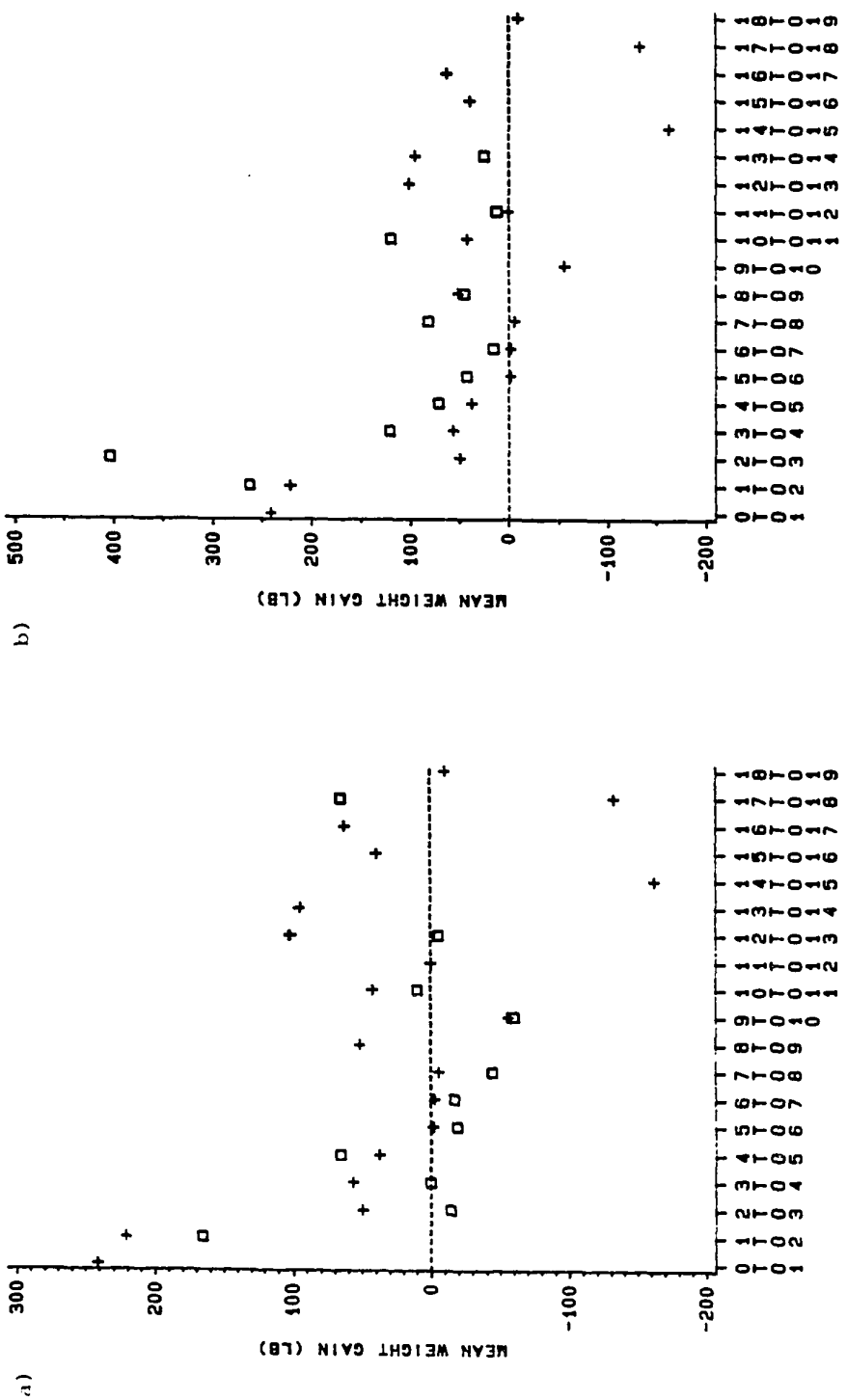

Figure 3.2. Mean Individual Weight Changes Compared with Difference of Mean Weights Between Consecutive Age Classes (DMW) for females at WCNP, (a) 1985-1986, (b) 1986-1987.

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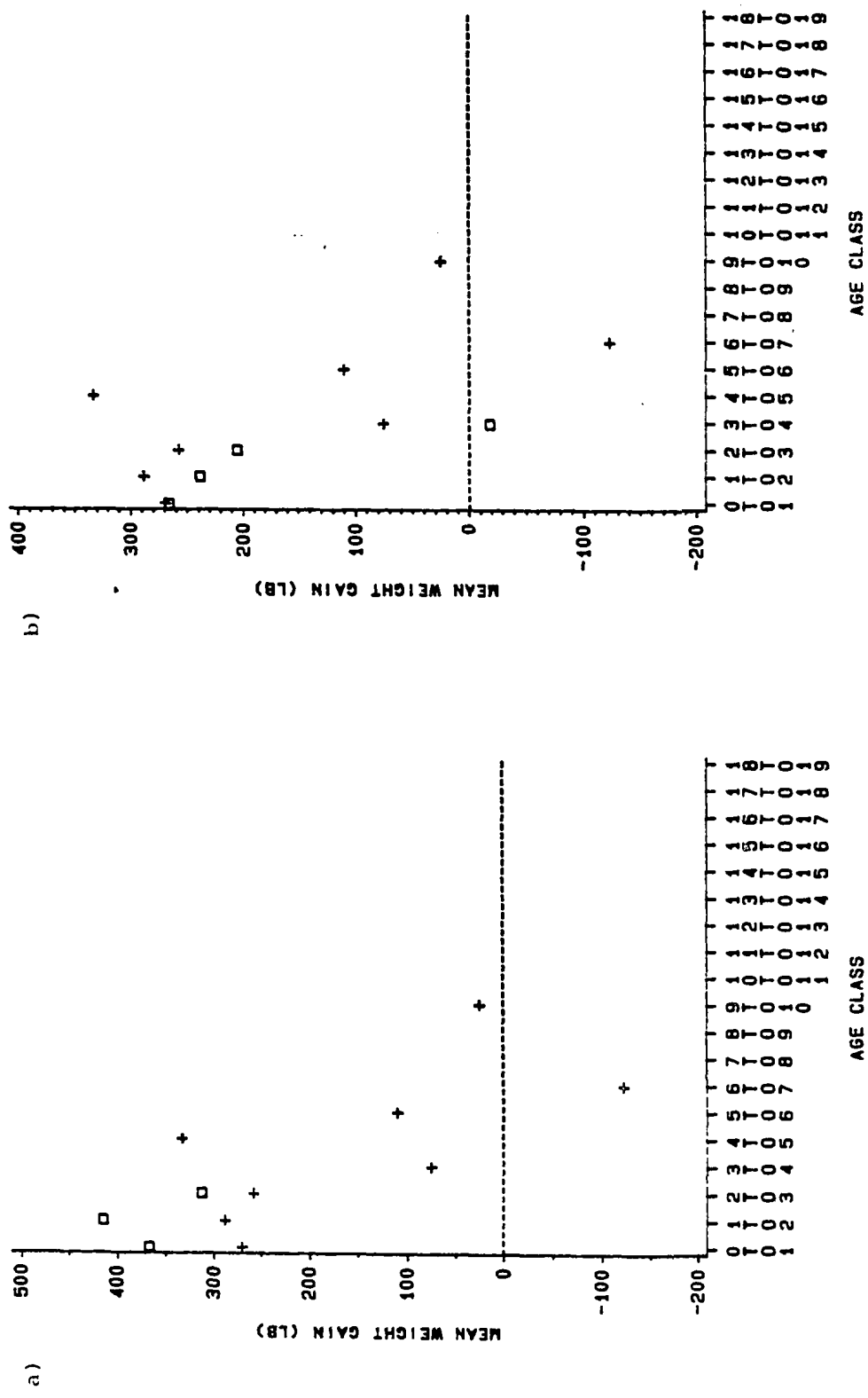

Figure 3.3. Mean Individual Weight Changes Compared with Difference of Mean Weights Between Consecutive Age Classes (DMW) for Males at WCNP, (a) 1983-1984, (b) 1984-1985.

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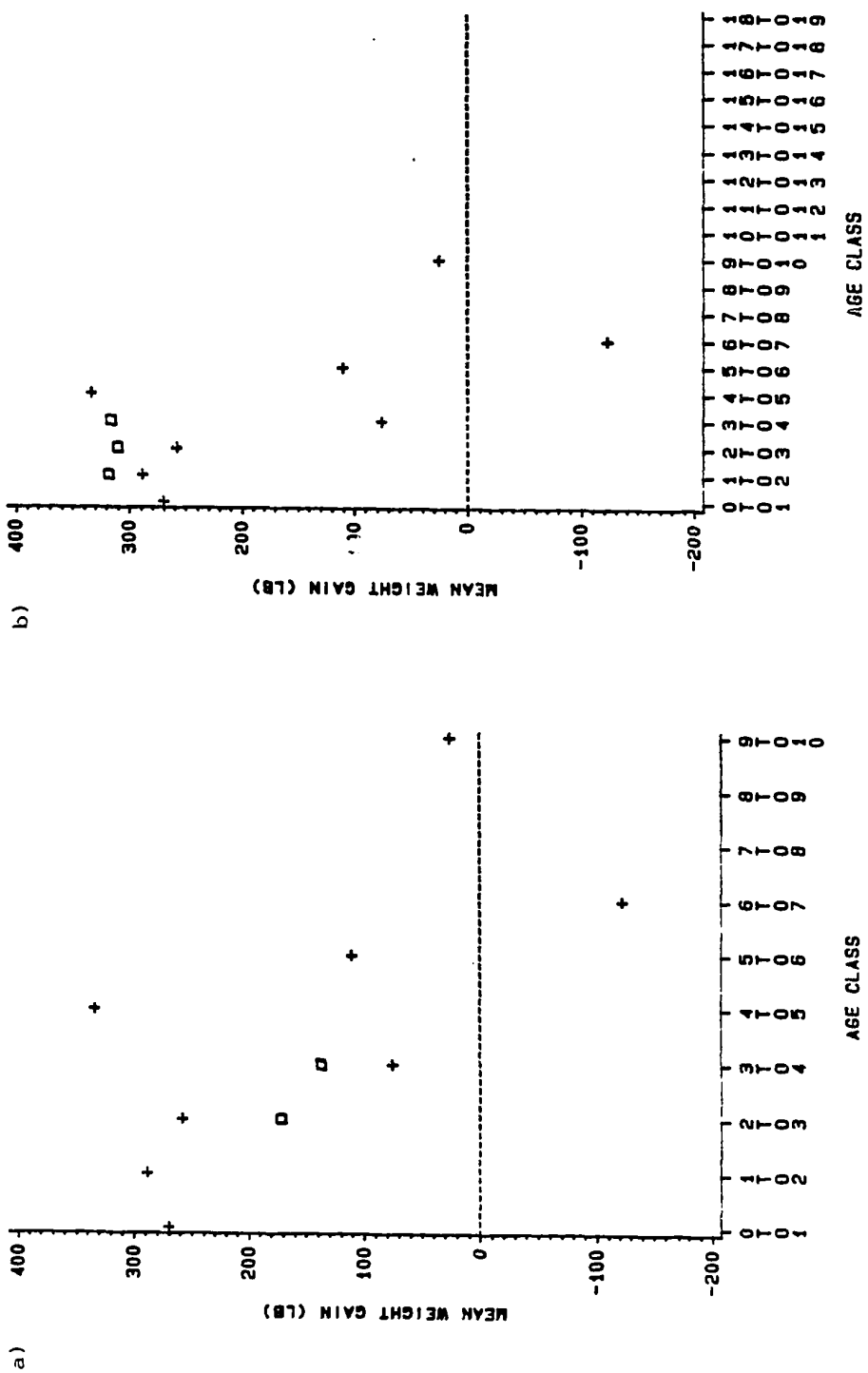

Figure 3.4. Mean Individual Weight Changes Compared with Difference of Mean Weights Between Consecutive Age Classes (DMW) for Males at WCNP, (a) 1985-1986, (b) 1986-1987.

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Table 3.7. Difference of Mean Weight (DMW) and the Percent Departure of Mean Individual Weight Change from DMW for Female and Male Bison, WCNP

Part A. Female Bison

Age Class	DMW (lb)	1983-1984 % Depart.	n	1984-1985 % Depart.	n	1985-1986 % Depart.	n	1986-1987 % Depart.	n
C-Y	241.0	26.3	(14)	8.8	(16)	----	----	----	----
Y-2	220.6	----	----	-16.3	(8)	-24.9	(8)	18.9	(24)
2-3	49.5	----	----	-10.5	(18)	-129.1	(9)	83.8	(10)
3-4	56.4	----	----	-52.5	(16)	-99.1	(13)	114.5	(10)
4-5	37.7	----	----	-20.4	(9)	74.5	(10)	90.5	(11)

Part A. Male Bison

Age Class	DMW (lb)	1983-1984 % Depart.	n	1984-1985 % Depart.	n	1985-1986 % Depart.	n	1986-1987 % Depart.	n
C-Y	269.9	35.9	(12)	-1.3	(25)	----	----	----	----
Y-2	288.0	43.8	(10)	-17.2	(8)	----	----	10.2	(2)
2-3	257.7	21.3	(2)	-20.3	(6)	-33.4	(2)	20.3	(1)
3-4	75.3	----	----	-124.3	(3)	82.6	(2)	318.3	(2)

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mean liveweight change is more in only two cases--calves to yearlings and six to seven year olds (Figure 3.1b, Table 3.7). The male mean individual liveweight gains during this same period (Figure 3.3b, Table 3.7), are all lower than the difference between the age class means (DMW), indicating below normal growth. During the next period, 1985-1986, mean liveweight changes for females are usually less than the difference of the corresponding age class means (Figure 3.2a, Table 3.7). The few male data for these years are mixed. Again, these data suggest that the years 1985 and 1986 were poor years for bison growth and liveweight increases at WCNP compared with the norms for 1983 to 1987.

Reviewing Figures 3.1 through 3.4 and Table 3.7, the question that immediately comes to mind is, are the differences between years significant? Unfortunately, the difference in mean liveweight (DMW) figures do not represent individual liveweight changes, but differences between the two mean liveweights for animals in consecutive age classes. Therefore, it is not possible to statistically compare these data. As an alternative, one might recalculate mean liveweights for each age class using only the data for individuals with multiple records, but these means would be affected by the relative sample sizes between paired years. If a large proportion of the records are associated with years that showed lower liveweight gains, and if sample sizes are small, the distributions would reflect these lower averages. This effect is registered to some extent in the means of the total sample as well, but by including data for individuals without multiple records, the sample size across all years is increased, and hopefully, lessens the impact of uneven distributions in yearly records. Measured over a much longer period of time (longer than the five years available), the variability in yearly differences in samples would be lessened in its effect

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on the mean. It is doubtful that DMW values would be negative (except in very old age classes) if sample sizes were larger.

Significance of Differences in Mean Individual Liveweight Gains

The mean individual liveweight gains data (Table 3.6) may now be used to study two relationships. They may be used to determine whether the magnitude of the mean liveweight changes of animals of the same age class differ significantly from year to year, thus indicating annual variability in their ability to meet their energy requirements. It should be noted that these data only represent annual deviations in liveweight changes. Seasonal changes might occur and be recooped and would not be evident in an analysis such as this one which is based upon annually collected records. The data in Table 3.6 also may be used to determine whether there are age or sex differences in how animals respond during periods of potentially low relative energy availability. To address these issues one must first determine whether the magnitude of differences noted between columns in Table 3.6 are significant.

Table 3.8 presents the results of a series of t-tests (differences are significant at $p < .01$, two-tailed test) comparing the distributions of liveweight changes between paired, consecutive years. It does not include data for females older than eight years because the sample sizes were much smaller in the older age categories. It should also be noted that no distinctions are made between pregnant and non-pregnant females in this analysis. In Table 3.9 when the difference in mean individual liveweight changes are significant, the years having the larger mean individual liveweight gains between the paired years are indicated with an inequality.

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Table 3.8. Comparison of Distributions of Mean Individual Changes in Bison Liveweights

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
C-Y	Mean (lb)	304.4	262.1	---	---	366.8	266.4	---	---
	n	14	16	---	---	12	25	---	---
	St. Dev.	69.6	54.7	---	---	117.2	53.5	---	---
	t	1.8589	---	---		2.8257	---	---	
	Prob>|t|	0.0736	---	---		0.0141	---	---	
Y-2	Mean (lb)	320.0	184.6	165.6	262.3	414.0	238.6	---	317.5
	n	16	8	8	24	10	8	---	2
	St. Dev.	96.1	88.9	26.2	55.3	67.2	48.9	---	74.2
	t	3.3303	0.5799	-6.6188		6.1744	---	---	
	Prob>|t|	0.0031[a]	0.5776	0.0001[a]		0.0001[a]	---	---	
2-3	Mean (lb)	---	44.3	-14.4	91.0	312.5	205.3	171.5	310.0
	n	---	18	9	10	2	6	2	1
	St. Dev.	---	85.2	87.8	46.6	88.4	73.3	30.4	---
	t	---	1.6722	-3.3203		1.7268	0.6090	-3.7192	
	Prob>|t|	---	0.1070	0.0040[a]		0.1349	0.5648	0.1672	

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Table 3.8. (continued)

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
3-4	Mean (lb)	---	26.8	0.5	121.0	---	-18.3	137.5	315.0
	n	---	16	13	10	---	3	2	2
	St. Dev.	---	108.6	70.9	58.0	---	315.4	10.6	7.1
	t	---	0.7506	-4.3600		---	-0.8549	-19.6919	
	Prob>|t|	---	0.4594	0.0003[a]		---	0.4825	0.0026[a]	
4-5	Mean (lb)	---	30.0	65.8	71.8	---	---	---	---
	n	---	9	10	11	---	---	---	---
	St. Dev.	---	59.1	186.0	71.0	---	---	---	---
	t	---	-0.5771	-0.0961		---	---	---	
	Prob>|t|	---	0.5755	0.9251		---	---	---	
5-6	Mean (lb)	---	-35.7	-19.0	43.1	---	---	---	---
	n	---	3	7	8	---	---	---	---
	St. Dev.	---	43.3	143.6	60.1	---	---	---	---
	t	---	-0.1914	-1.0660		---	---	---	
	Prob>|t|	---	0.8530	0.3183		---	---	---	

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Table 3.8. (continued)

Age Class	Statistic	Females				Males			
		83-84	84-85	85-86	86-87	83-84	84-85	85-86	86-87
6-7	Mean (lb)	---	10.0	-16.7	16.3	---	---	---	---
	n	---	5	3	4	---	---	---	---
	St. Dev.	---	30.5	62.6	59.5	---	---	---	---
	t	---	0.8318	-0.7092		---	---	---	
	Prob>|t|	---	0.4374	0.5099		---	---	---	
7-8	Mean (lb)	---	---	-44.0	81.7	---	---	---	---
	n	---	---	5	3	---	---	---	---
	St. Dev.	---	---	41.9	62.9	---	---	---	---
	t	---	---	-3.4488		---	---	---	
	Prob>|t|	---	---	0.0137		---	---	---	

[a] Difference is significant at $p < .01$.

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Table 3.9. Comparison of Significantly[a] Different Mean Individual Liveweight Changes Between Paired Years

Age Class	Results	Females			Males		
		83-84/84-85	84-85/85-86	85-86/86-87	83-84/84-85	84-85/85-86	85-86/86-87
C-Y	Decision	ns	---	---	ns	---	---
	Inequality	---	---	---	---	---	---
Y-2	Decision	s	ns	s	s	---	---
	Inequality	>	---	<	>	---	---
2-3	Decision	---	ns	s	ns	ns	ns
	Inequality	---	---	<	---	---	---
3-4	Decision	---	ns	s	---	ns	s
	Inequality	---	---	<	---	---	<
4-5	Decision	---	ns	ns			
	Inequality	---	---	---			
5-6	Decision	---	ns	ns			
	Inequality	---	---	---			
6-7	Decision	---	ns	ns			
	Inequality	---	---	---			
7-8	Decision	---	---	ns			
	Inequality	---	---	---			

[a] Difference is significant (s) at $p < .01$. Otherwise, difference in mean weight changes is not significant (ns). Inequality indicates which mean is larger when difference is significant.

Yearly Variability in the Magnitude of Mean Liveweight Changes

Inspection of Tables 3.8 and 3.9 shows two interesting relationships. First, the magnitude of change between consecutive years of record is not consistently significant as one ascends the table by age and sex categories. This indicates that, if small sample sizes and combined two year age groups are not responsible for the failure to find the differences significant, then age and sex may both be important in determining whether yearly changes in grassland productivity are registered through mean liveweight changes in bison. Second, when the magnitude of change in mean liveweights for males and females is large enough to indicate a significant difference between paired consecutive years, the direction of the inequality is similar for males and females for comparisons of two sets of records. This indicates that the mechanism that is operating to make the mean liveweight gains different for the two groups is producing the same effect for each age and sex class, when it is in operation. For example, when the mean liveweight changes for 1985-1986 and 1986-1987 are compared and found to be significantly different, the direction of the inequality does not change with changing age class, or between males and females. The direction of the inequality, when present, is the same for the entire column of tests, thus indicating a significant and consistent difference between paired years.

Reviewing these data, it is apparent that liveweight gains registered during the years 1984-1985 and 1985-1986 were relatively small and generally represent negative departures from normal liveweight increases (Table 3.7). These data suggest a period of below average energy balance. The period 1986-1987 showed few liveweight losses, much larger liveweight gains and positive departures from normal liveweight increases. The record for 1983-1984 included only animals in the youngest age categories, but these bison

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also showed positive departures from normal liveweight gains. Differences in the magnitude of their liveweight gains between 1983-1984 and the following years, 1984-1985, suggest the mean energy balance for the period 1983-1984 was well above that of 1984-1985. It should be noted, however, that this difference in magnitude was not significant until after the calf to yearling age class.

Although the liveweight data are presented in paired year records indicating gains or losses in liveweight for individuals from one year to the next, the consistent pattern of inequalities for these records can be interpreted to indicate in which year the lower gains were registered. It is apparent from these data that 1984 and 1987 both showed positive mean liveweight gains, while 1985 and 1986 both showed either liveweight losses or gains lower than normal.

Age, Sex and Significance of Mean Individual Liveweight Differences

Examination of Tables 3.7 through 3.9 shows that there may be age and sex differences in whether comparisons of mean liveweight gains registered significant differences between paired consecutive years of record. These differences are especially noticeable between age classes, but are more questionable between the sexes. I do not examine this issue further in regards to sex differences, because it appears that except for the youngest age classes prior to 1986, there are not enough male records to insure reliable results.

Age Class and the Significance of Mean Liveweight Gain Differences. Considering the record by age classes, several differences in response to varying conditions appear to be evident. First, the mean individual liveweight changes are significantly different only for animals older than

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the calf to yearling age class. This suggests that young animals, up to yearling status, are privileged consumers, buffered from poor conditions to some degree by their dependence upon their mothers.

The individual and mean liveweight gains for animals in the yearling to two year old age class is nearly always positive, but may vary significantly in magnitude (Tables 3.7 and 3.8). The positive direction of change indicates some degree of continuation of the privileged status of the young. It appears, however, that despite continued growth, registered as positive liveweight gains in this age category, the animals are not as privileged as the younger bison. That the rate of growth may be significantly slowed from one year to the next, is indicated by the negative departures from normal liveweight gains noted in Table 3.7 and the assessment that the mean individual changes between paired years are sometimes significantly different (Table 3.8).

Females between the ages of two and five are more likely to register significant yearly differences in mean liveweight gains than older animals. Significant differences were found between the 1985-1986 and 1986-1987 mean liveweight gains for females in these age categories, but not for older females during these same years. This may be attributed to the fact that at approximately five years of age, females reach mature weight, as indicated by the plateau in the growth curve (Figure 2.4). Prior to this, there is still a priority for energy use toward growth. After this period, excess energy is stored as fat, and in this case, was apparently enough to carry most of the females from 1985 through 1986, in better condition than the younger females.

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Bison Growth and Climatic Stress

Decreases in the rate of growth, or in actual liveweight, result from failure to maintain necessary levels of food intake relative to maintenance requirements. This might occur for several reasons. In some cases, it might result from increased maintenance requirements due to changes in external conditions (e.g., heat or cold stress); in other cases decreased food quantity and/or quality might be responsible. A combination of these and other conditions might also act to reduce animal condition as registered through liveweight gains.

The next step in this study is to assess whether or not the period of depressed mean liveweight gain found for the years 1984-1985 and 1985-1986 can be correlated with deteriorations in the climate, and/or concomitant deterioration in grassland productivity; and whether higher mean liveweight gains for 1983-1984 and 1986-1987 can be correlated with periods of improved climate conditions.

Geist (1987) suggests that there is a relationship between body size and duration of the annual productivity pulse. By this, Geist means that body size relates to the amount of time growing individuals have access to food of the highest quality. The relationship between growth and food quality may be considered on a short-term basis as well. During years of low food quality, growth should be less than during periods of high food quality. In an earlier section, nutrition, metabolism, and diet were discussed. In this section, before examining the record at WCNP, I provide a brief discussion of vegetation differences in mixed-grass prairies and the responses of that vegetation to changes in climate. After this, I examine the climatic record for the area around Wind Cave National Park.

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Latitudinal Variability in Grassland Composition

As noted above, Wind Cave National Park, from which data on individual changes in bison liveweight are available, is located within the mixed-grass prairie region. The closest study site that was part of the grassland biome study (Sims et al. 1978) was at Cottonwood, South Dakota (approximately 80 mi (128.7 km) east-northeast of the park). Sims et al. (1978:256) state that there is a shift in the dominant species between the northern and southern grasslands. At Dickinson, North Dakota, approximately 30-35 mi (48.3-56.3 km) east of TRNP, Stipa comata (needle and thread grass) and Agropyron smithii (western wheatgrass) are the most important species, with Bouteloua gracilis (blue grama) and Carex eleocharis (needleleaf sedge) of secondary importance. Farther south, at Cottonwood, South Dakota, Agropyron smithii is most abundant and Buchloe dactyloides (buffalo grass) replaces Carex eleocharis in the group of secondary species. Carex eleocharis is a cool season species, and Buchloe dactyloides is a warm season species. This suggests that the Cottonwood site would include more warm season species compared to the Dickinson site, and as Table 3.10 (from Sims et al. 1978:Table 4) illustrates, this appears to be true. Sims et al. (1978) note, however, that both the Cottonwood and Dickinson sites have a mixture of cool and warm season grasses. At Cottonwood, the proportion of warm and cool season grasses can be seen to fluctuate substantially between years. The annual temperature and precipitation means are listed for each year of record, including their departures from the 1951-1980 norms (Table 3.10). Changes in mean annual temperature and precipitation clearly affect the distribution of warm and cool season species. At WCNP, Coppock et al. (1983a) indicate that for locations beyond prairie dog towns, the percent contribution of warm and cool season grasses is somewhat different than at

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Table 3.10. Percent Contribution of Warm and Cool Season Species on Grazed Areas in the Mixed-Grass Prairies of Dickinson, North Dakota and Cottonwood, South Dakota Compared with Annual Departures in Temperature and Precipitation

Part A. Percent Contribution of Warm and Cool Season Species[a]

	Dickinson	Cottonwood		
Forage Type	1970	1970	1971	1972
Cool Season	48	11 +	30	31
Warm Season	37 +	88 +	70 +	68
Other	15	0	1	<1

Part B. Annual Records and Departures in Temperature and Precipitation

	Dickinson[b]	Cottonwood[c]		
Climate Record	1970	1970	1971	1972
Mean Annual Temperature (°F)	39.2	46.3	46.0	45.7
Percent Departure from Thirty Year Mean	-3.7	-1.5	-2.1	-2.8
Mean Annual Precipitation (in)	20.16	15.83	26.36	15.68
Percent Departure from Thirty Year Mean	23.3	-1.4	62.0	-2.4

[a] Source: Sims et al. (1978:271)

[b] Source: United States Department of Commerce (1970a)

[c] Source: United States Department of Commerce (1970b,1971,1972)

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Cottonwood. At WCNP, C-3 graminoids (cool season grasses and grass-like species) appear to represent approximately 35 percent of the total above ground live plant biomass, and C-4 graminoids (warm season species), a little over 50 percent (Coppock et al. 1983a:Figure 1b).

The Cottonwood site lies at an elevation of 744 m (2441 ft), whereas Hot Springs, the headquarters of Wind Cave National Park, is at 1077 m (3535 ft) in elevation. Coppock et al. (1983a) report elevations within Wind Cave National Park ranging from 1111 to 1528 m (3645 to 5013 ft). This difference in elevation may be important to the composition of the vegetation communities. An increase in elevation is generally correlated with an increase in precipitation and a decrease in mean temperature. Hot Springs, however, lies on the eastern slope of the Black Hills, and from the data presented in Table 3.11 (from United States Department of Commerce 1983b) appears to be in a rain shadow. Annual precipitation here is 383 mm (15.08 in) and mean annual temperature is 8.6°C (47.6°F). This is both warmer and drier than the area around Cottonwood, South Dakota, and warmer and drier still than the records for the Dickinson, North Dakota Experimental Station. Within Wind Cave National Park proper, the mean annual precipitation is 450 mm (17.7 in), the mean monthly temperature in July is 21°C (69.8°F), and the mean monthly temperature in January is -5°C (23°F). From these data, it appears that the Cottonwood vegetation data are still the best to use in application to Wind Cave National Park. Temperatures here are warm enough that grazed areas probably include more warm than cool season species (Sims et al. 1978:271). Coppock et al. (1983a:3:Figure 1b) show a larger percentage of warm season than cool season species in the total above-ground live plant biomass for uncolonized areas

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Table 3.II. *Thirty Year Temperature and Precipitation Averages for Two Grassland Study Sites and Two Bison Refuge Areas in North and South Dakota*

Month of Record	Cottonwood, S.D.[a]		Dickinson, N.D.[b]		Hot Springs, S.D.[a]		Medora, N.D.[b]	
	Mean Temp. (°F)	Mean Precip. (in)	Mean Temp. (°F)	Mean Precip. (in)	Mean Temp. (°F)	Mean Precip. (in)	Mean Temp. (°F)	Mean Precip. (in)
January	19.4	.45	9.3	.34	23.1	.34	12.0	.43
February	24.5	.45	16.2	.40	28.5	.44	19.8	.42
March	30.9	.79	25.4	.57	34.3	.72	28.8	.57
April	46.4	1.79	40.5	1.73	45.5	1.53	42.9	1.41
May	56.9	2.97	53.0	2.53	56.0	2.58	55.0	2.40
June	66.1	3.62	62.2	3.69	65.8	2.90	64.2	3.53
July	74.3	1.71	68.6	2.08	72.8	2.54	70.6	1.96
August	73.5	1.38	67.4	1.86	71.1	1.26	69.2	1.45
September	61.9	1.24	55.9	1.51	61.0	1.26	57.7	1.42
October	50.3	.91	45.0	.85	49.9	.81	46.2	.75
November	34.7	.40	28.3	.45	35.5	.36	30.1	.50
December	24.1	.35	17.1	.34	27.7	.34	19.1	.38
Annual Mean	47.0	16.06	40.7	16.35	47.6	15.08	43.0	15.22

[a] Source: United States Department of Commerce (1983b)

[b] Source: United States Department of Commerce (1983a)

outside prairie dog towns at WCNP. Approximately 35 percent are cool season species and a little over 50 percent are warm season species.

Climatic Record and Bison Growth at Wind Cave National Park

Climatic change, as registered through temperature and precipitation, may be evaluated at several levels. Annual, and seasonal (based on monthly records) changes in mean temperature and precipitation are considered here.

Mean Annual Temperature and Precipitation at Hot Springs, South Dakota

Table 3.12 lists the mean annual departures and percent departures of temperature and precipitation from the norm (determined for 1951-1980) for the years 1983-1987, at Hot Springs, South Dakota (United States Department of Commerce 1983b, 1984b, 1985b, 1986, 1987). From this table it is evident that 1983 was close to normal in temperature and rainfall, with a slight increase in temperature and a slight decrease in rainfall. The year 1984 was a little warmer and wetter than normal; 1985 was cooler and 23.5 percent drier than normal; 1986 oscillated back to warmer and much wetter conditions than normal; and 1987 was even warmer, but about normal in precipitation.

The decrease in mean individual liveweight gains (Tables 3.6 and 3.7) for yearling to two year old bison from 1983-1984 to 1984-1985 appears to correlate with a change from warmer, wetter conditions in 1984 to cooler, drier conditions in 1985. From the study of mean individual liveweight gains, the change from 1984-1985 to 1985-1986 was not found to be significantly different (Table 3.8), and the change from 1985-1986 to 1986-1987 was found to represent an improvement in bison mean liveweight gains. The mean annual departure from the precipitation and temperature norms for 1986 (Table 3.12), suggest that the period 1985-1986 and after, should all

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Table 3.12. Temperature and Precipitation Departures and Percent Departures from the Thirty Year Means for Hot Springs, South Dakota

Year	Annual Record[a]		Departure		Percent Departure[b]	
	Temperature (°F)	Precipitation (in)	Temperature (°F)	Precipitation (in)	Temperature (°F)	Precipitation (in)
1983	48.0	14.28	0.4	-0.80	0.8	-0.5
1984	48.3	16.14	0.7	1.06	1.7	7.0
1985	46.6	11.53	-1.0	-3.55	-2.1	-23.5
1986	49.3	17.29	1.7	2.21	3.6	14.7
1987	50.5	13.26	2.9	-1.78	6.1	11.8

[a] Source: United States Department of Commerce (1983b, 1984b, 1985b, 1986, 1987)

[b] Percent departure from 30 year means (1951-1980) for temperature (47.6°F) and precipitation (15.08 in).

show improvements in mean individual liveweight gains. This lack of congruence in the data suggests that either the annual records of departure are not detailed enough, the food source for the bison had not responded to the improved conditions of 1986, and/or some external factor was operating to prohibit forage intake at a level that would meet bison maintenance requirements.

Mean Seasonal Precipitation at Hot Springs, South Dakota

In a regression analysis of mean annual precipitation and vegetation biomass in different types of grassland (shortgrass, mixed-grass, tallgrass, etc.), French (1979b:176) found that, in most cases there is a strong positive correlation between the two variables. The exceptions to this positive relationship, however, were the mountain grasslands and the mixed-grass prairies. In the case of the latter, French suggested that the seasonal distribution of rainfall is a very important determinate of vegetation growth. Thus, if precipitation falls at normal or above-normal levels on an annual basis, poor vegetation growth might still occur if the distribution of the rainfall does not correlate with the growth patterns of the climatic climax.

In a study of shortgrass prairie species which included an assessment of their ecological responses to different precipitation distributions, Hyder et al. (1975:77-79) found differences in warm and cool season species responses to above-average precipitation in different quarters of the year. In their analysis, the spring quarter includes March, April, and May; summer includes June, July, and August; fall includes September, October, and November; and winter includes December, January, and February. These authors found that warm season species responded positively to above-average

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precipitation in summer and fall. Cool season species also responded positively to above-average precipitation, but during the spring and fall. Their response to above-average rainfall in the summer, however, was negative. Rauzi et al. (1969) studied the protein content and growth patterns of two species, Agropyron smithii (western wheatgrass), a cool season grass, and Bouteloua gracilis (blue grama), a warm season grass, both important components of the mixed-grass prairie at Cottonwood, South Dakota. Their results confirm the determination of Hyder et al. (1975) concerning the response of warm season species to fall precipitation, but dispute the positive fall response of Agropyron smithii to above-normal precipitation (Rauzi et al. 1969:49). At the Cottonwood site, Sims et al. (1978) indicated that Agropyron smithii was the predominant species, but from their analysis of the total composition of the live above-ground standing crop, it was found that warm season species provided a larger contribution than cool season species under grazed conditions (Table 3.10).

Changes in climate should have some effects upon the mixed-grass prairie at Hot Springs, South Dakota, depending upon departures in both the temperature and rainfall patterns from the norm. There are no records of vegetation patterns during this period (1983-1987) at Hot Springs. However, in Table 3.10 vegetation changes may be correlated with changes in mean annual temperature and precipitation at Cottonwood, South Dakota at an earlier date. From 1970 to 1971, cool season species increased from 11 to 30 percent of the total under grazed conditions, and the following year, 1972, it increased by one more percentage point (Sims et al. 1978:271). During this same period, temperature means were below normal, increasing each year in departure (United States Department of Commerce 1970b, 1971, 1972). Precipitation, however, fluctuated between negative and positive

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departures. In 1971, rainfall was 62 percent above normal, whereas, in the previous and following year, precipitation was slightly below normal. It appears that the increase in precipitation was probably responsible for the major increase in cool season species. This is clarified even more by comparison of the vegetation response with the seasonal departure data in Table 3.13.

Looking first at seasonal temperature departures for Cottonwood (Table 3.13), one can see that the decrease in mean annual temperature in 1971 was largely due to low temperatures in the winter quarter (December through February). Temperatures during the growing season (spring, summer, and part of fall) were almost all above normal. In 1972 temperatures were above normal in the spring, and cooler in the summer and fall. This appeared to have little if any effect on the vegetation contribution of warm and cool season species (Table 3.10). Precipitation over these three years was quite varied in its seasonal distribution (Table 3.13). In 1970 precipitation was below normal until the fall quarter when it rained 42.7 percent more than normal. After this, rainfall continued to be well above normal through the spring quarter of 1971, dropping back to normal for the summer quarter, before a very wet fall quarter. This pattern of above-normal precipitation in the spring and fall with normal precipitation in the summer favors the growth of cool season species (Hyder et al. 1975:78).

In 1972, spring quarter precipitation at Cottonwood was again above normal, but so was summer quarter (June through August) precipitation (Table 3.13). This would favor cool season plant growth in spring. However, the above-average summer precipitation might have been detrimental to cool season plant growth, instead favoring warm season species growth. At any rate, the improved conditions of 1971 appear to have carried over into 1972

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Table 3.13. Seasonal Temperature and Precipitation Departures from the Thirty Year Means for Cottonwood, South Dakota[a]

Year	Season (months)	Temperature (°F)			Precipitation (in)		
		Season Mean	Departure	Percent Departure	Season Total	Departure	Percent Departure
1970	- J F	22.3	0.3	1.4	.86	-.04	-4.4
	M A M	42.7	-2.2	-5.0	5.46	-.09	-1.6
	J J A	73.9	2.6	3.6	5.59	-1.12	-16.7
	S O N	47.5	-1.5	-3.0	3.64	1.09	42.7
1971	D J F	17.2	-5.5	-24.2	1.81	.56	44.8
	M A M	45.8	0.9	2.0	9.01	3.46	62.3
	J J A	72.2	0.9	1.3	6.74	.03	0.4
	S O N	48.3	-0.7	-1.4	8.75	6.20	243.1
1972	D J F	19.5	-3.2	-14.0	.82	-.43	-34.4
	M A M	47.3	2.4	5.3	6.41	.86	15.5
	J J A	70.3	-1.0	-1.4	7.20	.49	7.3
	S O N	47.1	-1.9	-3.9	1.37	-1.18	-46.3

[a] Means, totals and departures are from United States Department of Commerce (1970b, 1971, 1972)

with little change in the contribution of warm and cool season species (Table 3.10). It is probable, therefore, that the proportions of warm and cool season plants determined for the year 1970 is closer to the norm for this area, unless conditions prior to this time were abnormal as well.

The point of this discussion, however, was to demonstrate that changes in climate are registered in changes in vegetation productivity. In the following discussion, therefore, the absence of vegetation data may not completely limit the use of the climate data for the Hot Springs area for the period in question, and for the area around TRNP in the later discussion of the climatic patterns for that area.

Seasonal Pattern of Climatic Change at Hot Springs, South Dakota, 1983-1987

Figure 3.5 illustrates the percent departure from the mean monthly norms for temperature and precipitation (determined for the period 1951-1980) for the period January, 1983 through December, 1987 for Hot Springs, South Dakota (United States Department of Commerce 1983b, 1984b, 1985b, 1986, 1987). Table 3.14 summarizes the Hot Springs percent departure from precipitation and mean temperature by quarters, in the same manner as noted above for the years 1970-1972 at Cottonwood, South Dakota.

Seasonal Record for 1983. In 1983 (Figure 3.5, Table 3.14), above-normal precipitation fell in the months of March, October, November, and December. Below-average rainfall in April and May, however, produced a below-average total for the spring quarter. Similarly, the summer quarter had below-normal precipitation. The abundance of rain in October and November, was enough to offset a deficit in September, and produce an above-average fall quarter. The above-normal rainfall might encourage growth of cool season species other than Agropyron smithii, though above-normal

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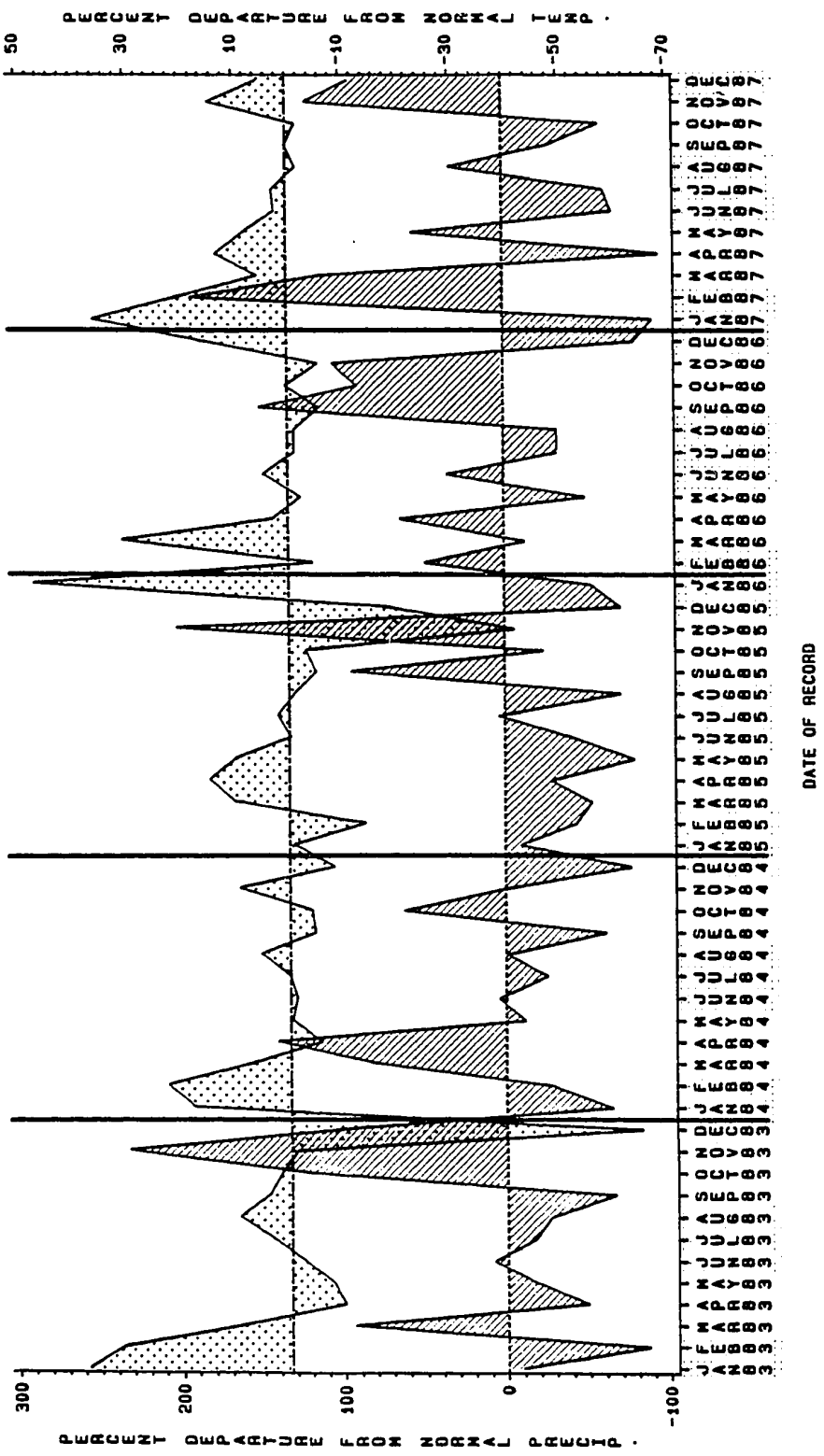

Figure 3.5. Percent Departure from Normal (1951-1980) Temperature and (°F) Precipitation (in) at Hot Springs, South Dakota, 1983-1987. Data derived from United States Department of Commerce (1983b, 1984b, 1985b, 1986, 1987).

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Table 3.14. Seasonal Temperature and Precipitation Departures from the Thirty Year Means for Hot Springs, South Dakota[a]

Year	Season (months)	Temperature (°F)			Precipitation (in)		
		Season Mean	Departure	Percent Departure	Season Total	Departure	Percent Departure
1983	D J F	32.8	6.4	24.2	.62	-.50	-44.6
	M A M	43.3	-2.0	-4.4	4.31	-.52	-10.8
	J J A	72.4	2.5	3.6	6.19	-.51	-7.6
	S O N	49.8	1.0	2.0	3.45	1.02	42.0
1984	D J F	23.9	-2.5	-9.5	1.12	0.00	0.0
	M A M	45.1	-0.2	-0.4	7.27	2.44	50.5
	J J A	70.9	1.0	1.4	6.18	-.52	-7.8
	S O N	48.2	-0.6	-1.2	2.17	-.26	-10.7
1985	D J F	24.3	-2.1	-8.0	.64	-.48	-42.9
	M A M	50.5	5.2	11.5	1.99	-2.84	-58.8
	J J A	70.1	0.2	0.3	4.71	-1.99	-29.7
	S O N	42.3	-6.5	-13.3	4.17	1.74	71.6
1986	D J F	28.0	1.6	6.1	.92	-.20	-17.9
	M A M	48.8	3.5	7.7	4.45	-.38	-7.9
	J J A	70.4	0.5	0.7	6.50	-.20	-3.0
	S O N	47.0	-1.8	-3.7	5.45	3.02	124.3
1987	D J F	32.6	6.2	23.5	1.39	.27	24.1
	M A M	49.4	4.1	9.1	5.65	.82	17.0
	J J A	70.6	0.7	1.0	3.26	-3.08	-46.0
	S O N	50.3	1.5	3.1	2.05	-.38	-15.6

[a] Records and departures are from United States Department of Commerce (1983b, 1984b, 1985b, 1986, 1987)

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rainfall in early spring (Figure 3.5) might have been enough to encourage productivity in that species. Late growth of warm season species in the fall, following potentially poor growth during the summer quarter, is probable. Temperatures during this period were above normal except for the spring quarter. Productivity of vegetation was potentially normal to below normal until the fall quarter when warm temperatures and abundant rainfall would have favored renewed growth of warm season species.

Seasonal Record for 1984. In 1984, precipitation in the winter quarter was average, coupled with warm temperatures; in the spring quarter rainfall was 50.5 percent above average, with approximately normal temperatures; in the summer quarter temperatures were slightly higher and precipitation was below average; in the fall quarter, rainfall continued at a below-normal level, and temperatures were slightly cooler. A period of above-average rain in October often encourages new plant growth. Based upon the work of Hyder et al. (1975), the rainfall distribution in 1984 should have favored cool season species and be somewhat marginal for warm season species.

Seasonal Record for 1985. Following the 1984 year of relatively better growth for warm than cool season species, the pattern was altered somewhat in 1985. In this year, rainfall was sharply below normal from the winter through the summer quarters, with one month in summer (July) having normal precipitation. This period of poor rainfall was coupled with a warmer than normal spring, and normal summer temperatures. The fall season had above-average rainfall and below-normal temperatures. Based upon Hyder et al. (1975) and Rauzi et al. (1969) one might expect poor vegetation growth for both warm and cool season species, perhaps with some improvement prior to the end of the growing season in the fall for the warm season species and most cool season species. Temperatures dropped into the upper twenties in

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late September limiting the possibility of fall season plant productivity. The magnitude of precipitation departures from normal during the spring and summer quarters following a dry fall and winter the previous year, probably cut vegetation productivity substantially.

Seasonal Record for 1986. In 1986, the winter was unseasonably warm beginning in January, with above-normal rain coming late in the quarter following below-normal precipitation. The spring quarter was alternating dry and wet, resulting in a quarter nearly eight percent below the norm. Temperatures were also above normal early in the period. The same pattern followed for summer, with most of the rain falling in the first month (June). Temperatures from mid-spring through mid-fall were approximately normal. Fall temperatures did not drop below freezing until the last day of September and did not do so significantly until mid-October. The amount of fall precipitation was 124.3 percent above normal and temperatures were cooler than normal. The year 1986 was essentially dry and warm with short periods of relief until the fall quarter when precipitation and temperatures should have prompted vegetation growth once again. This pattern favors growth of cool and possibly some warm season species in the fall. The cooler temperatures probably favor cool over warm season plant growth. The slightly lower than normal precipitation levels until the fall quarter, however, probably keep overall production somewhat lower, especially following the conditions of the previous year.

Seasonal Record in 1987. In 1987, winter and spring precipitation was above normal with concomitant higher than normal temperatures. December, January and April precipitation were below normal, but enough rain fell in February, March and May to bring the winter and spring season totals to above normal. The records for summer and fall were below normal in

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precipitation and above normal in fall temperatures. This pattern favors cool season vegetation growth over that of warm season species.

Bison Growth and the Climatic Record at WCNP

Reviewing the climate pattern for 1983 through 1987, it appears that climatic conditions were less favorable for cool than warm season species in 1983. In 1984, productivity was probably high, but especially so for cool season species. The year 1985 was probably a year of low productivity for both vegetation types, and 1986 was probably mixed until the fall quarter when cool season species growth was potentially good. The climate in 1987 would have favored cool season species. Productivity for this year may have been about normal, or possibly a little below normal.

The pattern for 1986 does not appear to be so dry or warm as to be responsible for poor mean individual liveweight gains registered during the 1985-1986 period, unless vegetation productivity was slow to recover from the effects of 1985. Ellison and Woolfolk (1937:333) remark that the effect of drought on plant growth extends into the following season, based upon their observations of plant growth in Montana in the years 1934 and 1935. These authors indicated precipitation was near normal for 1935 following the 1934 season in which summer rainfall was 62 percent below normal. This was coupled with high temperatures following an unusally warm fall, winter and spring. Despite the improved climate of 1935, plant recovery from the drought was slow.

Coupland (1958:287) notes that the immediate response of plants to drought is a reduction in the height of growth, and after prolonged drought, reduction in density and yield. He confirms Ellison and Woolfolk's assessment of delayed recovery following drought, noting that data from

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western North Dakota from 1933-1940 indicated full recovery of plant leaf height to pre-drought levels did not occur until four years following the end of the drought.

At Hot Springs in 1985, the spring quarter precipitation was 58.8 percent below normal, while the summer precipitation was only 29.7 percent below normal. The effects of these deficits should not be as extreme as those noted above for the dust bowl years, and recovery should be quicker as well. Nevertheless, the similar mean liveweight gains registered for bison for the period 1984-1985 and 1985-1986, probably reflect some delay in grassland recovery.

Direct Climatic Effects on Bison Growth

Climate also affects bison growth in a direct manner through weather conditions, in addition to the effects wrought indirectly by changes in the productivity of their food source. Three of several possible ways in which maintenance requirements might be increased, include (1) exposure to cold temperatures coupled with winds, as suggested by the work of Christopherson et al. (1979); (2) exposure to above-normal temperatures during the winter months when pelage insulation is high, thus leading to heat stress (Christopherson et al. 1979); and (3) exposure to heavy snowfall conditions which increase the maintenance costs associated with movement and gaining access to food (Meagher 1973:74).

It is possible that these factors were important in raising maintenance requirements for the WCNP bison during the winter quarters from December 1982 through February 1987. However, bison liveweights were recorded during roundup in the fall quarter each year. It is unlikely, therefore, that these influences on liveweight would not have been modified by later

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fluctuations in food availability and quality. These factors are considered again, however, when the condition of spring-collected specimens and the Theodore Roosevelt National Park herd is evaluated in light of the available climatic information.

Currently, there is little information available concerning bison susceptibility to heat stress. Christopherson et al. (1979) indicate that during the winter quarter, heat stress (indicated by raised metabolic rates) is induced in bison at temperatures of 10°C (50°F). After the winter quarter, temperatures of this magnitude are not high enough to initiate metabolic adjustments in bison (Christopherson et al. 1979). This is not to say that high temperatures, might not also have this effect. Indeed, it would be surprising if they did not show periodic responses to heat stress. The threshold value for this response in bison, however, is not known.

Evaluating the Condition of the TRNP Bison Herd

In order to understand what the values obtained from the carcass composition analyses mean, it is first necessary to know whether bison in the TRNP herd were in normal condition, or in a condition that would be considered above or below average. Were the data available as at WCNP, one could measure relative changes in animal condition by monitoring liveweight changes of individual animals across multiple years of study, correlating these changes with the climatic record. This type of analysis was done in the previous section in order to verify that changes in climate could be correlated with changes in bison liveweight.

Lacking these data at TRNP, the alternative is to infer changes in bison liveweight based upon changes in climate and assumed changes in grassland productivity, taking into consideration possible added energy

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requirements related to potential heat or cold stress. In Chapters 5 and 7, the results of the bone and carcass fat studies carried out on the four TRNP bison are presented and in one case, compared with the results of a similar study by Brink (1986) in Canada on bison from three locations near Edmonton, in the province of Alberta. The comparison of actual fat quantities in the four TRNP bison provides an assessment of whether the expected pattern of condition is evident in these individuals as well. The comparison of fat data from the TRNP specimens with that of other bison and wildlife species provides an indication of the relative condition of the TRNP herd as represented by these bison.

The remainder of this section includes (1) a review of the departure from the annual mean temperature and precipitation norms for Medora, North Dakota (which is adjacent to the south unit of TRNP) for the years 1983-1985 (based upon thirty year means for the period 1951-1980 (United States Department of Commerce 1983a, 1984a, 1985a)); (2) an analysis of the seasonal departures in the temperature and precipitation records for 1983-1985; and (3) an analysis of the potential for added maintenance costs associated with the direct effects of weather through possible heat and cold stress during the winter quarter of 1984-1985.

Record of Departure from Mean Annual Temperature and Precipitation

The mean annual temperature and precipitation for Medora, North Dakota was previously noted in Table 3.11. Mean annual temperature is 43.0°F (6.1°C) and mean annual precipitation is 15.22 in (386.6 mm) (United States Department of Commerce 1983a, 1984a, 1985a). Table 3.15 lists the annual departure and percent departure from the mean for both temperature and precipitation values for the years 1983-1985 at Medora, North Dakota. The

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Table 3.15. Temperature and Precipitation Departures and Percent Departures from the Thirty Year Means for Medora, North Dakota

Year	Departure[a]		Percent Departure	
	Temperature (°F)	Precipitation (in)	Temperature	Precipitation
1983	2.4	-2.16	5.6	-14.2
1984	2.2	-5.84	5.1	-38.4
1985	0.2	-2.17	0.5	-14.3

[a] Source: United States Department of Commerce (1983a, 1984a, 1985a)

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pattern here differs somewhat from that found previously for this same period at Hot Springs, South Dakota.

Considering the data on a yearly basis, it appears that the first three years of record, 1983-1985, all registered major precipitation deficits, with concurrent positive departures in mean temperature (Table 3.15). The year 1984 appears to be the most severe in terms of the magnitude of precipitation departure from the thirty year norm. The departure registered at Hot Springs, South Dakota in 1985 when liveweight records showed a substantial decline, was 23.5 percent. The departure in 1984 at Medora is even larger, registering 38.4 percent below normal precipitation. The fact that this is preceded and followed by additional quarters of negative departure of over 14 percent, during periods of above-average temperatures, suggests that liveweight records for TRNP bison, if taken, would probably have registered declines during the period 1983-1985.

Not anticipating delays in grassland recovery, the annual record at Medora, North Dakota suggests the years 1983 through 1985 would be poor years for grassland productivity. Increases in mean annual temperature suggest possible increases in the contribution of warm season grasses in this area which is usually dominated by cool season grasses under ungrazed conditions. The previous analysis of the WCNP bison liveweight data and the climatic record for Hot Springs, South Dakota, indicated a need for more refined analysis of climate than by yearly cycles of departure.

Seasonal Record of Temperature and Precipitation Departure at Medora, North Dakota

The importance of the seasonal variations in temperature and precipitation was previously demonstrated in reference to the Hot Springs,

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South Dakota record. Sims et al. (1978) indicated that an annual mean temperature of less than 10°C (50°F) in northern grasslands promotes the dominance of cool season over warm season plant species. French (1979b:176), however, noted that seasonal distributions of rainfall were much more important than total annual rainfall in determining the total live above ground standing crop biomass, and that seasonal changes in precipitation distribution affect whether warm or cool season species are more productive.

Figure 3.6 illustrates the monthly departures from the 1951-1980 normal values for temperature and precipitation at Medora, North Dakota (United States Department of Commerce 1983a, 1984a, 1985a). Table 3.16 lists the seasonal departure from the norm, in the same manner as previously described for the Hot Springs, South Dakota data, combining values for three month periods.

Seasonal Record for 1983

The annual record for 1983 showed above-average temperatures and below-average precipitation. The seasonal values of temperature and precipitation departures from the norm (Table 3.16) indicate that the winter quarter was much warmer and drier than normal. This would have the effect of decreasing soil moisture that would be used by the plants later in the year.

In the spring quarter, temperatures returned to normal, but precipitation remained below normal for the period. Figure 3.6 shows that March was wet, but was followed by three months of dry weather. The short period of above-normal precipitation would be positive for plant productivity only in its effect upon soil moisture, as it fell prior to the beginning of the growing season. The lack of spring quarter rainfall following a dry winter

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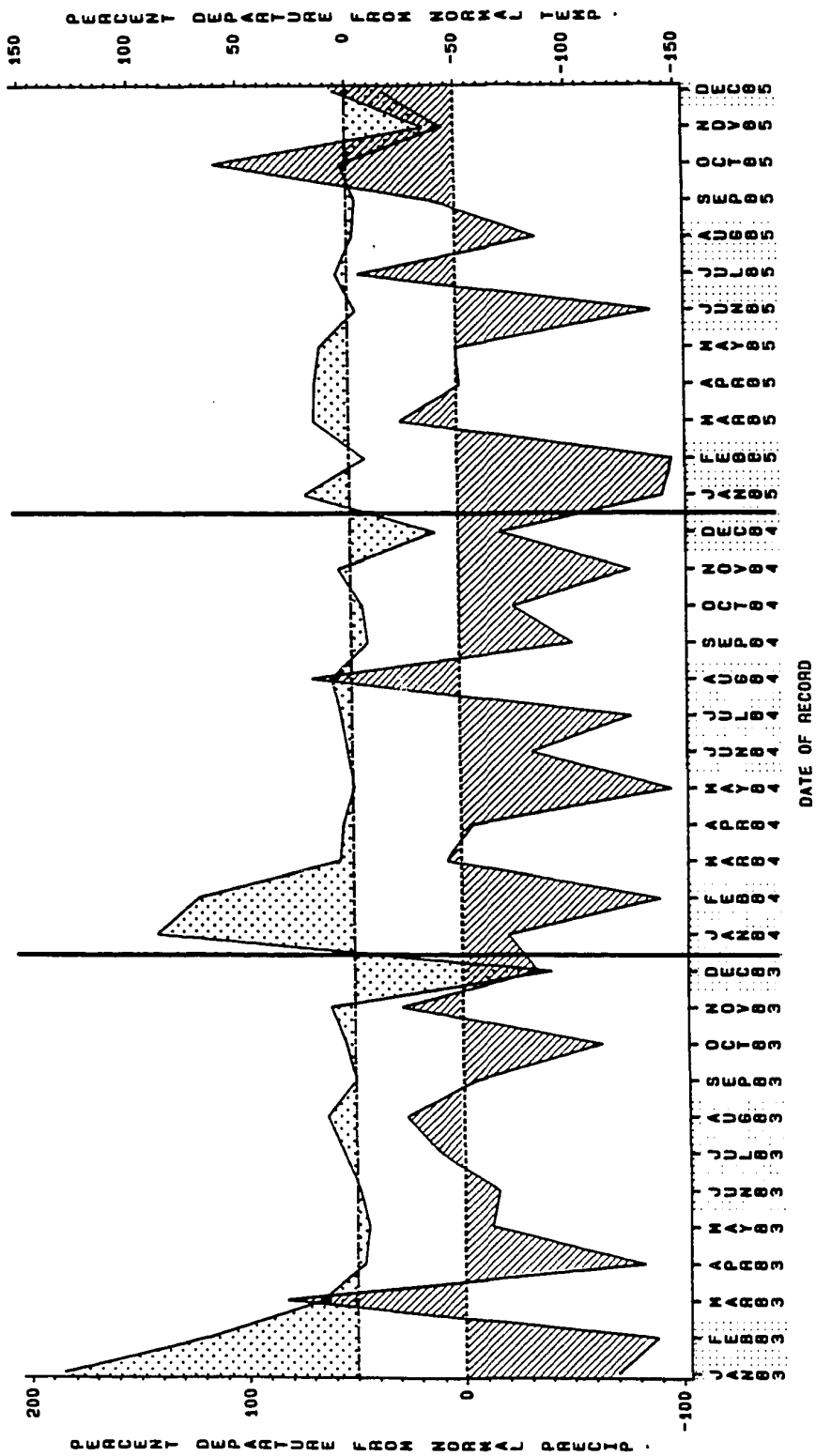

Figure 3.6. Percent Departure from Normal (1951-1980) Temperature (°F) and Precipitation (in) at Medora, North Dakota, 1983-1985. Data derived from United States Department of Commerce (1983a, 1984a, 1985a).

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Table 3.16. Seasonal Temperature and Precipitation Departures from the Thirty Year Means for Medora, North Dakota[a]

Year	Season (months)	Temperature (°F)			Precipitation (in)		
		Season Mean	Departure	Percent Departure	Season Total	Departure	Percent Departure
1983	D J F	28.3	11.3	66.3	.84	-.39	-31.7
	M A M	42.2	0.0	0.0	3.39	-.99	-22.6
	J J A	72.0	4.0	5.9	6.99	.05	0.7
	S O N	46.3	1.6	3.5	2.25	-.42	-15.7
1984	D J F	19.5	2.5	5.7	.63	-.60	-48.8
	M A M	43.4	1.2	2.8	2.05	-2.33	-53.2
	J J A	71.6	3.6	5.2	5.27	-1.67	-24.1
	S O N	43.0	-1.7	-3.8	1.37	-1.30	-48.7
1985	D J F	14.9	-2.1	-1.3	.35	-.88	-71.5
	M A M	48.3	6.1	14.5	4.52	.14	3.2
	J J A	68.0	0.0	0.0	4.18	-2.76	-39.8
	S O N	40.0	-4.7	-10.6	3.72	1.05	39.3

[a] Records and departures are from United States Department of Commerce (1983a, 1984a, 1985a).

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would adversely affect the growth and productivity of the cool season species which dominate ungrazed land in this part of the country. In grazed areas which show a higher proportion of warm season species (Sims et al. 1978), the contribution of cool season species would be potentially lower.

The summer quarter in 1983 had normal amounts of rainfall, but higher temperatures. Summer, however, includes the three months of the year with the highest amounts of precipitation, so if soil moisture deficits were not particularly high, warm season species might be relatively productive during this year.

The fall quarter showed continued above-normal temperatures, but they were not excessively so. Precipitation levels, however, were once again below normal until late in the quarter. The higher temperatures and low precipitation levels would discourage productivity in cool season species particularly, and might have had some effect upon the warm season species growth as well.

Due to the potentially poor growth of cool season species in the spring and fall, and the potentially lowered productivity of warm season species in the fall, total grassland productivity should have been lower than average during 1983. Warm season grasses and other plants probably faired relatively well during the summer months, but these were shown by Coppock et al. (1983a) to be of lower quality, as measured by shoot nitrogen content, than cool season species. This suggests potential below average productivity in bison, as measured by liveweight gains, for the 1983 season.

Seasonal Record for 1984

The seasonal record for 1984 looks particularly bleak for grassland productivity and thus bison liveweight gains. Deficits in rainfall were

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over 48 percent for every quarter except the summer quarter when precipitation was 24 percent below normal. At the same time, temperatures fluctuated between being well above normal, to slightly above normal, except for the fall quarter when temperatures fell below normal. At Wind Cave National Park, bison liveweight losses were registered in 1985 under conditions no worse than these (Table 3.14), and possibly better, given the high rainfall in the previous fall quarter there. Given the pattern of mean individual liveweight gains recorded for bison at WCNP during 1985 and 1986 (a year of below-normal precipitation followed by a year of above-normal precipitation, but with little improvement in bison liveweight gains), one would expect a similar lag in grassland productivity at TRNP during the year 1985 following the poor climatic conditions of 1984. Similarly low bison liveweights for 1984 and 1985 are expected at TRNP as well.

Seasonal Record for 1985

Unlike the year of improved conditions that followed the drought year at WCNP, the annual departures at Medora in 1985 showed nearly normal temperatures, but continued, below-normal precipitation. This principally was brought about by extremely low winter quarter rainfall, which normally accounts for only eight percent of the annual total. Nevertheless, after a spring quarter of slightly above-normal rainfall, the summer quarter (which acccounts for 45.6 percent of the annual total) was 39.8 percent below normal. The fall quarter showed a similar magnitude of positive departure from normal rainfall levels.

Under normal conditions, the pattern of temperature and precipitation departures noted above would be expected to encourage cool, but hinder warm

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season species growth and productivity. Under grazed conditions, warm season species are generally more productive than cool season species, although the absence of grazing results in the opposite relative contributions of warm and cool season species in this area (Sims et al. 1978). Total productivity in 1985, therefore, should be lower due to the decreased productivity of the warm season species.

As noted above, however, 1985 did not follow a year of normal climatic conditions and grassland productivity. The lower productivity expected from the 1985 climate is exacerbated by the previous year's poor conditions, so grassland productivity may be expected to be lower, and to be registered in poor bison growth and low or negative liveweight gains in 1985 and possibly into 1986.

Summary of the Implications of the Climatic Record on Bison Condition

The annual and seasonal climatic records both suggest that bison condition, as measured through liveweight gains, would probably be poorer than normal for the years 1983 through 1985 at TRNP. The year 1984 would have been particularly poor for forage productivity and bison growth and liveweight gains for 1983 through 1985 should have been lower than normal.

It is doubtful that the bison specimens shot April, 1985 would have improved dramatically following a year of potentially very poor grassland productivity. This is particularly true given the potential direct effects of weather conditions upon these animals for the winter and early spring months.

It should be noted that although precipitation levels returned to positive departures from normal in the fall of 1985, they were only slightly above normal in September. Furthermore, although the October departure was

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52.5 percent above normal, the fall study specimens were collected on the third day of October, and would not have benefited from this effect. Any improvement in animal condition for the fall animals would be attributable to potential new growth of cool and warm season species.

Direct Climatic Influences Upon Bison Condition

An earlier discussion of metabolic responses of bison to changes in winter temperatures (Christopherson et al. 1979) found that at temperatures of -30°C (-22°F) with winds of 4.7 km per hour (2.9 mph), bison metabolic rates increased to maintain core body temperatures, due to cold stress. During winter months, metabolic rates also increased in response to temperatures of 10°C (50°F), due to heat stress associated with the insulation properties of the winter pelage of these animals. These factors were not considered important to the changes in individual liveweight means registered at Wind Cave National Park due to the amount of time that elapsed between when these effects would be important and when the animals were weighed. However, at TRNP, these effects might be evident in weights of the spring collected study specimens. The record of the number of days with maximum temperatures of 10°C (50°F) or over and minimum temperatures of -30°C (-22°F) or lower for the winter months of 1984 to early 1985 is presented in Table 3.17 (United States Department of Commerce 1984c, 1985c).

Before reviewing these data for the winter quarter prior to the collection of the spring-killed study specimens, it should be noted that records of daily wind velocities are not available. Without the effects of wind, Christopherson et al. (1979) found no adjustment in metabolic rate, and no indication of cold stress at the given temperature. Therefore, even though days of potentially critical temperatures may occur, they may not

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Table 3.17. Potential Number of Days for Exposure to Heat and Cold Stress During the Winter Quarter for Bison at Theodore Roosevelt National Park, 1984-1985

Year	Month	Number of Days with Temperatures > = 50°F (10°C)	Number of Days with Temperatures < = -22°F (-30°C)
1984	December	3	1
1985	January	0	3
1985	February	4	3

Source: United States Department of Commerce (1984c, 1985c)

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indicate stressed conditions for the TRNP bison. Furthermore, in the presence of critical temperatures, animals may seek out protected areas which would reduce the effects of these conditions. On the other hand, the study did not carry over a range of temperatures and wind conditions, so it is possible that warmer temperatures with harsher wind conditions also might result in increased metabolic rates. Given these considerations, the following analysis is offered as evidence of potential increases in metabolic rate and thus maintenance costs, but can not be considered proof of such responses.

The period in question is the winter months preceding April 1985, which includes December, 1984 and January and February, 1985 (Table 3.17). During this time period, minimum and maximum temperatures exceded the specified limits a number of times. The fact that temperatures oscillated throughout the period, indicates that adjustments or acclimatization to either cold or warm conditions would not be likely, so periods of both heat and cold stress may have occurred. This oscillation is especially evident during the month of February.

Based upon these data, one may anticipate that these conditions might have resulted in increased metabolic rates and higher maintenance costs for short periods of time prior to the collection of the spring study specimens. Basically, this would indicate that the end of the winter was not a particularly easy one for the TRNP bison.

Conclusions

Given the climatic record for Medora, North Dakota, and the pattern of WCNP bison liveweight response registered for similar data at Hot Springs, South Dakota, it appears that the TRNP bison herd would probably have been

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in a condition that would be considered below average in 1985. This would have been registered by potentially lower rates of growth for the males, SAM, and possibly FYM, and by possible liveweight losses in the older females, SAF and FAF, primarily due to the mobilization of energy stored as fat. These expectations must be qualified, based upon two factors. First, they assume comparable vegetative and bison liveweight responses to somewhat similar climatic conditions, as registered at Hot Springs, South Dakota and Medora, North Dakota. Second, they ignore the potential for the effective influences of microclimates, which may result in areas of adequate vegetation growth and subsequent liveweight gains in some bison during periods of generally poor range productivity. The fact that individual animals registered liveweight gains during periods of potentially poor vegetation productivity at Wind Cave National Park, indicates that this is a real possibility that must be considered in later chapters in which the results of the fat extraction analyses are compared with those from Brink's (1986) study of bison in Canada.

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CHAPTER 4. PROCEDURES FOR ANALYSIS OF CARCASS COMPOSITION

The procedures used to collect the carcass composition data presented and discussed in the remaining chapters of this dissertation are the focus of this chapter. This discussion excludes description of the methods used to differentiate sex in archaeological collections of bone. Although sex data are used in Chapter 9 and are important to the evaluation of the models developed and presented here, this aspect of the procedures is excluded, because the bone data used in Chapter 9 are from published sources (Speth 1983, Frison 1970). The purpose of this chapter is to describe how the carcass composition data--the amount of meat, fat, and bone--were collected. This research draws upon methods used in the animal sciences, and although many of these analyses were carried out according to published procedures, in some cases modifications were necessary because of the nature of the material analyzed. Most of the methods used are described in order to facilitate understanding by the anthropological community.

In order to measure the relative value or utility of different parts of the bison carcass, as Binford (1978) did for sheep and caribou in his study of the relationship between economic anatomy and use, one must collect a variety of composition data. Composition studies are concerned primarily with the relative proportions of muscle, fat, and bone in the carcass (Berg and Butterfield 1976:15). The purpose of this chapter is to describe how these data were collected. These descriptions are presented in three sections. The first section, Butchering, Carcass Division and Preservation, describes how the carcasses of the bison were handled from the time the

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animals were shot until the carcass units were thawed for analysis. The second section, Analysis of Carcass Components, includes a description of the methods of determining the available weights of different carcass components. The third section, Analysis of Fat and Moisture Content, focuses on how meat, marrow, and bone grease samples were prepared and their fat and moisture content were analyzed and evaluated.

Butchering, Carcass Division, and Preservation

On each collection trip to Theodore Roosevelt National Park (TRNP), two bison, a male and a female, were shot and bled in the field. The exception to this was the spring adult male, SAM. The carcass of this bison was not bled immediately. No other field butchering was done prior to transporting the carcasses to a local meat packing plant for preparation. Butchering and division of each carcass into smaller units of study took place over a period of two days, with heading, skinning, eviscerating, and splitting of the carcasses done the first day, and division of the carcasses into smaller units, following overnight cooling of the quarters, taking place the next day. The procedure used to butcher each of the animals was the same, but occasional differences arose in the locations of the divisions. These errors were corrected in the laboratory so that all units from a given location are comparable.

The procedure used to butcher the carcasses was as follows. The head and shanks (metapodial and more distal bones) were removed with the associated hide intact. The head was separated from the body between the skull (occipital condyles) and the atlas vertebra, and the shanks were separated from the carcass between the metapodial and the associated tarsals or carpals. Next, the hide was removed from the carcass and the body cavity

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was opened for removal of the viscera. The heart and liver were separated from the pluck (the respiratory organs) which was removed after gastrointestinal evisceration. The carcass was split along the midline, and then washed and quartered prior to weighing and cooling overnight. Before freezing, the hide, tongue, eyes, and brain were removed from the head unit. Neither the brain, nor the eyes were preserved for analysis. During butchering, weights were collected for the hide, head (with and without hide, tongue, eyes, and brains), shanks, heart, liver, tongue, pluck (without heart or liver), gastrointestinal tract, and the washed carcass halves and quarters.

The next day, after overnight cooling, the carcasses were divided into smaller units to facilitate their transportation to Washington State University. In most cases, these divisions directly correspond to those used in the analysis of carcass composition. In some cases two adjacent analytical units were left together for transport and later division (e.g., tibia/tarsals, radius-ulna/carpals, and units of the shanks--the metapodials and phalanges). The rib and thoracic vertebrae units were treated somewhat differently due to the difficulty of rapidly dividing the muscles between such units. This portion of the carcass was subdivided into units that included a front and back section of ribs and vertebrae. The division between front and back units was between the seventh and eighth ribs and corresponding thoracic vertebrae. Later, in the laboratory, the meat and tissues of the front and back units were combined while establishing a division between the ribs and the thoracic vertebrae.

The division of the carcass used in this study is illustrated in Figure 4.1 and described in Table 4.1. These divisions were made in one of two ways: 1) cuts made across the grain of the muscles, thus dividing some

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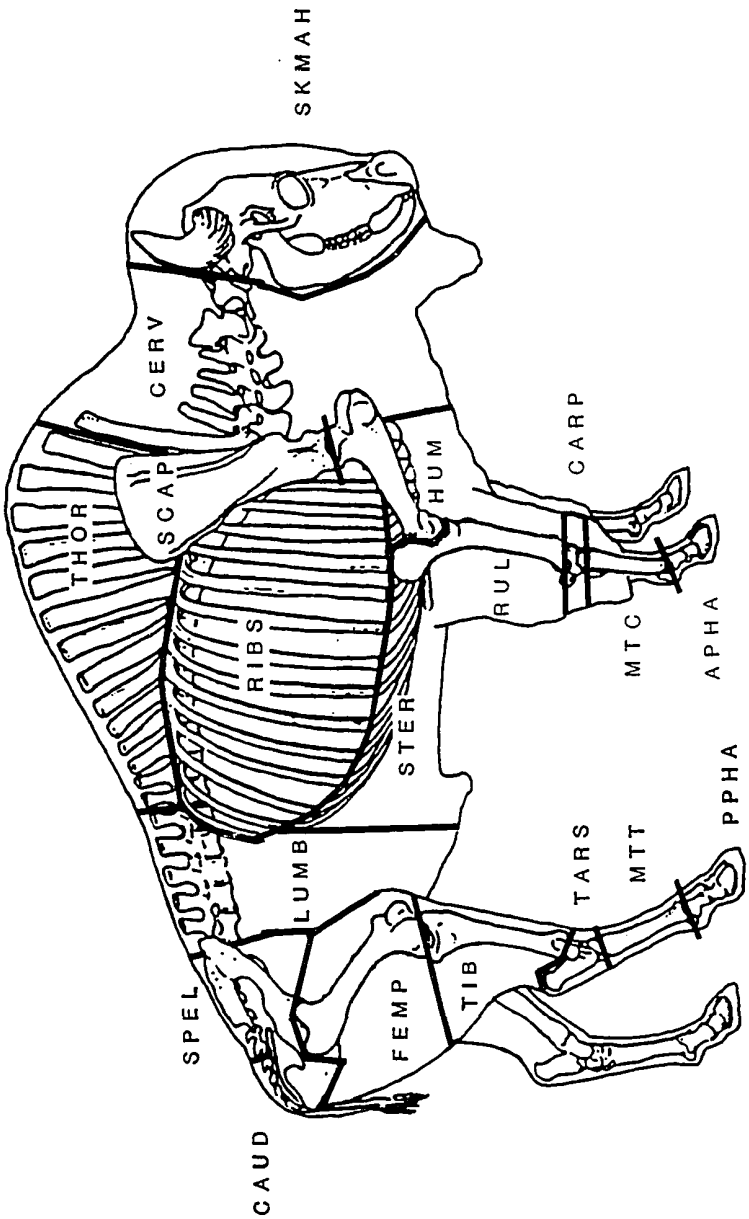

Figure 4.1. Carcass Unit Divisions

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Table 4.1. Description of Carcass Unit Divisions

Part A. Removal of the Thoracic Limb and Division of the Units

Division[a] Between Units		
Unit or Group	Unit or Group	Description
forelimb	thorax	First, the trapezius was cut along the scapular spine and peeled back off the lateral face of the scapula unit. The leg was lifted laterally and loosened from the body by cutting between the ascending (deep) pectoral and the limb muscles. The latissimus dorsi was cut at the posterior edge of the scapula. The rhomboideus was cut away from the medial face of the scapula and the leg was removed.
scapula (SCAP)	humerus (HUM)	A transverse cut was made between the glenoid cavity and the proximal head of the humerus. The muscles extending between the posterior border of the scapula and the humerus were cut at the scapula edge.
humerus (HUM)	radius-ulna (RUL)	A cut was made from the anterior edge of the joint through the ligaments connecting the radius and humerus. Then a cut was made from the posterior side of the limb at the most proximal edge of the ulna, following the dorsal to anterior perimeter of the olecranon.
radius-ulna (RUL)	carpals (CARP)	A cut was made at the joint between the radius and the proximal row of carpals.
carpals (CARP)	metacarpal (MTC)	A cut was made at the joint between the distal row of carpals and the metacarpal.
metacarpal (MTC)	phalanges (APHA)	A cut was made at the joint between the first phalanges and the distal metacarpal. The proximal sesamoids remain with the metacarpal.

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Table 4.1. (continued)

Part B. Removal of the Pelvic Limb and Division of the Units

Division[a] Between Units		
Unit or Group	Unit or Group	Description
hindlimb	pelvis	A cut was made along the dorsal line of the biceps femoris, extending from near the anterior end of the middle gluteal, posteriorly to the ischium. The biceps femoris was peeled down, exposing the proximal end of the femur. The femur was separated from the acetabulum by cutting through the ligaments. The tensor faciae latae was separated from the femur unit by cutting the facia. The gluteal muscles were separated from the femur by cutting their tendons at the femur. The semimembranosus and semitendinosus were cut from the ischium to go with the femur unit.
femur (FEM)	tibia (TIB)	A transverse cut was made at the joint and distal to the patella.
tibia (TIB)	tarsals (TARS)	The tendon attached to the tuber calcis was cut just proximal to the calcaneus. The ligaments connecting the tibia and astragalus were cut, separating the tibia from the tarsals. The lateral malleolus remained with the tibia.
tarsals (TARS)	metatarsal (MTT)	A transverse cut was made at the joint.
metatarsal (MTT)	phalanges (PPHA)	A transverse cut was made between the metatarsal and the first phalanges. The proximal sesamoids remain with the metatarsal unit.

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Table 4.1. (continued)

Part C. Division of the Axial Units

Division[a] Between Units		
Unit or Group	Unit or Group	Description
head (SKMAH)	neck (CERV)	A transverse cut was made through the muscles at the atlas-occipital condyle joint.
neck (CERV)	thoracic vertebrae (THOR), ribs (RIBS), and sternum (STER)	A transverse cut was made through the muscles following the anterior edges of of the dorsal spine of the first thoracic vertebrae, the first rib and the manubrium.
thoracic vertebrae (THOR), ribs (RIBS), and sternum (STER)	lumbar vertebrae (LUMB)	A transverse cut was made through the muscles along the posterior edges of the dorsal spine of the fourteenth thoracic vertebra, the fourteenth rib, and continuing along this line to the ventral edge of the abdominal wall.
lumbar vertebrae (LUMB)	sacrum-pelvis (SPEL)	A transverse cut was made between the fifth lumbar vertebra and the sacrum.
sacrum-pelvis (SPEL)	tail (CAUD)	The tail was separated from the carcass between the first and second caudal vertebrae.
sternum (STER)	ribs (RIBS)	The sternum was separated from the ribs by cutting through the costal cartilage and the muscles immediately ventral to the distal ends of the ribs.
ribs (RIBS)	thoracic vertebrae (THOR)	This division was made during the dissection process by grouping muscle and tissue associated with each unit, rather than by dividing the units and then processing them separately. The division between these units is not as easily made as the others.

[a] For a description of the division of muscle weights between carcass units, see Appendix 2.

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muscles between units, and 2) cuts made at muscle origins or insertions, or between muscles, thus leaving them intact.

Carcass units were wrapped in plastic and frozen prior to boxing for shipment to Washington State University. The frozen carcass units were transported via refrigerated truck and air from Billings to Spokane, Washington and then were brought the short distance to Pullman, by University vehicle without benefit of refrigeration. Here, the carcass units were removed from the boxes, wrapped in additional plastic, and stored at -23°C at a local market until they were removed for laboratory processing.

In their work on caribou and sheep, which served as the model for this bison project, Binford (1978) and Binford and Bertram (1977) collected weights on the carcass parts in the field with the use of a dairy scale. For marrow samples that needed more accurate measurement, the samples were frozen and transported for later study. In this study of bison carcass composition, the animals were transported prior to dissection and thus, unlike the study of caribou and sheep, they had to be thawed before further study. Several different methods were used to thaw the carcass pieces prior to laboratory processing. Initially, carcass units were removed from the lockers and stored in a freezer that operated at refrigerator temperatures. When the freezer quit working, units that were small enough, were thawed in a refrigerator. Larger units were left out overnight in the laboratory to thaw at room temperature. Due to their large size, this generally resulted in thawing of the outer flesh, while the inner remained frozen or partially frozen.

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Analysis of Carcass Components

Data were gathered for three purposes in this project. Many of the data were gathered to construct utility indices like those created by Binford (1978) and by Metcalfe and Jones (1988) for sheep and caribou. Thus, many of the same kinds of data are similarly recorded here. Other data were needed, however, to construct utility indices modeled after Binford's example, but which incorporate or emphasize other carcass resources. Finally, some information was collected in order to provide baseline data for modification of these indices or models of utility, given regional or temporal differences in butchering patterns. The carcass components analyzed here include total meat and individual muscle weight, fat and other tissue weight, demuscled bone weight, bone marrow and bone grease weight, marrow cavity volume, dry bone weight, and measures of bone density and volume.

The procedures used to gather the composition data were generally consistent between carcasses, but sometimes varied when methods of recovery needed to be adjusted or when an error was made. The general procedure was as follows. After a carcass unit was partially thawed, the weight of the unit was recorded using one of two scales. If the unit weighed less than 20 pounds, a hanging scale with divisions to one ounce was used. Heavier units were weighed on a hanging scale with one pound divisions. In most cases, thawing resulted in some water loss, so the combined weights of the carcass units from each animal are somewhat less than the quarter weights recorded at the time of butchering.

Treatment of the carcass units at this stage primarily involved separation of the meat, fat, bone, and other tissue (e.g., ligaments, tendons, fasciae, and some cartilage). Once the bone was separated from the

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muscle and tissue, the marrow was collected when present, and the bones subsequently boiled for collection of bone grease. After additional degreasing, dry weight, density, and volume were determined for each bone. The remainder of this section provides a description of those procedures and modifications.

Total Meat and Individual Muscle Weights

Binford's (1978) work with sheep and caribou anatomy records gross weights for carcass units, noting when variations in butchering procedures resulted in inflated values for some units. These weights are not specifically meat weights, but include all components of the carcass unit, including bone, meat, fat, and other tissue. Binford factors in a loss based on dry bone weight to account for the inedible portion of the unit weight. In this study of bison anatomy, total meat weight and individual muscle weights were specifically recorded for one side of each of the spring-killed animals (SAM and SAF). This was done in order to provide data that might be used to adjust the utility indices when differences occurred in butchering patterns such as those described by Frison (1973:85-88) at the Wardell Buffalo Trap and the Glenrock Buffalo Jump, as well as to provide a more accurate measure of the proportion of the unit weight represented by edible meat. Thus, the proportion of edible tissue is not inflated by including the weight of other non-meat tissue in the determination of meat utility.

Gathering data on meat and muscle weights for each carcass unit involved identifying and separating the muscle from the fat and fasciae, weighing each muscle or muscle fragment, and then recording the total muscle weight for the carcass unit. This process was very time consuming so

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weighing of individual muscles was discontinued in the analysis of the two fall-collected animals. Separation of the muscles was not significantly different for the right side carcass units, however, as fat deposits (excluding intramuscular fat) also were separated from the muscle tissue as in the fall season specimens. Meat, fat, and other tissue was not separated in carcass units from the left sides of the fall collected animals (FAF and FYM) in order to decrease processing time, and based upon an assumption of lateral symmetry.

Fat Tissue Weight

Binford (1978) in his study of sheep and caribou anatomy did not separate fat from muscle tissue when recording gross weight for carcass units. In this study of bison anatomy, separable fat was collected apart from muscle, so the contribution of fat to gross weight could be determined. This factor is important in determining the rank of carcass units during periods when fat resources have high relative subsistence value compared to lean meat.

During the processing of the thawed carcass units, fat tissue was generally separated into the following groups: subcutaneous, intermuscular, and cavity fat. Subcutaneous fat is associated primarily with the axial skeleton, but extends onto the proximal appendicular units (i.e., the scapula and femur), and cavity fat is found within the body cavity and therefore, is limited to axial skeleton units. Unfortunately, no division was made in the cavity fat between kidney and channel fat. Intramuscular fat, another important depot, is found within the muscle tissue and was not separated or measured at this stage of the project. Distinguishing between intermuscular and intramuscular fat was sometimes difficult. Fat tissue

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that was easily removable was considered intermuscular, rather than intramuscular. Tissue that was not easily separated from the muscle tissue was considered intramuscular and left with the muscle.

No effort was made at this stage to separate the fat from the fascia, or tissue, associated with it. The tissue and fat were weighed according to the categories noted above, and refrozen for later rendering.

Other Tissue Weight

As previously noted, Binford (1978) did not separate what is classified here as "other tissue" (e.g., tendon, ligament, fasciae, and cartilage) from edible meat and fat in his construction of utiltiy indices. Weights of this tissue type were recorded for the carcass units in this study of bison. For example, the knuchal ligament was separated from the muscle and fat, and weighed with these tissues. Tendons were removed by cutting at the point where the muscle tissue terminated along the tendon. Additional tendon and ligament fragments and cartilage were included in this category from cleaning the bones. No additional processing of these tissues was done and they were discarded after total tissue weight for the carcass unit was recorded.

Bone Weight and Other Bone Data

After the meat, fat, ligament, and tendon were cleaned from the bone(s) of each carcass unit, weight and other data were recorded. These include demuscled and dry bone weight and volume, as well as weights of marrow and bone grease associated with the bone.

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Demuscled Bone Weight

Binford (1978:15) reports that bone weight was recorded after meat and tendon were cleaned from the bones, and that this weight was used to determine the quantity of meat that would result from boning an animal. However, when the meat utiltiy index is constructed (Binford 1978:20-21), dry bone weight was used rather than fresh or demuscled bone weight, and the combined meat, fat, and other tissue weight data that would result from the subtraction of the fresh bone weight from the carcass unit weight, were never presented.

In this bison study, demuscled bone weight was recorded as well. After each carcass unit was cleaned of muscle and fat, the ligament and tendon adhering to the bone were removed. The cartilage was left intact except on the scapulae. Weights of the scapulae were recorded before and after removal of the cartilage at the proximal end of the blade. Once cleaned, all bones were weighed and refrozen for later processing of the bone marrow and grease. Demuscled bone weight thus includes the weight of the associated bone marrow and grease.

Marrow Collection and Weight

Marrow was collected in a different manner than the method described by Binford (1978:16) in his study of the economic anatomy of caribou and sheep. Binford reported that marrow from the sheep and caribou was collected from the shafts of the long bones after first separating the heads from the shafts. The marrow was bagged and stored frozen until later, when it could be accurately weighed.

Although Binford focuses much of his discussion on differences between utility values for proximal and distal ends of bones, there is no statement

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about how the samples were subdivided. His reference to, and use of the data resulting from the work of Irving (1972:149), which is reporting the work of Meng et al. (1969), as well as his own presentation of the sheep data (1978:24), suggest that differences occurred in the division of the bones for these two species. Meng et al. (1969:187) collected data on three sections of caribou bone--proximal, middle, and distal thirds. Binford uses the figures reported for the proximal and distal ends for his analyses (1978:24). His data for sheep, collected by Robert Grange, are reported for the proximal and distal ends of the long bones, suggesting the marrow removed from the shafts was divided in half.

Rather than isolating the marrow cavity, and dividing its contents into two units of equal size, I cut the long bones (except for those from the left side of FAF) at the midpoint of total element length. This procedure allows one to treat the marrow weight data in two ways. First, by combining the marrow weights from the two ends and then dividing by two, the data are comparable to that used by Binford for sheep. Second, by maintaining the distinction between proximal and distal ends (based upon total bone length), real differences in marrow distribution (in terms of weight) are emphasized, thus more accurately reflecting differences in the relative value of the proximal and distal ends of the bones.

The marrow from the left side of the fall female (FAF) was collected in a different manner. This marrow was recovered in the process of breaking bone in preparation for maximizing bone grease collection. The marrow was removed and weighed to compare it with that collected (as described above) from the right side elements. Shafts from all of the limb bones broke easily, exposing the marrow cavity and minimizing differences attributable to differences in the method of recovery.

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Bone Grease Collection and Weight

Bone grease samples were also collected in a manner somewhat different than that described by Binford (1978). His measure of the relative importance of elements for the production of bone grease was based upon a combination of factors, including measures of bone density, volume, and the relative percent of total fatty acids comprised by oleic acid (a low melting point fatty acid believed to correlate with perceived differences in fat quality). Binford (1978:32) used samples of bone grease from cancellous tissue to determine the percent oleic acid, which he used as a measure of grease quality. He used measures of bone density and volume to reflect quantitative differences in bone grease production.

In the present study, although bone volume and density measures were also recorded, a direct measure of bone grease production was attempted by boiling each skeletal element in water for seven hours, cooling overnight, and then collecting the fat. Elements from the left side of the female bison, FAF, were broken into smaller pieces before boiling, in an effort to maximize grease recovery. These bones were broken with a two-pound hammer while they rested on a rock anvil. As previously noted, the shafts of the limb bones broke easily, exposing the marrow. However, greater difficulty was encountered in breaking the articular ends of the long bones, where the cancellous tissue containing bone grease is located. These epiphyses probably were not broken up as much as in aboriginal preparations for recovery of bone grease, but a measure of the difference between total grease weight and recovered grease weight can be made by comparing the bone weights after boiling for grease collection with the weights of the dry, defatted bone.

The appendicular elements from the right side of FAF were boiled whole

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(if they were not marrow producing bones), or as proximal or distal ends (if they did produce marrow). A bone grease sample was collected for each element, or element end, with the exception of the phalanges, carpals, tarsals and radius-ulna, which represent multiple element samples. The grease samples from the first through third phalanges were combined producing anterior and posterior phalanges samples. In older animals, the ulna is fused to the radius, and although they are often separated proximally in butchering of the forelimb, or in preparation of bone grease, they were maintained together as a unit in this study. Appendicular bone grease samples from the other bison (SAM, SAF, and FYM) were collected in the same manner as those from the right side of FAF.

Elements from the axial part of the skeletons had been divided along the midline at the time the carcasses were split. The vertebrae and the sternum therefore, were split between the left and right sides. The tails were removed from the carcasses prior to splitting, so unlike the rest of the vertebrae, they are complete--excepting the first caudal vertebra which, in each case, remained with the sacrum. No additional bone breaking was done of the vertebral elements of FAF prior to boiling for the rendering of bone grease. The ribs from the left side, however, were cut into thirds. The ribs from the right side of this animal and the other animals were boiled as complete elements. Bone grease samples were not collected from either the skulls or mandibles of these animals, nor was any bone grease collected from the skeletal elements of the fetal bison, SFM.

The specific procedure for collecting bone grease samples and determining the quantity of bone grease production was as follows: 1) holes were drilled into the cancellous tissue of the articular ends of the bone to facilitate extraction of the bone grease by boiling; 2) the bones were

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weighed; 3) each skeletal element was boiled in a covered pot or pan of water for approximately seven hours; 4) the water was cooled, allowing the fat to congeal; 5) the fat was collected and any excess water collected with the fat was separated and discarded; 6) the separated fat (bone grease) was weighed; 7) the bone was cleaned of any remaining ligament, tendon, or cartilage; 8) each bone was allowed to dry for two days before they were reweighed. The difference in bone weights recorded prior to a subsequent defatting process and prior to boiling for collection of the bone grease samples reflects weight losses due to loss of bone grease (generally incomplete), other tissue (ligaments, tendons, and cartilage), and water.

It should be noted that aboriginal procedures for collecting bone grease are frequently reported to have involved breaking the bones into small pieces, boiling these in water, and collecting the grease that floats to the top (Leechman 1951). Breaking up the bone exposes more surface area, thus facilitating the mobilization of fat.

Additional Defatting of the Bone

After boiling the bone for seven hours in water in order to collect the bone grease, they were set aside to dry while other carcass units were processed. Many of the bones that were degreased in the early stages of the process, and had dried for several weeks, showed signs of residual fat deposits moving to the surface of the bones, thus indicating incomplete degreasing of the elements. The construction of the utility indices required the collection of dry bone weights (i.e., without residual grease), so additional efforts were made to more thoroughly degrease the bones.

Although there are several methods available to degrease bones, many of these require the use of hazardous chemicals, or long periods of time to

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complete the process. The following process was detailed in a laboratory procedure guide prepared for an anatomy laboratory class at Washington State University (Paul Johnson, personal communication) and has the benefits of posing few hazards and taking relatively little time. According to the procedure, holes are drilled in the bones to improve exposure of the cancellous tissue to the defatting solution. The bones are then placed in a container filled with a solution consisting of an ammonia based detergent, such as Alconox (1.5 kg), ammonium hydroxide (500 ml at less than 40 percent ammonia), and water (90 l). The solution is changed weekly until the defatting process is complete.

The bison bones from this study were treated to this process, after first recording their weights. The bones were either suspended in the defatting solution or submerged in porous bags tagged for identity. The solution was changed weekly, as recommended. After a period of six weeks, because the defatting process was proceding so slowly, the bones were removed to another container in which the proportion of the ammonium hydroxide was doubled, producing a solution of 1.5 kg Alconox, 1 l ammonium hydroxide, and 90 l of water. Bones were left in this solution for one week, with the exception of the caudal vertebrae which were left an additional week. Weekly changes of the solutions included rinsing the bones in hot water to remove adhering fat. Following treatment, the bones were thoroughly rinsed in hot water and laid out, covered, to dry slowly for one week. The bones were then reweighed and the difference between pre- and post-defatting weights recorded as additional bone grease and water loss.

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Measurement of Marrow Cavity Volume

The method of measurement used to determine marrow cavity volume is one described by Grover Krantz (personal communication 1987) in his Human Osteology class at Washington State University. He uses this method to measure cranial capacity of human skulls. At his suggestion, poppy seeds were used rather than millet, because they are smaller and more accurately measure cavity volume where small areas must be filled.

The volume of the cavities of the marrow yielding bones from the right sides of each bison were measured by determining the volumes of poppy seeds necessary to fill the cavities. Volume was determined by pouring the poppy seeds removed from the marrow cavity into a graduated cylinder.

This method differs from that employed by Binford and Bertram (1977) and Brink (1986) to measure cavity volume. These researchers coated the interior walls of the bone cavity with parafin and plasticene, respectively, in order to delineate the marrow cavity from the surrounding cancellous tissue. When the coating substance had dried, water was poured into the cavities and the volume of the water measured in a graduated cylinder.

Differences in these methods may vary somewhat in the results they produce. The volumes derived by coating the cavity with a water insoluable material may be smaller than if they had been derived using the poppy seed method. The coating material has volume itself, whereas, the poppy seeds are in direct contact with the interior walls of the bone. On the other hand, there are interstitial spaces between each sphere of the poppy seeds. I assume that the poppy seed method is an adequate measure of marrow cavity volume.

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Measurement of Dry Bone Weight

Measures of dry bone weight are used extensively in the construction of body part utility indices developed by Binford (1978), and in a subsequent study (Metcalfe and Jones 1988) attempting to simplify the construction. Binford and Bertram (1977) describe their method of measurement, noting that humidity affects the weight of bone. Their solution to humidity-related changes in bone weight was to submerge each bone for five seconds in water and then heat it in an incubator (at 102°F) for seven days prior to taking the measurement (Binford and Bertram (1977:107). Lacking access to similar equipment, a method had to be found to compensate for any changes in weight over the period of measurement for dry bone weights.

The solution sought here was to control changes in the humidity of the room, which would alleviate the need to dry out the bone. Humidity, however, is affected by temperature, in that warm air can hold more moisture than cold air. As temperature rises, the amount of moisture the air can hold increases and the humidity reading decreases if the amount of available moisture does not increase as well. Bone weight apparently changes with humidity, probably as a result of absorbing moisture from the air. Therefore, by maintaining the relative humidity of the room, relative differences in dry bone weights should reflect actual differences in bone weight and not weight differences combined with additions or losses of moisture in the bone.

Dry bone weights were collected on two separate occasions and reflect these differences in weight due to changes in room humidity. The first period of dry bone weight measurement was done at the end of October, 1987 following nearly two and one half months with little or no rain in the Pullman area. The relative humidity in the lab at this time was maintained

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at approximately 47 ± 1 percent. At a later date, the original weights (collected before the need for additional defatting was determined) were found to be unsuitable. The second time dry bone weights were collected, humidity was maintained at approximately 59.5 ± 0.25 percent. These, rather than the earlier weights are used for the dry bone weights in construction of the utility indices.

Measurement of Bone Volume and Density

Binford (1978:33) used bone density and volume as proxy measures of bone grease production in his construction of utiltiy indices. Bone volume serves as a proxy for relative differences in bone size, while bone density serves as an indicator of the amount of cancellous tissue present. Together, they provide an indirect measure (and as shown in Chapter 5, a potentially inaccurate measure) of the amount of fat, in the form of bone grease, available in a given bone when direct measures of production are not available.

Binford and Bertram (1977:107) report that to measure bone density they used the formula:

$$\text{density} = \frac{\text{dry bone weight (gm)}}{\text{bone volume (ml)}}$$

where density is expressed as weight per unit volume. Bone volume was measured by water displacement after each element was coated with parafin and allowed to cool slowly (Binford and Bertram 1977:108). This coating prevents water absorption into pore spaces.

Lyman (1984:267), in a review of methods of determining bone density, suggests that the volume measures Binford and Bertram derive are inaccurate and somewhat inflated because the volume of the parafin coating is not

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subtracted from total volume. The magnitude of the error varies with bone size. It is doubtful that it represents a constant proportional volume as was assumed in their calculations.

In place of measuring bone density using Binford and Bertram's method of bone volume measurement, Lyman (1984:265) suggests that density can be determined using the formula:

$$Db = M/Vt$$

where Db equals bulk density, M equals mass or dry bone weight (Wa), and Vt equals the volume of the bone including pore space volume. Bulk density is used rather than true density (Dt), which uses a volume measure (Vs) which includes the volume of the bone only, thus excluding pore space volume. If density and volume are used as a proxy for the quantity of bone grease available in the construction of the utility indices, a measure that includes pore space volume is desirable. Lyman determines Vt by substracting the weight of the bone, saturated with water, from the weight of the bone suspended in water.

I used Lyman's method of bone density measurement, in part, in order to avoid having to remove the parafin coating on completion of the volumetric measurements, but also due to Lyman's arguements of greater accuracy of density measurement. The method he (1984:265) describes requires that each bone is boiled in water for two hours, cooled, and weighed--once suspended in water, and once as water saturated bone. Using this procedure, the bison bone was not saturated after two hours of boiling, and attempts to weigh the bones were unsuccessful. Rather than increasing the period of boiling and thus contributing to the degradation of the bone, they were boiled in water two hours and then were placed in a water bath overnight and weighed the next day. All bones were water saturated using this process and consistent,

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saturated bone weights were recorded. I suspect that increasing the duration of the period the bones are boiled in water might provide similar results. The large difference in size between bison bones and those of other ungulates such as sheep, caribou, or deer probably is responsible for the lack of success in applying Lyman's method prior to making the described modification in procedure.

Renderable Fat Weights

While processing each carcass unit, fat tissue was separated from the dissected muscle and divided into three groups: subcutaneous, intermuscular, and cavity fats. Each of these was not always present in every unit. Tissue from each group was bagged separately and refrozen until a later date when the fat was rendered. Rendering at first, was accomplished by cutting up the tissue and boiling it in a covered pot of water and collecting the separated fat. This process frequently took many hours of boiling, and cycles of fat collection, draining the water from the tissue, breaking up the tissue further, and reboiling. Later, in order to speed up the process, the tissue was homogenized in a blender after the initial boiling and fat collection. This process facilitated separation of the fat from the tissue. Excess water that was collected with the fat was subsequently poured off and discarded. The rendered fat was then weighed.

Although it would have been desirable to do so, no additional analysis was done of the moisture and fat content of the rendered carcass fat component. It is expected that the moisture content is probably relatively low.

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Analysis of Fat and Moisture Content

The initial butchering and dissecting of the carcass units produced three products that were subjected to additional laboratory analyses to determine their moisture and fat content. These were the muscle, marrow, and bone grease from each carcass unit. Additional fatty acid analyses of some marrow and bone grease samples were planned, but could not be carried out within the time frame of the project. Future studies of bison carcass composition could profit by including that analysis, as well as a similar study of the rendered carcass fat. The following sections describe the methods of sample preparation and analysis procedures used to determine fat and moisture content in meat, marrow and bone grease, as well as the methods used to determine the acceptability of the analysis results.

Sample Preparation

Preparation of meat, marrow, and bone grease samples differed somewhat in the extent they were processed prior to testing for moisture and fat content. In each case, the procedures were designed to homogenize the sample to assure that laboratory tests would reflect differences due to sample location and not differences due to the part of the samples analyzed. Despite these efforts, there were differences in the success of producing homogenized test samples. These differences were sometimes the result of the apparent need for additional sample homogenizing. For example, some meat samples contained connective tissue which differed in consistency from the muscle tissue and was therefore, resistant to homogenization. Other differences occurred due to differences in the optimum temperature of the material for preparing the test samples. Meat samples generally performed best when the meat was completely thawed prior to conducting the fat and

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moisture analyses, but fat samples varied according to differences in their melting points. Fat with low melting points generally had to be kept frozen until the test samples were prepared, whereas fat with high melting points produced more homogenous results if they were allowed to stand at room temperature for one or more hours prior to preparation of the test samples.

The following sections detail how meat and fat samples were prepared for analyses, and include descriptions of the methods used to homogenize them.

Meat Samples

The frozen meat that had previously been removed from the carcass unit was prepared for analysis by first grinding and then homogenizing it. The meat from the axial and forelimb carcass units of the two spring-collected animals was ground by hand using a Chop-Rite #10 Chopper with a 3/16-inch plate. Only a single pass through the grinder was possible using this hand operated equipment because as the meat thawed, it clogged the grinder plate. The excessive time required to process the meat from some of the relatively large carcass units (e.g., the femur) necessitated changing equipment. An electric Toledo Chopper (Model 5222 with 3/4 Hp motor) was used to prepare the meat samples from the hindlimbs of the spring animals and both fall animals. Using this apparatus, the meat was ground through a 1/4-inch plate, and then through a 1/8-inch plate, often remaining in a frozen or partially frozen state throughout the process.

After all of the meat from a carcass unit had been ground, it was mixed briefly by hand, and a subsample composed of ten handfuls of ground meat was selected. When the total amount of meat from a carcass unit was relatively small, subsampling at this stage was not necessary. The ground meat sample

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was placed in a plastic bag, double wrapped with freezer paper, and placed in frozen storage -23°C.

At a later date, each ground meat sample was partially thawed for further subsampling and preparation of a homogenized sample. At this stage, ten large pinchs of ground meat were collected and homogenized using a Sorval Omni Mixer and an ice water bath. The product was stored in glass jars sealed with masking tape, and refrozen until subsequent moisture and fat analyses were performed.

Marrow Samples

Due to the small quantities available, marrow samples did not require subsampling. Homogenization of these samples, in most cases, involved hand mixing of the material with a small metal spatula. The exception to this was the samples from the mandibles of SAM and SAF (none were collected from FAF or FYM), which were ground in a blender to break up the other non-marrow tissues (e.g., nerves) that were present in the mandible marrow samples.

Bone Grease Samples

Like the marrow samples, the bone grease samples did not require subsampling. There was some difficulty encountered, however, in homogenizing the samples. Small amounts of other tissue were sometimes present, but broke up easily with hand-mixing. The major difficulty encountered in the analysis of the bone grease samples was the tendency of the water and the fat in the samples to separate. As a result of this difficulty, multiple samples had to be run in the analysis of the moisture and fat content and the results averaged.

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Measures of Fat and Moisture Content

Three carcass products--the meat, marrow, and bone grease--were subjected to laboratory tests to determine the percent fat and moisture. The percent fat in meat samples is a measure of the quantity of nondissectable, intramuscular fat. This and a measure of the tissue weight provide information on the amount of energy obtainable from the carcass unit. Measures of intramuscular fat and moisture content might also be used to construct an index of body part utility when the meat is dried for storage. The percent fat in the marrow serves as a potential indicator of relative differences in animal condition. The percent moisture in the meat and marrow samples should directly vary with respect to the percent fat (e.g., Marquesz and Coblentz 1987), as no additional moisture was introduced to the samples through the collection process. Moisture content in meat and marrow samples, therefore, reflects differences in the actual water content of these products. The bone grease samples, however, were collected by boiling the bones in water. The introduction of water into these fat samples makes measurement of the percent moisture meaningless, except as required by the procedures to determine the percent fat.

The following sections include brief discussions of (1) the formulae for determining the percent moisture and fat in the samples; (2) the procedure for determining moisture content; (3) the procedure for determining fat content; (4) variations of these procedures; and (5) the method used to determine the acceptability of the extraction results.

Formulae for Determining Percent Moisture and Fat

In this study, the determination of the percent fat is dependent upon prior determination of the percent moisture, because fat was extracted in

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groups of multiple samples, rather than by individual treatment. The formulae commonly used to calculate the percent moisture and fat are as follows:

$$\text{percent moisture} = \frac{\text{wet weight - dry weight}}{\text{wet sample weight}} \times 100$$

$$\text{percent fat} = \frac{\text{(wet weight-extraction weight) - (moisture weight)}}{\text{wet weight}} \times 100$$

where wet weight equals the pre-analysis weight, dry weight equals the post-moisture-analysis weight, and extraction weight equals the post-fat-extraction weight. The actual formula used to determine the percent sample moisture also included calculations of the dish weight; the formula used to determine the sample fat content included calulations of the weight of the filter paper the sample was treated in, as well as calculations to adjust for average loss of moisture from the filter paper.

Procedure for Moisture Content Analysis

The procedures used to determine the percent moisture in these samples differ from those described in the AOAC (1975) in some detail. This difference involved an increase in the length of time the samples were placed in the 100°C oven. Drying for this extended period of time is reported in studies of broiler chicken carcasses by Verstrate et al. (1980).

The procedure I used to determine the percent moisture in the meat, marrow, and bone grease samples included the following steps. An aluminum dish was numbered and weighed to 0.0000 gm using a Metler H10 balance. A small amount of the wet sample material (approximately five gm for meat samples and two gm for marrow and bone grease samples) was placed in the dish, and the combined dish and sample material weighed. The samples were then placed in a gravity convection oven to dry at 100°C for approximately

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18 hours. The dried samples were cooled for 45 minutes in a dessicator and reweighed as dry samples.

The difference between the weights of the wet and dry samples represents the loss of moisture weight. As previously noted, this value divided by the original wet sample weight equals the percent moisture when multiplied by 100.

Procedure for Fat Extraction

The AOAC (1975) description of the fat extraction procedure includes the use of anhydrous ether for individual treatment of samples. An alternate method, involving the concurrent extraction of fat from multiple samples was used. The differences between the multiple and single sample methods are that, in the former, sample material is placed in filter envelopes rather than filter thimbles and the envelopes are placed together in a large chamber for extraction, rather than in individual goldfisch beakers. The specific procedure is described below.

To determine the fat content of the samples, by weight, the following procedure was used. First, an envelope of Whatmann No. 1, 15 cm diameter filter paper was numbered in pencil and weighed to 0.0000 gm using a Metler H10 balance. A small amount of sample material (ca. two gm for fat samples and five gm for meat samples) was placed in the filter envelope, and weighed. This was secured with a stapel and reweighed. Samples were then placed in a stainless steel pan and dried for 24 hours in an oven at 100°C removing all water moisture. When dry, the samples were placed in a dessicator until 20 to 50 samples were ready for extraction.

Once 20 to 50 samples were prepared, they were placed in an extraction apparatus that operates as a still. Using this apparatus, anhydrous ether

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is heated in a flask, converting it to a gas which rises and is condensed upon contact with glass tubing containing cold running water. The condensed ether drips into a funnel leading to the chamber containing the samples. Gradually ether fills the chamber until it reachs a level where it syphons back into the flask, carrying with it approximately 50 percent of the fat available in the samples. The process is continuous as long as sufficient ether remains to be reheated and converted to gas. The conversion of the liquid ether to gas cleans it of the extracted fat, which remains in the flask. With each cycle, in which the chamber fills and empties, approximately one half of the remaining fat is extracted from the samples. Depending upon whether meat or fat samples were being processed and the expected percent fat content, 12 or 16 syphoning cycles were run to assure that the fat was extracted. This process generally took approximately 26 hours when 16 cycles were required.

When a sufficient number of cycles were completed, the heat source was removed to stop the process. The samples were then removed from the extraction chamber, placed in a stainless steel pan and put in a vented, heated cabinet where the samples dried as the remaining ether evaporated. Following evaporation of the ether, the samples were placed in a dessicator for 45 minutes to cool, prior to post-extraction weighing.

The weight loss recorded from comparison of the post-extraction weight and the wet sample weight, represents the combined weight loss of the sample moisture and fat, as well as moisture loss from the filter paper. The fat content is determined by subtracting the corresponding loss of sample and paper moisture from this total and dividing by the original wet sample weight.

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Variation in Moisture and Fat Content Procedures

In most cases, separate samples were run to determine the moisture and fat content. The percent fat for each sample was determined using the average result of the moisture content analyses. If the total sample weight available for the analyses was small, however, then the moisture content analysis was run in conjunction with the fat extraction.

Under these conditions, the samples were prepared as for fat extraction, except that they were placed in pre-weighed, individual beakers to first determine moisture loss. This stopped the melted fat of one sample from mixing with that of another. After weighing to determine moisture loss, the sample envelopes were then placed in the extraction apparatus to remove the remaining fat. For these samples, the calculation of the percent sample fat uses the corresponding sample percent moisture, rather than an average for the samples from that carcass unit location.

A variation in the procedure used to determine the percent sample moisture was initiated when the bone grease samples were analyzed. These samples, as previously noted, were not well homogenized and many had small amounts of water, poorly mixed with the fat. When these samples were placed in open aluminum dishes in a 100°C oven for 18 hours, they frequently came out with fat on the bottoms of the dishes, from splattering. Due to the small amount of material available to rerun samples, a different method of analysis was tried. These samples were treated like fat extraction samples, with the material placed in filter paper envelopes and dried in individual, pre-weighed beakers. All weight changes could then be attributed to moisture loss and did not reflect contamination of one sample with splattered fat from another.

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Assessment of Extraction Results

The initial runs of the moisture content and fat extraction analyses included two samples from each sample location. The material from each sample location had been ground and homogenized, so it was expected that the analysis of two subsamples of this material should produce similar results. When this occurred, the resulting values were then averaged to represent the percent fat or moisture for that carcass location. A measure of similarity had to be defined to determine when differences in the results were acceptable given the assumption of sample homogeneity. If the results were too dissimilar, additional samples would then be run.

In a previous study of fat content in animal products, Sersland (1982:27) used the coefficient of variation to determine acceptance or rejection of the sample runs. She cites Young et al. (1976) as the precident for the use of 3.42 as the limit above which samples must be rerun to assume homogeneity. The coefficient of variation expresses the sample standard deviation as a percent of the sample mean. In applying this statistic to the results of the moisture and fat content analyses, however, it became evident that the value of the mean, strongly affects how large a difference in results can occur and still be acceptable. For example, if the mean percent sample moisture is 80 percent, then the standard deviation from the mean of the results can be quite large before a value of 3.42 for the statistic is reached. However, if the mean percent moisture is 5 percent, a much smaller standard deviation results in rejection of the hypothesis of sample material homogeneity. For meat samples, generally high in moisture content, it would be relatively easy to get acceptable levels of variation in the analysis results for tests of moisture content, but correspondingly difficult to get acceptable results for tests of the fat

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content because moisture content is high and fat content is low. The same would be true for the analyses of the marrow and bone grease samples, except that rejection of the results would be difficult for the fat content analyses and easy for the moisture evaluations, due to high proportions of fat and low proportions of moisture in these materials.

Inquiry into the method used in the Animal Sciences to determine acceptability of the results (Merton Pubols, personal communication) led to the use of a slightly different, but similar evaluation tool. In this case, samples from a homogenized material were rerun if the range of the results were more than ten percent of the mean of the sample results. That is,

$$\frac{\text{range of the sample results}}{\text{mean of the sample results}} \times 100 \leq 10\ \%$$

would result in acceptance of the sample results and a value greater than 10 percent would result in a rerun of the analysis for that sample location. However, this statistic suffers from the same problems of acceptance and rejection as the previous statistic, specifically, that a large mean allows greater variability in the analysis results before rejecting a hypothesis of homogeneity. After reviewing the results of the early moisture and fat content analyses, it became evident that rejection of the hypothesis of homogeneity was too difficult for samples with high proportions of fat or moisture and too easy for samples with low proportions. A more restricted range of acceptable results was decided upon for samples with high proportions, and a more lenient range of variability was found acceptable for samples with very low proportions.

Despite these changes, for many samples, the homogeneity of the sample material was clearly a problem. Rejection of the results of the first two samples run for a sampling location required additional analysis. Where

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adequate material was available, the second run of the analysis included three samples. Often, this second run would produce acceptable results, but occasionally it would not. Initially, a third set, again including three samples, was run to test for homogeneity and the relevent percent moisture or fat. Eventually, however, after checking the results of multiple sets of samples and taking care to mix samples again before running the test, it became clear that running additional samples rarely produced better results. The problem of getting comparable results could be attributed to poor homogenization rather than errors or inconsistencies in sample treatment during the analysis. It suggests as well, that the described levels of acceptable difference between samples may have been too small.

Limitations in time, money, and total sample material, and the lack of improved results with multiple series of extractions suggested that after two runs, it was reasonable to accept that the sample was not homogeneous at the designated levels of acceptable differences and average the results of the runs. Prior to this decision, when a third run did not produce results indicating similar results, all eight samples previously run as three sets, were averaged for determination of the percent sample moisture or fat. Clearly, it would be desirable to run a large number of samples to improve the probability of obtaining an accurate estimation of the sample mean of fat or moisture content, but this was not possible under the limitations of the study. Despite these problems, it is my opinion that the fat and moisture content data presented in later chapters represent acceptable results.

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CHAPTER 5. VARIABILITY IN CARCASS COMPOSITION, PART ONE: BONE AND BONE PRODUCTS

In order to construct and apply models of carcass utility in appropriate ways, one must first understand how carcass composition varies between classes of animals, and then determine whether these variations are important to model construction. In this, and the next two chapters, I present the results of the analyses of the bone, bone marrow, bone grease, meat, meat fat, and other carcass fat recovered from the Theodore Roosevelt National Park bison. The discussions of these analyses focus on three questions concerning variability in their distribution and quantity in the bison carcass. First, do males differ from females in the quantity of the product available (referred to as production or yield in these chapters) in the carcass units or in the carcass as a whole, and are these products distributed differently within the carcasses of animals of different sex? Second, how do differences in animal age influence the production and distribution of these products in the carcass? Third, under fluctuating nutrition conditions, do production or distribution of the carcass products change, and if so, do these changes correspond to areas of greater product availability, or significantly alter the ranking of carcass units as sources of that product? Studies of cattle, other wildlife, and human physiology provide the basis for some of the interpretations presented in these chapters.

Carcass composition studies usually detail the proportion of the animal carcass that is comprised of bone, muscle, and fat. These studies

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frequently include an assessment of the distribution of these products throughout the carcass. These three major components of the bison carcass are discussed in this and the following chapters: Chapter 5 concerns bone and bone products, including bone marrow and bone grease; Chapter 6 pertains to muscle and intramuscular fat (considering carcass organs separately from other muscles); and Chapter 7 focuses on carcass fat, including subcutaneous, intermuscular, and some body cavity depots.

Units of Measurement

In this and later chapters, I frequently compare the bison data to the results of published studies of cattle or other wildlife data with the expectation that the patterns seen here for bison might be clarified by studies of larger sample size. This requires that the data are similarly organized. A primary unit of measure in many research projects studying domestic livestock is the standard dressed carcass weight which is the weight of the skinned, eviscerated carcass, excluding the head, tail, and distal limbs (metapodials and below). The anthropological study of carcass composition, on the other hand, requires consideration of the complete carcass. Where necessary, both sets of data are presented.

Influence of Age, Sex, and Condition on Carcass Composition

Before separately considering the variability of bone, meat, and fat present in the bison carcasses studied, it is important to briefly consider how these components shift with age in the proportion they represent of total carcass weight. Cattle serve as a model of this pattern of change. Berg and Butterfield (1976:22-23) indicate that with increasing cattle liveweight, the weight of all three carcass components rise, but at

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different rates. With increasing carcass weight, therefore, the proportion each component contributes to the total carcass weight changes. In young animals, fat is a relatively minor component of carcass weight, and muscle and bone make up the largest percentages. The faster rate of postnatal development of muscle over bone, however, leads to the gradual decrease in the proportion of the carcass that is bone. At a later age, the relationship between muscle and fat in cattle changes when an animal enters the fattening stage, and the major impetus for growth shifts from muscle to fat. At this stage, the proportion of the carcass that is fat increases to different degrees, depending upon genetics, sex, and feeding regimes. Berg and Butterfield's (1976) study of cattle indicates that variability in carcass composition should be expected in animals of different ages and outlines the direction of these changes.

Berg and Butterfield (1976) also indicate that differences in composition may be associated with differences in animal sex and condition. They found marked differences in fattening and minor differences in the distribution of muscle weight between males and females, noting that females are usually fatter than males (measured at the same weight or age), and that the hindquarters are proportionately heavier in females, whereas the forequarters are heavier in males. Changes in animal condition are evident in differences in composition as well. A loss of liveweight, due to below-maintenance energy consumption, primarily results in fat loss, although weight loss in other components also occurs. A change in composition should be more readily seen in males than females because of the smaller reserves of energy stored as fat in males. The effect of a decline in liveweight, with its greater decrease in the fat component in all animals results in an increase in the proportion of the total carcass weight that is muscle and

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bone. Depending upon the severity of the weight loss and the extent that it includes other body tissues in addition to fat, this change in component proportions may differ for males and females. Berg and Butterfield's work clearly indicates that variability is evident in the carcass composition of cattle, and is affected by age, sex, and animal condition. Their work also suggests that examination of this subject in bison may be profitable for studies of the prehistoric and historic use of bison. In the remainder of this chapter, I focus on the variability found in bone, bone marrow, and bone grease in the Theodore Roosevelt National Park bison.

Bison Bone, Marrow, and Grease Production and Distribution

When the animal carcass is considered as a source of food products, the importance of bone lies in the fact that it is a vehicle for what archaeologists refer to as bone marrow and bone grease. Prehistorically and historically, marrow from the medullary cavities of bone was extracted by breaking the bone and removing the marrow. Bone grease from the cancellous tissue of bone, is not as easily collected. It was extracted by boiling broken pieces of bone in water and collecting the fat as it separated and rose to the surface. These products are often directly correlated with fat in the minds of archaeologists, but the amount of fat present varies. Marrow and bone grease are mixtures of fat, water, and other tissue. It is important that marrow and grease as recovered from bone, are distinguished from marrow fat and bone grease fat. The need for this distinction lies in the fact that there is not always a one to one correlation between fat weight and marrow or bone grease weight, and it is the fat component which provides the major source of food energy in these products. In the following discussions some consideration is given to the amount of material

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recovered (marrow and bone grease), but the primary consideration here is to examine variability in the fat production of these products in bison of different age, sex, and condition.

Bone generally is all that remains of the bison carcass for archaeologists to make inferences about the availability of marrow, bone grease, and other carcass products. Animal age and sex are two characteristics that can be determined for archaeological bone with varying degrees of detail. Animal condition is difficult to assess from bone. However, because all three of these characteristics provide important influences upon the amount of fat resources available to prehistoric hunters, the relationship between these factors must be considered. Where animal age and sex may be determined, these data can provide the baseline estimates of marrow and bone grease fat availability. These fat estimates might be further refined by consideration of the effects that changing animal condition has on their availability. It is my goal to define in Chapters 5, 6 and 7, the variability in resource availability, and provide some expectations of how changing condition influences that availability in bison of different age and sex. It is a task that can be fulfilled only in part, given the small size of the bison sample.

Before considering variability in the production and distribution of marrow, bone grease, and their fat components, some consideration needs to be given to (1) whether understanding the physiological function of these products provides any clue to expected variabilities in quantity between classes of animals, and (2) whether the quantity of these products is correlated with characteristics of bone that archaeologists might measure.

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Classification and Function of Bone Marrow

The products that archaeologists refer to as marrow and bone grease are studied as a single product by physiologists and referred to collectively as bone marrow. Table 5.1 lists the product names as used by these two groups of researchers. Archaeologists and physiologists differ somewhat in their sub-classifications of these products as well. Binford (1978) uses color designators as indicators of quality (distinguishing between white and yellow bone grease), whereas physiologists (e.g., Tavassoli and Yoffey 1983) use color designators as indicators of structure and function (distinguishing between red and yellow marrow). Note should be made that the yellow color designator is used by both groups, but in reference to different subcategories of fat. Careful attention, therefore, must be given to whether archaeological or physiological classes are referenced.

Examination of these classifications illustrates that despite the differences of these two schemes, there is one underlying characteristic which is expressed similarly--differences in fatty acid composition. This similarity leads to roughly comparable, though not identical, divisions in the archaeologists' bone grease (between white and yellow grease) and the physiologists' red and yellow marrow. The fact that physiologists do not divide the subclass of yellow marrow into divisions comparable to the archaeologists' bone marrow and white bone grease may be due to their focused interests on red marrow. There are no detailed studies of yellow marrow that distinguish appendicular marrow found in cancellous tissue from that found in medullary cavities. In the following discussion, I examine the physiological and archaeological classifications of these bone products, consider possible composition differences between marrow and grease fat, and identify where functional differences in bone grease and bone marrow may

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Table 5.1. Classifications of Bone Products

Fat Origin	Archaeological[a] Classification		Physiological[b] Classification	
	Major Division	Minor Division	Major Division	Minor Division
Medullary Cavities of the Limbs	Bone Marrow	---	Bone Marrow	Yellow Marrow (except in the young[c])
Cancellous Bone of the Limbs	Bone Grease	White Grease	Bone Marrow	Yellow Marrow (except in the young[c])
Cancellous Bone of the Tail	Bone Grease	Yellow Grease	Bone Marrow	Yellow Marrow
Cancellous Bone of the Axial Skeleton (excluding Tail)	Bone Grease	Yellow Grease	Bone Marrow	Red Marrow

[a] Source: Binford (1978)
[b] Source: Tavassoli and Yoffey (1983)
[c] In young animals this may be red marrow.

lead to variability in fat availability in animals of different age and sex classes.

Physiological Classification and Variability in Fat Production

Tavassoli and Yoffey (1983) provide an extensive summary of studies of the structure and function of bone marrow in man and animals. Their work is the source for much of what is presented below.

Red and Yellow Marrow. Bone marrow is found in the medullary cavities of the limb bones, in the cancellous bone of these and the axial elements. Physiologists distinguish between yellow and red marrow, noting differences in their function and structure. Yellow marrow is composed primarily of fat, and in adults is found in the medullary cavities and cancellous tissue of the limb elements. The fat in yellow marrow provides a relatively protected source of energy that normally is not used until after mobilization of other fat sources has been initiated. Red marrow contains some fat, but differs from yellow marrow in its function, its location, the amount of fat present, and the stability of the fat associated with it. Red marrow is hemopoietic tissue--that is, its function is to produce blood cells and platelets. In newborn animals, red marrow is found in some of the bones of the appendicular skeleton as well as in the axial skeleton. As the animal matures, red marrow sites become focused in the axial skeleton and that in the limbs is largely converted to yellow marrow (Tavassoli and Yoffey 1983:111). As in other aspects of growth, the conversion from red to yellow marrow in the limbs of maturing animals begins distally and extends proximally. Once red marrow sites have been converted to yellow marrow, they seldom participate in blood formation, even under conditions of in-creased hemopoietic demands (Tavassoli et al. 1977). This is discussed below.

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Red marrow volume is determined by animal age, size, and conditions that affect blood requirements. A much higher percent of total marrow volume is red in fetal, neonatal, and young animals, and possibly in species of small body size. Tavassoli and Yoffey (1983:122) suggest that studies of red marrow volume differences between large and small bodied animals may be misleading. They argue that age differences in test animals probably had more influence on red marrow volume than animal size.

The point here, that is important to hunters and to archaeologists is that animals with high proportions of red marrow have correspondingly low proportions of yellow marrow. Red marrow is not without fat, however. It has a hemopoietic tissue fraction and a fat fraction. The fat fraction in red marrow serves as a cushion of space available for use during periods when expanded hemopoiesis is necessary. Fatty, or yellow marrow has also been considered reserve space for red marrow expansion--a hypothesis disputed by Tavassoli and Yoffey (1983:122-123) and which is discussed in the next section.

Red marrow volume also may be affected by animal sex. Differences between males and females in the production of red blood cells may correspond to differences in the proportion of red marrow that is fat. Krantz and Jacobson (1970:157-158) discuss the effects of the hormones androgen and estrogen on erythropoiesis (the production of red blood cells), noting that experiments with varying levels of these hormones produced different results in red cell production. They conclude that androgens increase erythropoiesis while estrogens decrease it, and suggest that this may explain the normally higher red cell counts in males than in females. Although no discussion was found of the relationship of this factor to the volume of red marrow and its fat component, these data suggest that a sex

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difference may exist in the relative volume of red marrow, and thus, in the proportion of red marrow that is fat. If the introduction of androgen results in the expansion of hemopoietic activity and an increase in red marrow volume, this might occur at the expense of red marrow fat volume. This assumes that the proportional increase in male to female bone size and the associated increase in hemopoietic tissue volume is not large enough to compensate for this difference and red marrow volume is increased at a greater proportion. Under these conditions, the proportion of red marrow fat to total marrow fat might be smaller in males than in females. Depending on the absolute difference in red marrow volume, it is possible that proportionately less fat might be renderable from the red marrow bones of fully mature males than from females.

Fat Mobilization and Hemopoietic Need. Physiologists have spent little effort on the study of yellow marrow, except as it relates to the replacement of red marrow with growth, and to differences in fat stability which results in the resistence of yellow marrow fat to mobilization in response to increased hemopoietic need. The yellow marrow fraction of total marrow, as noted, is mostly fat, but this fat differs in character from that found in red marrow. Tavassoli et al. (1977) suggest that the fat associated with yellow marrow is relatively stable compared to the fat of red marrow which is readily mobile. (Fat may be mobilized to allow for the expansion of hemopoietic tissue or to provide a source of energy under conditions of nutritional stress. The result of mobilization, in either circumstance, is a loss of fat weight.) The difference between red and yellow marrow fat, they argue, is probably attributable to differences in fatty acid composition, as well as to differences in the temperature of the bone sites in which they are found.

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Yellow marrow contains higher percentages of palmitoleic and myristoleic fatty acids, both of which are mono-unsaturated fatty acids with low melting points. Yellow marrow is found primarily in cooler temperature bones peripheral to the body, including the limbs and tail. In red marrow, the proportions of the saturated form of these fatty acids (palmitic and myristic acids) are larger. Saturated fats have higher melting points, making their predominance at the body core understandable.

The differences in red and yellow marrow fat mobility result in major differences in their response to changes in external temperature stimuli, animal condition, and to changes in the need for hemopoietic activity. Red marrow fat is readily mobilized to allow expansion of hemopoietic tissue and the fat associated with this tissue behaves similarly to fat found outside of bone in the animal carcass, mobilizing during periods of nutritional stress. Yellow marrow fat (at least the fraction found in the medullary cavities of bone) resists mobilization and is usually the last fat reserve of the body to be depleted under conditions of nutritional stress (Harris 1945).

Tavassoli and Yoffey (1983:122-123) argue that site temperature is as important to fat mobility characteristics as fatty acid composition. If hemopoietic activity is stimulated artificially, marrow fat is not mobilized to allow the expansion of hemopoietic tissue unless the site temperature is comparable to that found for sites in the axial skeleton. Under laboratory conditions, fat from either red or yellow marrow may be mobilized and hemopoiesis expanded. For yellow marrow fat to mobilize in response to hemopoietic activity, however, the site temperature must be raised from its normally cooler level. Temperature change alone, however, does not result in an increase in red marrow volume. Both conditions, increased hemopoietic

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need and appropriate site temperature, are required to allow expansion of red marrow volume (accompanied by decrease in red or yellow marrow fat). Under normal field conditions, therefore, one would not expect yellow marrow fat to mobilize in response to increases in hemopoietic activity. The change in marrow fat volume associated with increases in hemopoietic activity normally is limited to red marrow sites.

The greater recorded stability of yellow marrow fat (resulting in part, from slower rates of mobilization) helps to explain the observation that marrow found in the medullary cavities of bone frequently shows little change in fat content, unless poor nutrition conditions are persistent and severe. Given this assessment, one might expect to see less variability in marrow fat weight (from the medullary cavities) than in other sources of fat, including the other carcass fat depots, as well as bone grease fat from the axial skeleton.

Archaeological Classification of Marrow and Bone Grease

Binford's (1978) classification of bone marrow and bone grease (Table 5.1) reflects some of the same functional differences noted by the physiologists. It was constructed, however, to account for differences in how marrow and bone grease are evaluated, collected, and used by Nunamiut hunters. The primary division in the archaeological classification of the fat found in bone is between fat found in the medullary cavities of bone, called bone marrow (here referred to as medullary marrow to avoid confusion) and the fat found in the cancellous tissue of bone, called bone grease. This division is based upon differences in the recovery methods used to process these fat products.

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Quality differences are noted by Binford for both medullary marrow and bone grease. In the case of the former, this does not result in subclassification, but in the case of bone grease, it results in division of bone grease into yellow and white categories (Table 5.1). Binford suggests that differences in the fat quality in both marrow and bone grease greatly influence how they are used, and that the quality differences are governed, in large part, by differences in the fatty acid composition as they affect the melting points of these fats. His analyses focus upon differences in the prevalence of one of the most abundant fatty acids in these products: oleic acid, a low melting point fat. He notes that highly valued medullary marrow and grease have higher proportions of this mono-unsaturated fatty acid and assigns these fats higher quality values. Apparently, the factor which influences fat softness is highly correlated with the factor that affects the distribution of red and yellow marrow, and the stability of the fat in these products.

Binford also comments on the importance of marrow and grease quantity and efficiency of recovery, indicating that hunter preference is governed by the interaction of quantity, quality, and extraction characteristics. Bones producing small amounts of high quality fat may not be as highly valued as bones producing larger amounts of slightly lower quality fat, especially if it is difficult to extract. At some point, however, quality differences override differences in quantity. Given that quantity is often important, it would be beneficial to understand what factors influence its stability. Obviously, any factors resulting in differences in the resistance of fat to mobilization become important. Furthermore, archaeological indices of carcass utility must be constructed that recognize the potential importance of fat quantity fluctuations. Although Jones and Metcalfe (1988) argue that

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marrow indices based on estimates of quantity, rather than a mixture of quality and quantity, provide better predictions of carcass use, physiological studies of red and yellow marrow fat composition suggest that this might not be true for bone grease fat or for medullary cavity marrow fat, when animals are in poor condition. Unlike bone marrow from medullary cavities, in which the fat content is generally closely related to the marrow volume itself (due to the resistance of this fat to mobilization), red marrow (bone grease from the axial skeleton) is as mobile as the fat found outside bone in the carcass depots (Tavassoli and Yoffey 1983). Fatty acid composition, therefore, may play a more important function in the evaluation of fats that are more mobile and thus, subject to greater fluctuations in quantity.

Factors affecting fat mobility and thus quantity, need to be evaluated in addition to factors which affect fat softness (fat quality). In each case, fatty acid composition is important in determining these characteristics. The fatty acids that Tavassoli et al. (1977) suggest are responsible for greater fat stability are in the same class (mono-unsaturated) as the fatty acid that Binford (1978) uses to denote quality differences. The divisions in quality that Binford denotes for bone grease (between white and yellow classes) apparently are related to functional differences in marrow types.

Fat Mobility and Fatty Acid Composition

The bison sample used here is too small to adequately determine whether yellow marrow in the appendicular skeleton may be divided into marrow and grease categories based on more than differences in the recovery processes. However, differences in the extent of variability between the two female

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bison (one of which is in better condition than the other) for the marrow and white grease fat weights suggest that differences in fat mobility might exist. The weights for medullary marrow fat and white bone grease fat were compared by elements (proximal and distal portions, where appropriate) for SAF and FAF (Table 5.2). Figure 5.1 illustrates differences in the degree of variability between animals and fat types, and suggests there may be variability in the mobility of the fat from these two marrow sources, with white grease fat having greater mobility than medullary cavity marrow fat.

Paired-comparison t-tests (Thomas 1976) were run for the medullary marrow and for the white bone grease values of the bone elements (proximal and distal ends) of SAF and FAF. The older female, FAF, was in poorer condition than the younger female, SAF, when killed. If there is a difference in the mobility of medullary marrow fat when compared with white grease fat, with medullary marrow fat having greater stability, then (1) the mean difference in the values for SAF and FAF should differ, and (2) the mean difference for weights of medullary marrow fat should be smaller than that for white grease fat. The results of the tests show the mean difference for the medullary marrow fat weights of SAF and FAF to be 3.68 gm (standard deviation = 5.65; $p < 0.0163$) and for the white grease fat weights is 8.96 gm (standard deviation = 17.67; $p < 0.0352$). These distributions do show the expected differences in the magnitude of their means if fat mobility differs. The distributions overlap, however, and the distribution for marrow is within one standard deviation of the mean for white grease fat.

Examination of stem and leaf plots (Hartwig and Dearing 1979) for these two distributions (Figure 5.2) shows the major differences arise from outliers in the white grease fat distribution, in which the fat weights for

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Table 5.2. Comparison of Marrow and White Grease Fat Weight Differences Between Female Bison in Different Condition

Marrow Fat Weight (gm)				White Grease Fat Weight (gm)			
Unit	SAF	FAF	Difference	Unit	SAF	FAF	Difference
SCAP	2.8	0.0	2.8	SCAP	20.3	21.2	-0.9
PHUM	44.8	43.5	1.3	PHUM	83.0	86.5	-3.5
DHUM	59.4	46.8	12.6	DHUM	34.1	30.9	3.2
PRAD	51.5	38.0	13.5	PRUL	33.5	20.4	13.1
DRAD	22.2	21.2	1.0	DRUL	57.5	41.7	15.8
ULNA	12.3	9.9	2.4	CARP	10.7	3.4	7.3
PMTC	18.3	19.5	-1.2	PMTC	5.0	5.0	0.0
DMTC	4.2	4.4	-0.2	DMTC	21.2	18.0	3.2
APHA	1.2	1.9	-0.7	APHA	28.4	31.3	-2.9
PELV	3.4	5.7	-2.3	PATE	4.3	4.5	-0.2
PFEM	86.9	73.0	13.9	PFEM	66.3	50.3	16.0
DFEM	39.8	34.3	5.5	DFEM	142.0	78.6	63.4
PTIB	74.6	68.4	6.2	PTIB	76.8	26.5	50.3
DTIB	59.4	49.5	9.9	DTIB	19.5	21.1	-1.6
PMTT	22.9	21.0	1.9	PMTT	5.4	3.4	2.0
DMTT	6.6	10.0	-3.4	DMTT	27.2	21.0	6.2
PPHA	4.0	4.7	-0.7	PPHA	18.4	25.8	-7.4
				TARS	4.9	3.7	1.2
				AST	10.3	5.9	4.4
				CALC	21.7	12.1	9.6
n = 17; mean difference = 3.68;				n = 20; mean difference = 8.96			
standard deviation = 5.65				standard deviation = 17.67			

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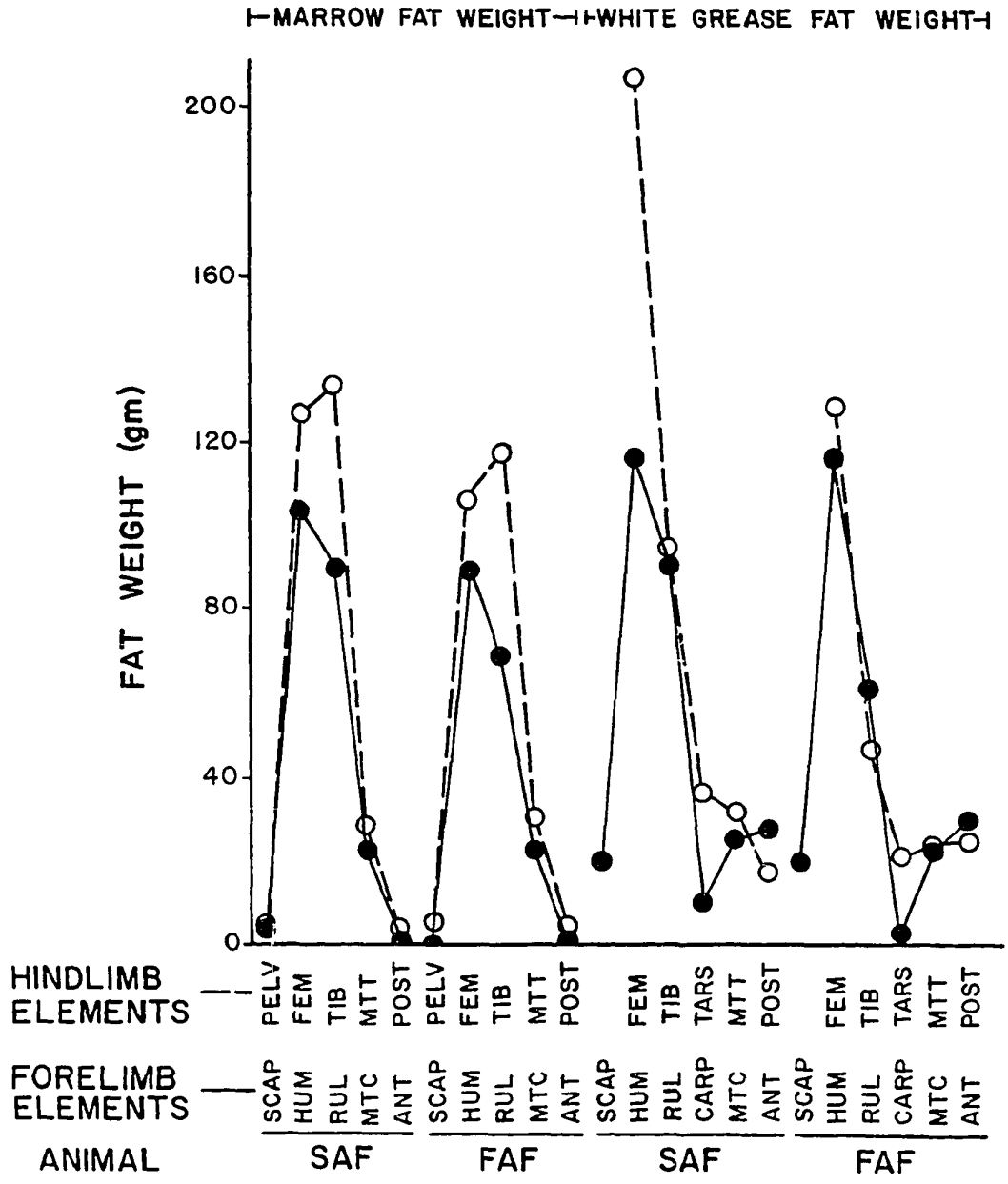

Figure 5.1. Comparison of Bone Marrow and Grease Fat Weight Differences Between Female Bison.

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Figure 5.2. Stem and Leaf Plots of the Compared Weights of the Medullary Marrow and White Grease Fats in the Females SAF and FAF

Part A. Medullary Marrow Fat Weight (gm) Differences (SAF - FAF)

Weight Differences							Unit Identification	
- 0	- 0.2	- 0.7	- 0.7	- 1.2	- 2.3	- 3.4	- 0	DMTC APHA PPHA PMTC PELV DMTT
0	1.0	1.3	1.9	2.4	2.8		0	DRAD PHUM PMTT ULNA SCAP
5	5.5	6.2	9.9				5	DFEM PTIB DTIB
10	12.6	13.5	13.9				10	DHUM PRAD PFEM

n = 17 mean = 3.68 standard deviation = 5.65

Part B. White Grease Fat Weight (gm) Differences (SAF - FAF)

Weight Differences							Unit Identification	
- 5	- 7.4						- 5	PPHA
- 0	- 0.2	- 0.9	- 1.6	- 2.9	- 3.5		- 0	PATE SCAP DTIB APHA PHUM
0	0.0	1.2	2.0	3.2	3.2	4.4	0	PMTC TARS PMTT DMTC DHUM AST
5	6.2	7.3	9.6				5	DMTT CARP CALC
10	13.1						10	PRUL
15	15.8	16.0					15	DRUL PFEM
20							20	
25							25	
30							30	
35							35	
40							40	
45							45	
50	50.3						50	PTIB
55							55	
60	63.4						60	

n = 20 mean = 8.96 standard deviation = 17.67

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SAF were much larger than for FAF. Otherwise, the distributions both show their modes focusing around zero. Though perhaps not significant, the differences for medullary marrow fat are most frequent in the 0 to -5 range, while those for white grease fat are from 0 to +5. The fact that there are no major outliers for the medullary marrow data and there are fewer major differences in fat weight here than in white bone grease, suggests medullary marrow fat is less mobile. The statistical differences noted here in the distributions of marrow and bone grease fat weight differences between the two females, however, are small. It remains to be clearly demonstrated that white grease fat mobilizes prior to marrow fat. However, it is my opinion that some of the data above suggest that such a difference may exist and it should be investigated in future research to clarify the the relationship between fat availability, classification, and use.

As previously noted, Tavassoli et al. (1977) attributed some differences in fat stability and mobility to differences in the temperatures of the sites from which the marrow was recovered. This does not appear to be an important factor in the differences noted between medullary marrow and white bone grease fat weight differences. This explanation for the observed differences in fat weights may be dismissed because the grease sites are adjacent to the marrow sites, so any temperature differences should be minor, if they occur at all. Given the work of Tavassoli et al. (1977), difference in fatty acid composition is a likely factor controlling differences in fat mobility between marrow from the medullary cavities and cancellous tissue of appendicular bone.

Consideration of fatty acid composition and its effect on fat stability and mobility was discussed for red versus yellow marrow by Tavassoli et al. (1977). The fatty acids they focused on in their comparison of red and

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yellow marrow fat are myristic and palmitic acids, with some discussion of the more abundant stearic and oleic acids. As noted above, differences were found in the porportions of all of these fatty acids in red versus yellow marrow, with marrow that has larger proportions of the unsaturated fats (myristic and palmitic acids) being more stable.

Their site comparisons of oleic acid were somewhat ambiguous. In whole tissue assessments, no significant differences were found between the oleic acid proportions in red and yellow marrow, but in assessments of the fat cells, significant differences were found with higher percentages present in the more stable appendicular elements. This correlates with what Binford (1978) found for oleic acid grease values in sheep and caribou appendicular and axial cancellous bone samples. Appendicular fats had higher proportions of oleic acid than axial element fats. Tavassoli et al. (1977), however, concluded that the proportions of the less abundant palmitic and myristic acids may influence stability more than the abundance of the oleic and stearic acids, based on the whole tissue assessment in rabbits.

Assuming that the data presented above, of grease and medullary marrow differences in the two female bison, do reflect differences in fat stability, then the influence of oleic acid might be assessed by comparing these values in the marrow and grease of Binford's (1978) caribou. The percent of oleic acid in medullary marrow and bone grease for the appendicular skeleton (Table 5.3, Figure 5.3) in caribou (Binford 1978) shows a significant linear relationship ($p < 0.0001$) with a high coefficient of determination ($R^2 = 0.9792$). A t-test of the hypothesis that the parameters equal zero showed the slope, but not the y-intercept, to be significantly different from zero ($p < 0.0001$). The estimate of the slope of the regression line is 1.06. If bone grease fat is less stable than

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Table 5.3. Percent Oleic Acid in Caribou Marrow and Bone Grease

Anatomical Unit	Percent Oleic Acid[a]	
	Bone Marrow	Bone Grease
mandible	24.5	26.0
pelvis	34.0	37.0
scapula	32.0	33.0
proximal humerus	43.0	40.0
distal humerus	42.0	40.0
proximal radius	52.0	48.0
distal radius	64.0	67.0
proximal metacarpal	70.0	73.0
distal metacarpal	73.0	78.0
proximal femur	42.0	44.0
distal femur	51.0	53.0
proximal tibia	46.0	54.0
distal tibia	67.0	71.0
calcaneus	66.0	70.0
proximal metatarsal	66.0	71.0
distal metatarsal	73.0	76.0
first phalanges	73.0	76.0
second phalanges	75.0	78.0

[a] Source: Binford (1978:24, 33)

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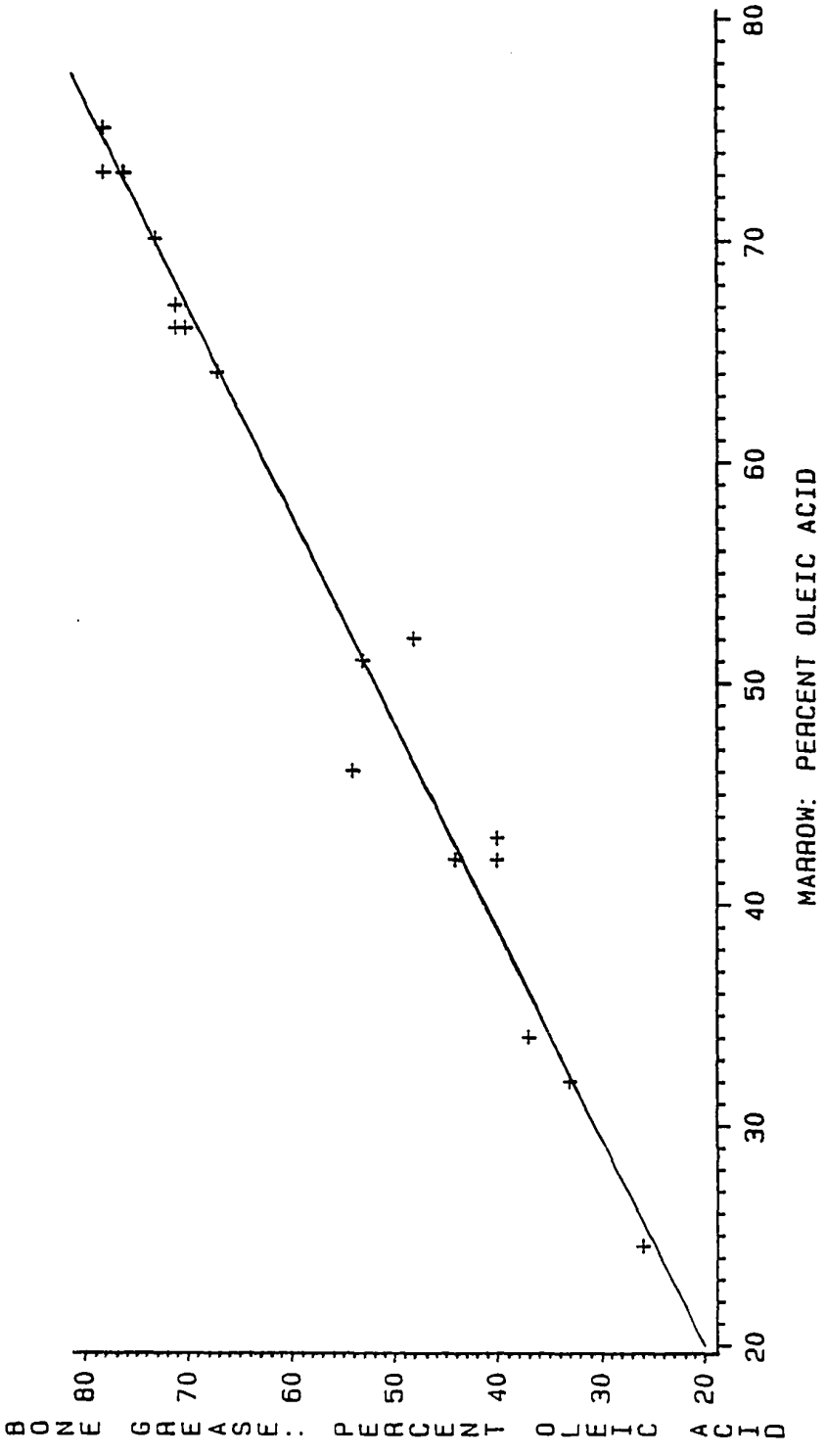

Figure 5.3. Regression of Oleic Acid Percentages from Caribou Marrow and Bone Grease Fat Showing Similar Fatty Acid Content. (Source: Binford 1978)

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marrow fat, and if the abundance of oleic acid influences this stability, one would not expect the relationship between the values of oleic acid for grease fat and marrow fat to be best represented by a line with a slope of one and an intercept not significantly different from zero. This regression suggests instead, that the percent oleic acid for one type of fat may be used interchangeably for the other. If this is true, then oleic acid differences may not be influential in producing the observed differences in marrow fat stability.

A paired t-test of the oleic acid data for caribou bone grease and medullary marrow (Binford 1978) adds further doubt to the possibility that differences in the abundance of this fatty acid could account for differences in fat stability. In the study by Tavassoli et al. (1977), when a significant difference was found in the percent oleic acid, the relationship indicated that more oleic acid was associated with the more stable marrow fat. If oleic acid influences stability, then one would expect more oleic acid in the fat of medullary marrow than in that of bone grease. The paired comparisons t-test tests the hypothesis that the mean difference between grease and medullary marrow values is equal to zero. Although the regression above indicates a nearly perfect correlation, a slope of one and a intercept of zero, the paired comparisons t-test indicates a significant difference ($p < 0.0011$) between the mean difference and zero. Marrow and grease oleic acid values are not quite the same, although the best fit least squares line is one where these values are the same. Furthermore, inspection of the values of the percent oleic acid for each element (Table 5.3) shows the larger oleic acid proportions are found in the bone grease samples, rather than in the medullary marrow, as would be expected if this fatty acid were influencing stability.

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Given these data, it is doubtful that oleic acid extends much influence over the stability of marrow and grease fats. Tavassoli et al. (1977) conclude that fatty acid composition is closely related to fat mobility in red and yellow marrow, and suggest that myristic and palmitic acids are more important than oleic acid in controlling this fat characteristic.

The lack of influence of oleic and stearic acids on fat stability is clarified by further reference to their work and to the work of zoologists studying differences in animal condition as reflected by marrow fat content. The order of fat mobilization in red versus yellow marrow in rabbits and the order of fat depletion within major marrow bones in caribou and impala indicate the probable order of fat mobility. Based on these data it appears that, under stress, red marrow fat mobilizes prior to yellow marrow fat (Tavassoli et al. 1977). Comparing yellow marrow fat from the medullary cavities, the fat from proximal elements tends to mobilize prior to the fat from the distal elements (Reich 1981:416, Davis 1987:365) although in individual animals the order of depletion may vary for the intermediate and more distal bones. Reich (1981:418) also indicates that in the impala he studied, fat tended to mobilize in the hindlimb at a faster rate than in the forelimb. The proximal to distal order of mobilization may be compared with the data Tavassoli et al. (1977:50-51) present on the fatty acid composition of rabbit vertebrae, femora, and os calcis (calcanei) marrow in order to identify which fatty acids complement the mobility pattern. One might expect that for a fatty acid to be influential in the mobility of fat, the proportion it represents of the total fatty acids (moving from central to peripheral sites, and therefore, from highly mobile to less mobile sites) must increase or decrease in order, but not change directions so that the intermediate site has the highest or lowest proportion of that fatty acid.

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Table 5.4 and Figure 5.4 present these data from Tavassoli et al. (1977), including the mean fatty acid values and their standard deviations. The values for stearic and oleic acids do not progress in a linear direction comparable to that found for fat mobility and might, therefore, be tentatively dismissed as influential fatty acids for fat mobility in rabbits. The other fatty acids studied (including palmitic, palmitoleic, myristic, and myristoleic acids) all show linear progressions in the percent they represent of total fatty acids, and as Tavassoli et al. (1977) suggest, may influence fat mobility. In their analysis, mobile fat has higher proportions of the saturated forms of the fatty acids (i.e., myristic and palmitic acids), whereas less mobile fat has higher proportions of the mono-unsaturated forms of the fatty acids (i.e., myristoleic and palmitoleic acids). Based upon their rabbit data, it does not appear that oleic acid values are useful in assessing fat stability.

In Binford's caribou, however, the correlation between fat mobility and oleic acid composition was consistent, with high fatty acid values correlated with sites of low mobility (Table 5.3). Does this indicate that oleic acid is important to fat stability in caribou, but not in rabbits? I think not. Rather, it appears that in this case, comparing red versus yellow sites, the correlation was positive, whereas in rabbits, it was not. When oleic acid values are compared between more mobile grease and less mobile medullary marrow for the same bone (Table 5.3), the relationship did not hold up, indicating either that the correlation is not indicative of cause, and other fatty acids, perhaps myristic and palmitic acids (and their mono-unsaturated derivations), are more important (as suggested by Tavassoli et al. (1977) in the comparison of red and yellow marrow), or possibly that the differences noted in fat weights for grease and marrow are a

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Table 5.4. Fatty Acid Content in Whole Red and Yellow Marrow of New Zealand White Rabbits[a]

Source	Marrow Type	Descriptive Statistic	Proportion of Total Fatty Acids					
			Myristic Acid (14:0)	Myristoleic Acid (14:1)	Palmitic Acid (16:0)	Palmitoleic Acid (16:1)	Stearic Acid (18:0)	Oleic Acid (18:1)
thoracic vertebrae	red	mean	2.2	0.4	30.1	3.4	34.9	23.4
		st. dev.	0.1	0.1	2.4	0.2	1.0	1.9
femora	yellow	mean	1.7	0.8	26.3	5.4	29.5	25.7
		st. dev.	0.3	0.7	2.0	1.0	1.1	0.9
calcanei	yellow	mean	1.5	1.2	17.6	14.4	35.1	23.2
		st. dev.	0.3	0.3	0.6	0.6	2.6	2.6

[a] Source: Tavassoli et al. (1977:50-51)

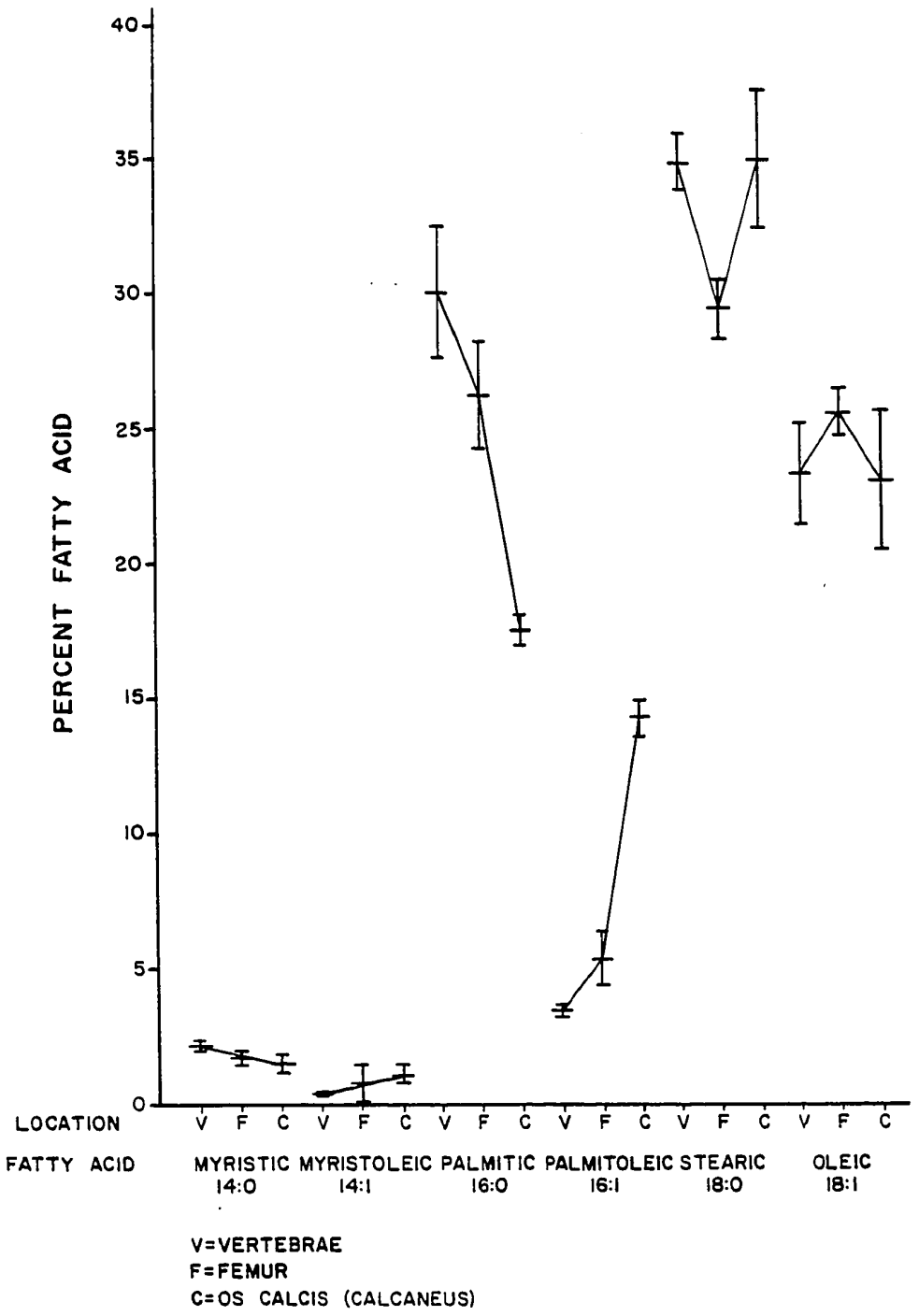

Figure 5.4. Fatty Acid Contribution in Rabbit Bone Marrow from Central to Peripheral Locations. Means ± standard deviation (Source: Tavassoli et al. 1977).

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non-respresentative case of the relationship. Obviously, additional research is needed in this area to determine which fatty acids control fat mobility and how differences in the percentages of the fatty acids present in different skeletal elements affect the character of fat in different parts of the carcass.

Implications of Functional and Structural Differences in Marrow

It is evident that variability might be expected in the fat content of the marrow and grease products of bone, and furthermore, that these differences may indicate a need to consider these products as separate resources (in terms of expectations of their variability, though perhaps not always in terms of their selection for use). These descriptions of bone marrow suggest that: (1) higher fat levels should be found in the red bone marrow of mature than immature animals, because more of the space available for marrow is devoted to hemopoietic activity allowing less space for the storage of fat in immature animals; (2) mature males may have lower fat levels than mature females in red marrow because, based on human physiology, males have higher erythropoeitic activity than females under the influence of male hormones (c.f., Letsky in Forbes 1987:200), except during pregnancy when red marrow hemopoietic activity increases to take care of increased blood plasma and red cell mass needs, thus suggesting fat levels in pregnant cows may be lower than in barren cows, and possibly, though not necessarily, than in adult bulls; (3) if an animal is not fully mature, and conversion of appendicular red marrow to yellow has not been completed, fat levels should be lowest in the elements closest to the body because of the distal to proximal progression of marrow conversion within individual bones; (4) the extramedullary marrow fat of appendicular elements (physiologically yellow

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marrow) is more stable than that of the axial units (physiologically red marrow), and therefore, should show less variability between animals of similar maturity, but different condition, than those of the axial skeleton; (5) if there are differences in fat stability between yellow marrow locations (marrow versus grease), then marrow fat may be more stable than bone grease fat; (6) if bone grease and marrow fat levels and stability in appendicular elements vary, they should not be affected by temperature, but probably by differences in fatty acid composition; and (7) medullary cavity bone marrow fat levels should be higher in mature animals than in young animals that still have some of this marrow volume devoted to hemopoietic activity (although the age at which the change from red to yellow marrow in the appendicular skeleton of bison is not known).

Relationship Between Bone Characteristics and Fat

The material that archaeologists have to work with to estimate the amount of food resources recoverable from prehistoric bison kills is the remains of bone left at kill sites, transported to processing sites, or returned to camps or villages. If there is no correlation between bone characteristics and the quantity of the food products available, then the statements archaeologists can make about the available products based on the composition of the bone assemblage are severely limited. In this section, I examine through regression analyses, whether bone measurements may be shown singularly, or in combination, to correlate with quantities of bone grease or medullary marrow fat weights.

In these regression tests, the relationship being tested is between a measure of fat weight recoverable from a bone (medullary marrow fat weight or bone grease fat weight) and some measurable bone characteristic such as

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medullary cavity volume, dry bone weight, bone volume, or density. The sample sizes are relatively large because bones are the focus of measurement rather than individual animals. In the regressions of bone grease fat weight on bone measurements, analyses were first run on all bones, and subsequently in separated groups including axial and appendicular units to represent red versus yellow marrow fats. The results of the medullary marrow regression analyses are presented first, followed by the results of the bone grease fat analyses.

Relationship Between Marrow Cavity Volume, and Medullary Marrow and Fat

Table 5.5 presents the results of the regression analyses comparing medullary cavity volume to the total weight of the marrow and to the weight of just the marrow fat. For each set of data, measurements from all bones of all animals (Figures 5.5 and 5.6), and then from individual animals were compared. In all tests, the relationships between medullary cavity volume and the total marrow and marrow fat weights are significant ($p < 0.0001$), and the coefficients of determination (R^2), measuring the goodness of fit of the regression equations, are all very high indicating that, in this sample, both marrow weight and marrow fat weight may be predicted with a high rate of success using the volume of the medullary marrow cavity. The parameter estimates for the y-intercepts are not significantly different from zero, and the estimates for the slopes are smaller for the marrow fat weight data than for the total marrow weight data. This means that the regression lines for marrow weight are steeper than those for marrow fat weight, and indicates that it takes a larger cavity volume to produce the same weight of marrow fat as marrow.

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Table 5.5. Regressions of Marrow Weight and Marrow Fat Weight on Marrow Cavity Volume

Marrow Sample Weight	Marrow Fat Weight	All Animals	By Animal	Prob > F	R^2	Parameter Estimates	
						Intercept	Slope
x		x		0.0001	0.9861	-0.37	0.85
x			FYM	0.0001	0.9937	-1.02	0.90
x			SAM	0.0001	0.9852	0.12	0.84
x			SAF	0.0001	0.9834	-0.49	0.82
x			FAF	0.0001	0.9908	-1.16	0.87
	x	x		0.0001	0.9711	-0.47	0.72
	x		FYM	0.0001	0.9922	-0.83	0.77
	x		SAM	0.0001	0.9649	-0.51	0.71
	x		SAF	0.0001	0.9703	-1.15	0.74
	x		FAF	0.0001	0.9844	-0.52	0.69

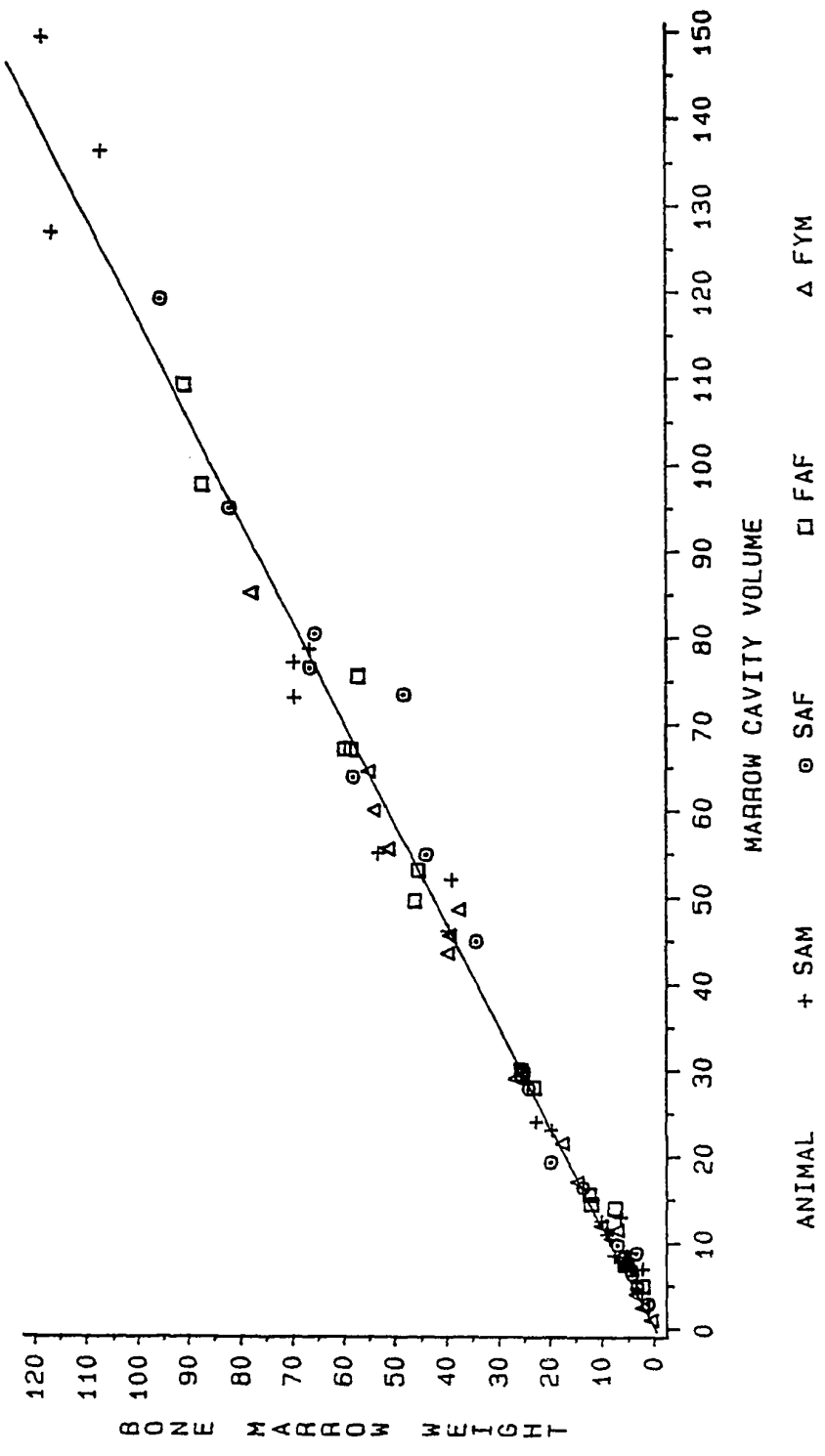

Figure 5.5. Regression of Marrow Weight on Marrow Cavity Volume without Differentiation by Animal or Bone Location. Corresponds to first regression reported in Table 5.5.

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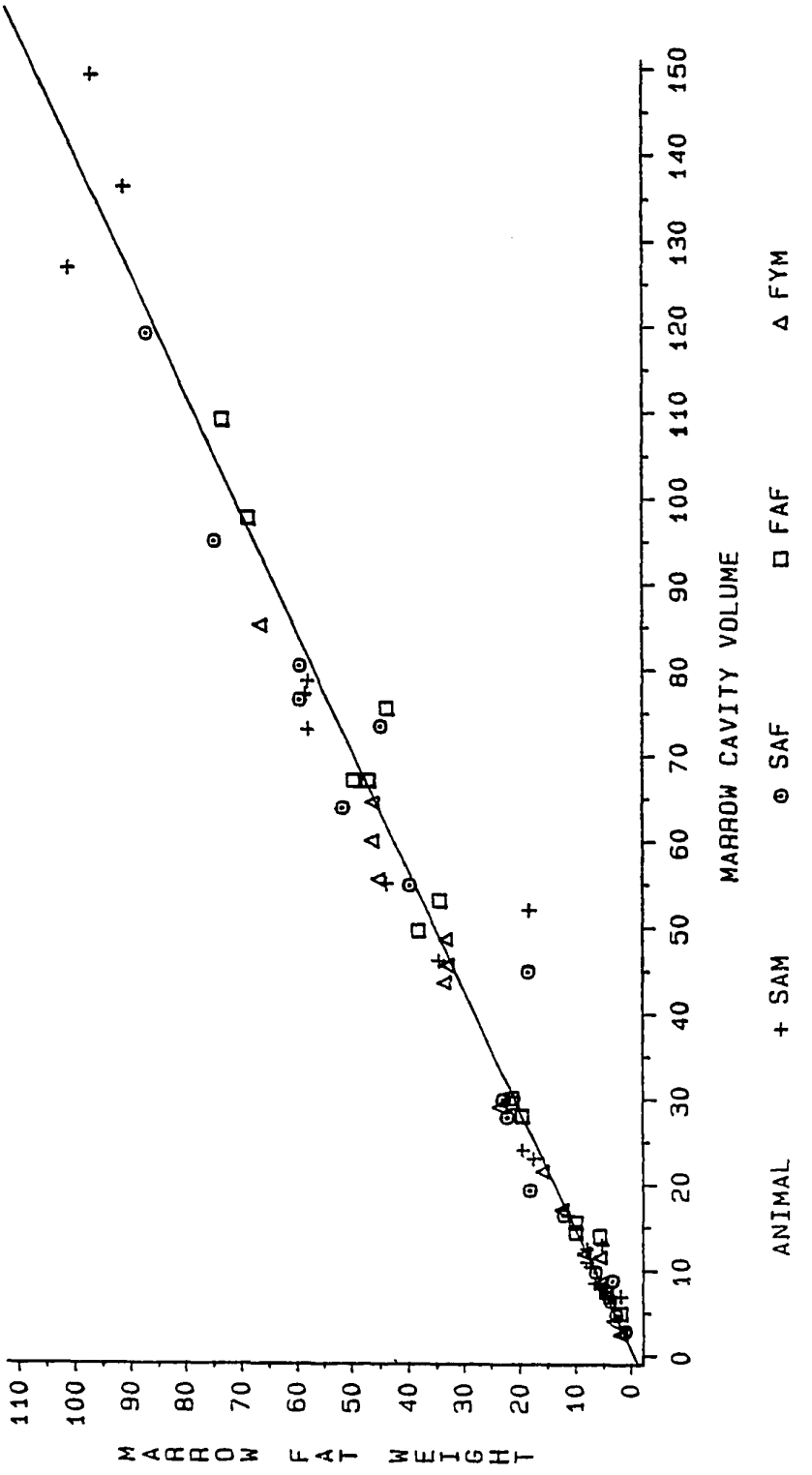

Figure 5.6. Regression of Marrow Fat Weight on Marrow Cavity Volume without Differentiation by Animal or Bone Location. Corresponds to sixth regression reported in Table 5.5.

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Comparison of the regression equations for the total marrow weights compared with the marrow fat weights illustrate that although both may be predicted using medullary cavity volume, the weight of the former is more accurately predicted than that of marrow fat weight, based upon the coefficients of determination (R^2). This is true for the combined animal data, and for the paired regressions by animal. In each case the difference in the coefficients of determination are quite small, but the direction of better fit is always the same. One may suggest that the poor conditions for the maintenance of animal liveweight suggested by the climatic data for Theodore Roosevelt National Park (see Chapter 3 above) were not harsh enough or sustained for a long enough period of time for nutritional stress to be registered in the regression of marrow fat weights and marrow cavity volumes of these animals. For this to occur, the animals would have to respond differently to nutritional stress, so that the combined relationships provide a poorer coefficient of determination. If all animals respond similarly, the scatterplot might still show a linear relationship, but perhaps with smaller slope estimates indicating the decline in marrow fat weight associated with a given marrow cavity volume. Marrow fat weights, however, are still relatively high in these animals (see marrow production and distribution section), and one could expect that as nutritional stress is prolonged, and marrow fat is mobilized to provide energy, age and sex differences between animals in how rapidly they must respond to nutritional stress using this energy resource, should result in poorer coefficients of determination for marrow fat weight as predicted by marrow cavity volume.

In this sample of four bison of different ages, it did not substantially improve the fit of the regression line to consider the distributions by animal, rather than as a group. If age, sex, or animal

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condition had large differential effects upon the weight of marrow or marrow fat, one would expect the combined data to have poorer coefficients of determination, or possibly to not prove to be linear at all. Apparently these animals have not yet reached a stage of fat mobilization that would be registered differently in the representatives of these age and sex classes. In these animals, which may have been exposed to a period of drought, the effects of possible poor nutritional condition is not yet registered in markedly differing marrow weights or marrow fat weights between animals.

Based upon these data, it is clear that marrow cavity volume provides an easily determined and accurate estimate of marrow availability. Marrow weight is more accurately predicted than marrow fat weight, but the difference in this sample is minor. Care should be taken, however, in applying these data to other samples. It is probable that due to the substitution of water for fat during fat mobilization, the relationship between cavity volume and marrow weight will change little, but the fit may be expected to be poorer, and the slope smaller for marrow fat weight, under conditions of persistent nutritional stress.

Relationship Between Bone Grease Fat Weight and Bone Measurements

Three measures of bone (dry bone weight, bone volume, and bone density) were determined for the bones from the four Theodore Roosevelt National Park bison. Using regression analyses (Lewis-Beck 1980), these data were compared with the weight of bone grease fat determined by computation of the results of an ether extraction analysis for each sample of bone grease recovered. Bone grease fat weight is used in place of the weight of the bone grease sample itself, because the availability of fat as a food source is the question of interest. Table 5.6 presents the results of the

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Table 5.6. Regressions of Bone Grease Fat Weight (Y Variable) on Bone Measurements (X Variable)

Reference Number	Independent Variable (X)			Sample Composition				Analysis of the Regression			
				Bison Included		Bones Included					
	Bone Volume	Dry Bone Weight	Bone Density	All Four Bison	Sub-Sample	All Bones	Part of Carcass[b]	Prob > F	R^2	intercept	slope
1		x		x		x		0.0001[a]	0.2530	9.43	0.03
2	x			x		x		0.0001[a]	0.2559	9.89	0.04
3			x	x		x		0.1184	--	--	--
4		x			FYM	x		0.3036	--	--	--
5		x			SAM	x		0.0149[a]	0.1939	9.33	0.02
6		x			SAF	x		0.0032	0.2709	14.64	0.05
7		x			FAF	x		0.0001[a]	0.4461	9.55	0.04
8	x				FYM	x		0.2092	--	--	--
9	x				SAM	x		0.0039[a]	0.2607	8.47	0.02
10	x				SAF	x		0.0012[a]	0.3168	13.96	0.06
11	x				FAF	x		0.0001[a]	0.4833	9.85	0.05

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Table 5.6. (continued)

Reference Number	Sample Composition: Independent Variable (X)			Sample Composition: Bison Included		Sample Composition: Bones Included		Analysis of the Regression			
	Bone Volume	Dry Bone Weight	Bone Density	All Four Bison	Sub-Sample	All Bones	Part of Carcass[b]	Prob > F	R^2	intercept	slope
12			x		FYM	x		0.7968	--	--	--
13			x		SAM	x		0.0634	--	--	--
14			x		SAF	x		0.1794	--	--	--
15			x		FAF	x		0.0672	--	--	--
16		x		x			axial	0.0001[a]	0.4129	4.55	0.03
17		x		x			append	0.0001[a]	0.2855	2.84	0.07
18	x			x			axial	0.0001[a]	0.3991	3.51	0.03
19	x			x			append	0.0001[a]	0.4139	1.41	0.09
20			x	x			axial	0.0558	--	--	--
21			x	x			append	0.0007[a]	0.1393	68.72	-37.35

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Table 5.6. (continued)

Reference Number	Independent Variable (X)			Sample Composition				Analysis of the Regression			
				Bison Included		Bones Included					
	Bone Volume	Dry Bone Weight	Bone Density	All Four Bison	Sub-Sample	All Bones	Part of Carcass[b]	*Prob > F*	R^2	*intercept*	*slope*
22		x			FYM		axial	0.2843	--	--	--
23		x			SAM		axial	0.1854	--	--	--
24		x			SAF		axial	0.0229[a]	0.4963	7.98	0.04
25		x			FAF		axial	0.0007[a]	0.7840	3.52	0.04
26		x			FYM		append	0.0637	--	--	--
27		x			SAM		append	0.0031[a]	0.3930	-1.24	0.06
28		x			SAF		append	0.0016[a]	0.4329	-5.16	0.14
29		x			FAF		append	0.0057[a]	0.3536	3.14	0.07

Table 5.6. (continued)

Reference Number	Independent Variable (X)			Sample Composition				Analysis of the Regression			
				Bison Included		Bones Included					
	Bone Volume	Dry Bone Weight	Bone Density	All Four Bison	Sub-Sample	All Bones	Part of Carcass[b]	Prob > F	R^2	intercept	slope
30	x				FYM		axial	0.2819	--	--	--
31	x				SAM		axial	0.1418	--	--	--
32	x				SAF		axial	0.0187[a]	0.5191	5.31	0.05
33	x				FAF		axial	0.0007[a]	0.7829	1.40	0.05
34	x				FYM		append	0.0084[a]	0.3275	5.26	0.04
35	x				SAM		append	0.0001[a]	0.6345	-2.98	0.07
36	x				SAF		append	0.0001[a]	0.6802	-8.95	0.19
37	x				FAF		append	0.0001[a]	0.6057	-0.45	0.11

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Table 5.6. (continued)

Reference Number	Independent Variable (X)			Sample Composition				Analysis of the Regression			
				Bison Included		Bones Included					
	Bone Volume	Dry Bone Weight	Bone Density	All Four Bison	Sub-Sample	All Bones	Part of Carcass[b]	Prob > F	R^2	intercept	slope
38			x		FYM		axial	0.2053	--	--	--
39			x		SAM		axial	0.9534	--	--	--
40			x		SAF		axial	0.3481	--	--	--
41			x		FAF		axial	0.4931	--	--	--
42			x		FYM		append	0.0354[a]	0.2233	32.89	-19.36
43			x		SAM		append	0.0027[a]	0.4023	93.10	-59.96
44			x		SAF		append	0.0064[a]	0.3458	149.97	-92.06
45			x		FAF		append	0.0005[a]	0.4952	121.49	-70.56

[a] Significant at $p < .05$.

[b] Part of Carcass: appendicular bones (append); axial bones (axial).

regression analyses run comparing these measurements to bone grease fat weight. This table represents a series of regression analyses that measure the relationships between the bone characteristics (1) by grouped or individual animals, and (2) for all bones, or for axial and appendicular groups of bone. Each regression from this table is assigned a reference number which is used in the text of this section. Referenced analyses are from Table 5.6 unless otherwise specified. Multiple regressions were run that included two or more bone measurements as independent variables, but these were discarded due to the existence of colinearity between the bone measurements, and given the expectation that archaeologists would be reluctant to spend the time and effort needed to produce multiple measurements per bone. These multiple regression analyses are not included in Table 5.6.

Regression Analyses with Grouped Bones and Animals

The first three analyses (No. 1-3, Table 5.6) examine the relationship between bone grease fat weight and (1) dry bone weight, (2) bone volume, and (3) bone density (which is equal to weight divided by volume), when measurements for all bones (excluding skulls and mandibles) of all animals are included. Although the regression of bone density and bone grease fat weight (No. 3) failed to show a significant relationship between the variables, dry bone weight and bone volume both show signficant relationships to grease fat weight, but with very low coefficients of determination (R^2 values). When measurements are grouped in this manner, these variables explain little of the variability seen in bone grease fat weight--a relationship much different from that seen for marrow cavity volume and marrow productivity measurements.

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Regression Analyses of Individual Animal Data

Analyses No. 4-15 (Table 5.6) present the results of regressions when individual animals are studied, thus serving as representatives for animals of the same age and sex class, and in the case of the females, of animals in good and relatively poorer condition. Once again, a significant relationship was not found between bone density and bone grease fat weight for any of the bone assemblages from individual animals (No. 12-15). The regressions of dry bone weight and bone volume for the bones of the immature male, FYM (No. 4, 8) also were not significant. The results of the analyses for the other three animals reveal positive linear relationships between bone volume and dry bone weight measurements and grease fat weight (No. 5-7, 9-11). The improvement in the R^2 values over those lumping the data from all animals (No. 1-2), however, are variable with increases in this value apparently following the increase in animal age. In the male, SAM, the improvement is slight in one case (compare No. 2 and 9), and negative in the other (compare No. 1 and 5), but in the older female, FAF, the improvements are substantial, nearly doubling in the analysis of bone volume and grease fat weight (compare No. 2, 10 and 11, and No. 1, 6 and 7).

Regression Analyses with Axial-Appendicular Divisions of Bone

The next step in the analysis of the relationship between bone meaurements and bone grease fat weight was to evaluate how differences in bone grease fat classification (i.e., from axial versus appendicular units) might affect the regression results (Table 5.6). In the first set of analyses (No. 16-21), the axial and appendicular groups from all of the animals were studied. In the second set, the axial and appendicular groups were analyzed for each individual animal (No. 22-45). The results of the

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first set of data show continued significant relationships for each regression, except for that of bone density when axial skeletal elements are measured (No. 20). Interestingly, a significant relationship is shown between bone density and grease fat weight when appendicular elements are studied (No. 21), but the R^2 value is very low. Previous tests could not establish a significant relationship between this bone measurement and grease fat weight. The improvement in R^2 values for the dry bone weight and bone volume data (No. 16-19) is encouraging, but they still fall substantially below 0.50, suggesting the relationships are not particularly strong ones.

Dry Bone Weight Regression Analyses. When the bones of the individual animals are considered separately, along with differences in bone location (axial versus appendicular), the first coefficient of determination above 0.50 is seen, and the lack of significant relationships seen in earlier data begins to make sense. Looking first at regressions of dry bone weight and grease fat weight (No. 22-29, Table 5.6), one sees that neither set of regressions (axial or appendicular) is significant for the immature male, FYM, nor is the axial regression for the older, but not fully mature male, SAM. (This is discussed shortly.) Where significant linear relationships do occur, the R^2 values for the axial data are better than those for the appendicular data, and the R^2 values for the axial data for SAF and FAF (No. 24, 25) show marked improvement over previous tests where the axial-appendicular division alone was used (No. 16). In the appendicular data analyses (No. 27-29), considering the data by animal and bone division only slightly improves the fit of the regression line over that found using the axial-appendicular divisions alone (No. 17).

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Bone Volume Regression Analyses. The regressions of bone volume and grease fat weight delimiting animals and axial-appendicular units (No. 30-37, Table 5.6) again show significant linear relationships for all but the axial data of FYM and SAM. The axial data of SAF and FAF (No. 32, 33) show a better fit to the regression line (R^2) than when the axial-appendicular division alone is used (No. 18). Bone volume is roughly equivalent to dry bone weight in its ability to predict bone grease fat weight in axial bone elements, although dry weight provides slightly higher coefficients of determination. The appendicular element regressions (No. 34-37) show an improvement in the fit of the regression line to the data (R^2 values) for all but the immature animal, FYM, compared to the regression using the axial-appendicular division alone (No. 19).

Bone Density Regression Analyses. Although none of the axial regressions of bone density and grease fat weight by individual animals (No. 38-41, Table 5.6) were significant, the appendicular regressions were (No. 42-45). Including both animal and axial-appendicular divisions substantially improved the fit of the regression line to the data over that found for grease type divisions alone (No. 21). The R^2 values, however, are still quite small.

Ease of Measurement and Regression Analysis Results

The measurement of bone density is derived by dividing bone weight by volume. Given that the R^2 values for bone density and grease fat weight regressions of appendicular units by animal (No. 42-45) are not as good as those determined for the other measurements (bone volume and dry weight) individually, one should not use density to try to predict bone grease fat weight. No further discussion of this measure is presented.

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Measurement of bone volume is relatively tedious and much more time consuming than measurement of dry bone weight. One must evaluate, therefore, whether the effort of making these measurements is worthwhile given the differences in the fit of the regression lines. Comparing the axial data first (No. 24, 25, 32, and 33), it is apparent that bone volume offers no improvement over dry bone weight in predicting bone grease fat weight. Axial data therefore, are best evaluated using dry bone weight. Furthermore, division of the population into adult females and others should be done, as the regressions for data from males that were not fully mature, were not significant. Comparing the appendicular data (No. 27-29, 35-37), the R^2 values using bone volume are much higher than those using dry bone weight. Apparently, if one wants to predict bone grease fat weight in limb elements using bone measurements, bone volume offers a much better estimate of fat weight than dry bone weight. The researcher must evaluate whether the cost of determining bone volume is offset by the improvement in the R^2 values, although it is my opinion that the improvement argues for the need for this increased effort.

Implications of Regression Analyses

Several observations are suggested by these data, and in two cases these observations lead to additional analyses and conclusions.

Reassessment of Bone Divisions and Reanalysis of the Regression Results. The scatterplots of the regressions of bone volume and dry bone weight to grease fat weight (e.g., Figure 5.7) show two elements, the sacrum-first caudal vertebra unit (SAC1), and the scapula unit (SCAP), consistently behaving in opposition to the expectations of their grease fat weight, given that they are respectively, axial and appendicular units. The

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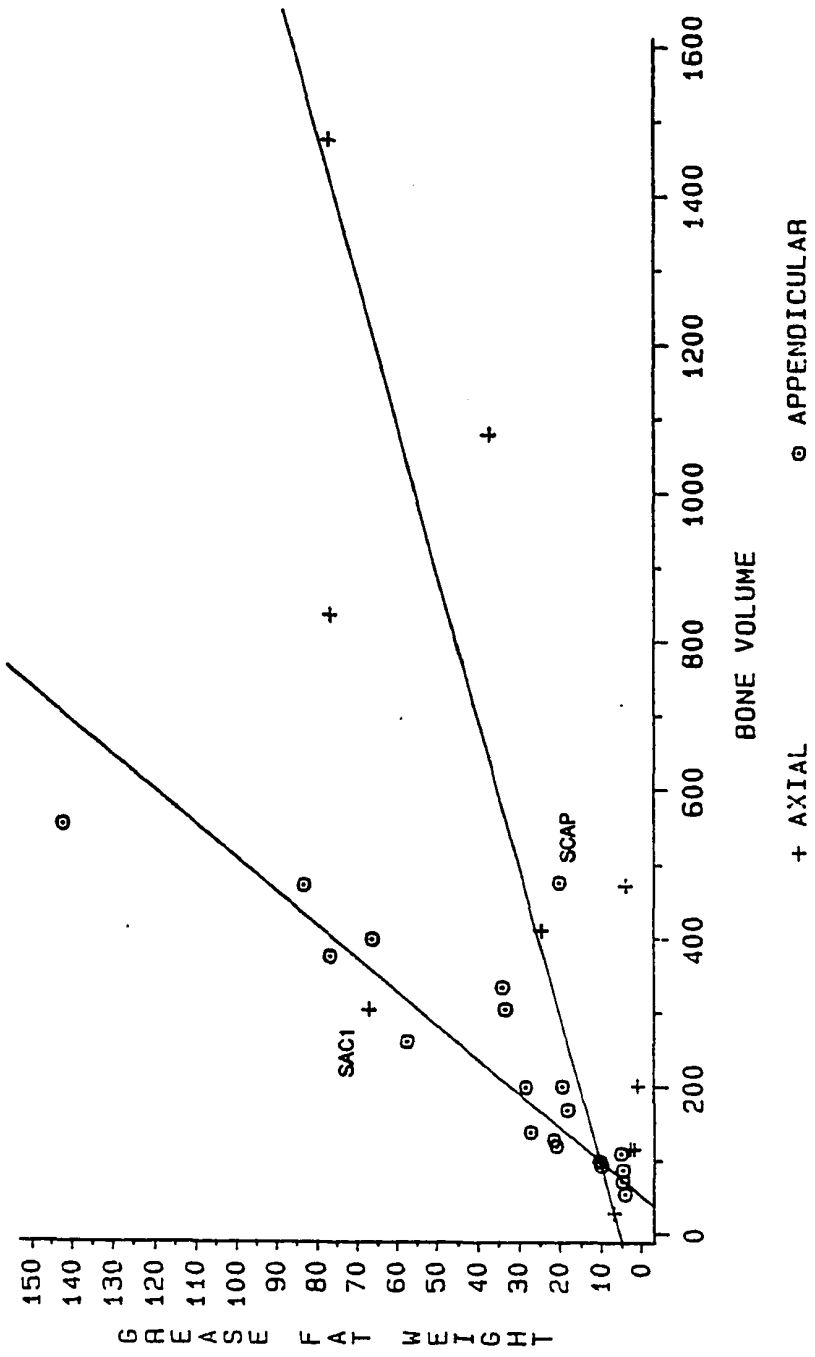

Figure 5.7. Regression of Grease Fat Weight on Bone Volume in SAF with Indication of Axial and Appendicular Location. Corresponds to regression No. 10 in Table 5.6.

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sacrum-first caudal vertebra unit (except in the immature animal, FYM) appears more closely allied with the appendicular units, while the scapula falls far below the expected fat weight for its volume and appears to behave more like an axial than an appendicular unit, in terms of grease fat production. The low fat weights of the latter may be easily understood given the relatively small amount of cancellous bone compared to compact bone found in this element. The unexpectedly high fat weight for the sacrum-first caudal vertebra is more difficult to account for. As part of the axial skeleton, and given its location in a warm temperature environment, one might expect this bone to contain red marrow and relatively minor amounts of fat. Although the caudal vertebrae are known to contain yellow marrow, and this unit includes one such vertebra, this cannot account for the high fat weight, unless, like the tail, the sacrum contains primarily yellow marrow. Regardless of what kind of marrow is found in this and the scapula, if one is trying to estimate bone grease fat weights, one would be advised to use the regression equation for the data set the bone best fits. For the sacrum unit, the appendicular regression equation would be best, while for the scapula, the axial equation best predicts grease fat weight.

Table 5.7 presents a reanalysis of the regressions previously described, but with the sacrum-first caudal vertebra unit given the same designation as the similarly behaving appendicular units, and the scapula given the same designation as the axial units. The caudal unit is also assigned to the group including appendicular units based upon Tavassoli and Yoffey's (1983) assessment that it contains yellow rather than red marrow, despite it association with the axial skeleton. Included in Table 5.7 are the R^2 values for the corresponding regressions analyses on the previously

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Table 5.7. Regressions of Bone Grease Fat Weight (Y Variable) on Bone Measurements (X Variable) Using Adjusted Axial and Appendicular Designations for the Sacrum-First-Caudal, Caudal, and Scapula Units

Ref. Number[b]	Independent Variable (X)			Sample Composition: Bison Included		Sample Composition: Bones Included		Analysis of the Regression				R^2 Table 5.6
	Dry			All Four	Sub-	All	Element[c]					
	Volume	Weight	Density	Bison	Sample	Bones	Type	Prob > F	R^2	intercept	slope	
16		x		x			axial	0.0001[a]	0.5038	-0.80	0.03	0.4129
17		x		x			append	0.0001[a]	0.4313	-1.85	0.10	0.2855
18	x			x			axial	0.0001[a]	0.4853	-1.54	0.03	0.3991
19	x			x			append	0.0001[a]	0.5499	-1.55	0.11	0.4139
20			x	x			axial	0.1356	--	--	--	--
21			x	x			append	0.0042[a]	0.0958	57.80	-29.09	0.1393

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Table 5.7. (continued)

Ref. Number[b]	Independent Variable (X)			Sample Composition: Bison Included		Sample Composition: Bones Included		Analysis of the Regression				R^2 Table 5.6
	Volume	Dry Weight	Density	All Four Bison	Sub-Sample	All Bones	Element[c] Type	Prob > F	R^2	intercept	slope	
22		x			FYM		axial	0.3768	--	--	--	--
23		x			SAM		axial	0.2019	--	--	--	--
24		x			SAF		axial	0.0042[a]	0.7134	-2.78	0.05	0.4963
25		x			FAF		axial	0.0001[a]	0.8922	-3.44	0.04	0.7840
26		x			FYM		append	0.0047[a]	0.3509	3.90	0.04	--
27		x			SAM		append	0.0001[a]	0.6138	-5.69	0.07	0.3930
28		x			SAF		append	0.0001[a]	0.6348	-12.28	0.19	0.4329
29		x			FAF		append	0.0001[a]	0.5650	-3.91	0.11	0.3536

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Table 5.7. (continued)

Ref. Number[b]	Independent Variable (X)			Sample Composition: Bison Included		Sample Composition: Bones Included		Analysis of the Regression				R^2 Table 5.6
	Dry Volume	Dry Weight	Dry Density	All Four Bison	Sub-Sample	All Bones	Element[c] Type	Prob > F	R^2	intercept	slope	
30	x				FYM		axial	0.3652	--	--	--	--
31	x				SAM		axial	0.1461	--	--	--	--
32	x				SAF		axial	0.0028[a]	0.7432	-5.36	0.06	0.5191
33	x				FAF		axial	0.0001[a]	0.8922	-5.15	0.05	0.7829
34	x				FYM		append	0.0010[a]	0.4422	4.08	0.04	0.3275
35	x				SAM		append	0.0001[a]	0.8693	-5.87	0.09	0.6345
36	x				SAF		append	0.0001[a]	0.8634	-12.34	0.22	0.6802
37	x				FAF		append	0.0001[a]	0.8187	-4.82	0.14	0.6057

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Table 5.7. (continued)

Ref. Number[b]	Independent Variable (X)			Sample Composition				Analysis of the Regression				R^2 Table 5.6
				Bison Included		Bones Included						
	Dry Volume	Dry Weight	Density	All Four Bison	Sub-Sample	All Bones	Element[c] Type	Prob > F	R^2	intercept	slope	
38			x		FYM		axial	0.5329	--	--	--	--
39			x		SAM		axial	0.9085	--	--	--	--
40			x		SAF		axial	0.4742	--	--	--	--
41			x		FAF		axial	0.5476	--	--	--	--
42			x		FYM		append	0.2619	--	--	--	0.2233
43			x		SAM		append	0.0130[a]	0.2833	74.33	-45.54	0.4023
44			x		SAF		append	0.0269[a]	0.2323	116.45	-66.88	0.3458
45			x		FAF		append	0.0039	0.3629	96.96	-54.07	0.4952

[a] Significant at $p < .05$

[b] Reference numbers are identical to those in Table 5.6

[c] Axial group (axial) includes the scapula, and excludes the sacrum-first-caudal and caudal units.
Appendicular group (append) includes the sacrum-first-caudal and caudal units and excludes the scapula unit.

run, unadjusted data. The same reference numbers are used for these regression analyses for easy reference to Table 5.6.

In all of the regression analyses of dry bone weight and bone volume, the R^2 values for the adjusted data are much better than those seen when bone elements are split strictly between axial and appendicular units. Poorer results are seen in the regression analyses of bone density and grease fat weight, and the regressions of the appendicular data for FYM is no longer significant. The same relationships are noted for analyses run on the bones of all the animals grouped as one sample. As before, the R^2 values are much lower for this grouped data than for the individual bison data.

Examination of the scatterplot of the relationship between bone volume and grease fat weight (Figure 5.8) shows (1) the data points fanning out as bone volume gets larger, and (2) the distributions for males and females separating. Table 5.8 presents the results of a series of regression analyses on the adjusted axial-appendicular data where the data are separated by sex. Table 5.9 summarizes the coefficients of determination (R^2 values) for these regressions by sex, but also includes the results from the regressions by individual animals and for the combined group. It is evident in these data that the best results are produced for regressions including the bones of single animals. Nevertheless, the results when grouping the animals by sex remain relatively high and suggest that grouped data provide adequate assessments of bone grease fat availability.

In terms of selecting one set of data over another to predict grease fat weight, the adjustment of the axial and appendicular assignments of the three elements did not alter that assessment. Dry bone weight is still best for predicting axial unit grease fat weight, and bone volume is still best

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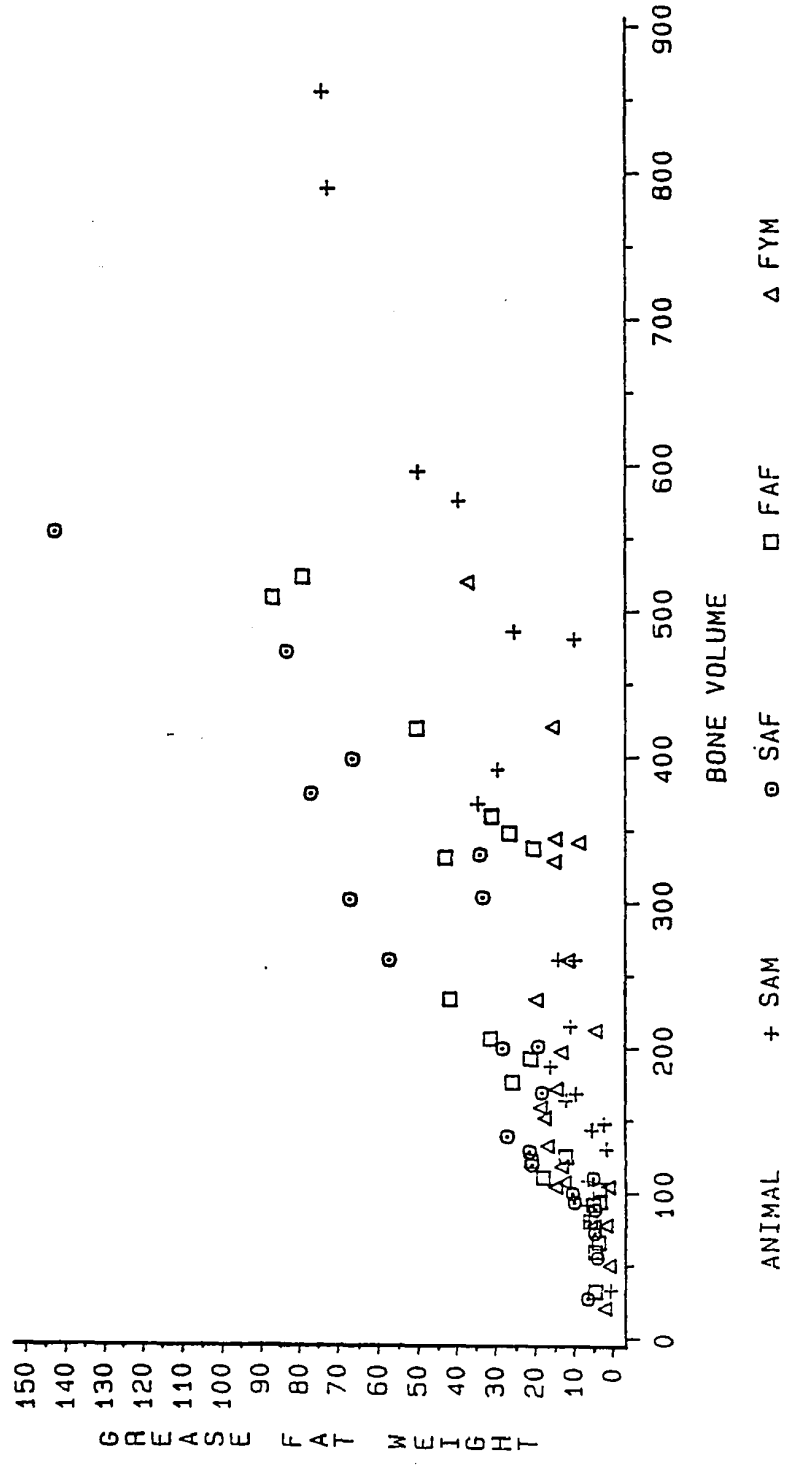

Figure 5.8. Regression of Grease Fat Weight on Bone Volume in Appendicular Units without Differentiation by Animal, Using Adjusted Axial-Appendicular Groups. Corresponds to regression No. 19 in Table 5.7.

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Table 5.8. Regressions of Bone Measurements on Grease Fat Weight with Data Grouped by Bison Sex and Using Adjusted Axial-Appendicular Groups

Part A. Results of the Regression Analyses

Ref. Number[b]	Independent Variable (X)		Sample Composition		Analysis of the Regression			
	Bone Volume	Dry Bone Weight	Sex	Bone Group[c]	Prob > F	R^2	intercept	slope
46	x		males	axial	0.0127[a]	0.3297	-0.10	0.02
47	x		females	axial	0.0001[a]	0.8033	-4.96	0.05
48	x		males	append	0.0001[a]	0.7841	-2.54	0.08
49	x		females	append	0.0001[a]	0.7868	-8.31	0.18
50		x	males	axial	0.0227[a]	0.2844	1.31	0.02
51		x	females	axial	0.0001[a]	0.7847	-2.73	0.05
52		x	males	append	0.0001[a]	0.5847	-1.53	0.07
53		x	females	append	0.0001[a]	0.5396	-6.87	0.15

Table 5.8. (continued)

Part B. Units Falling Outside a Studentized Residual of ±2.0

Reference Number[b]	Units with Studentized Residuals < -2.0	Units with Studentized Residual > +2.0
46	none	SAM PELV (3.51)
47	none	SAF PELV (2.99)
48	SAM PRUL (-3.06)	SAM DFEM (2.15)
49	FAF PRUL (-2.34), FAF PTIB (-2.04)	SAF DFEM (3.90)
50	none	SAM PELV (3.56)
51	none	SAF PELV (3.24)
52	SAM PRUL (-3.06)	SAM PHUM (2.99), SAM DFEM (2.46)
53	FAF PRUL (-2.29)	SAF DFEM (3.78)

[a] Significant at $p < .05$

[b] Reference numbers continue from Table 5.6

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Table 5.9. Summary of R^2 Values for Regressions of Bone Measurements on Grease Fat Weight Using Adjusted Axial-Appendicular Unit Designation

Bone Measurement	Element Type	R^2 Values Given Different Sample Composition						
			Individuals				Sex	
		All Animals	FYM	SAM	SAF	FAF	Females	Males
volume	axial	0.4853	--	--	0.7432	0.8922	0.8033	0.3297
volume	append	0.5499	0.4422	0.8693	0.8634	0.8187	0.7868	0.7841
dry weight	axial	0.5038	--	--	0.7134	0.8922	0.7847	0.2844
dry weight	append	0.4313	0.3509	0.6138	0.6348	0.5650	0.5396	0.5847

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for predicting appendicular unit fat weight in individual animals. In data grouped by sex, bone volume is best for estimating both axial and appendicular fat.

Implications of Cases Showing No Significant Relationships. Given the lack of significance and poor R^2 values in the individual regressions of SAM and FYM, and in the grouped male analyses (Table 5.9), one might be tempted to suggest that grease fat weight in the axial elements of males is not related to measurements of bone density, volume, or dry weight. Caution should be exercised here, however, given what is known about the ages of these two males and the changes in hemopoietic tissue volume in animals that are growing, compared to those that are fully mature. It is my expectation that the lack of a significant linear relationship for these two males in the measurements of axial bones and fat weight occurs for two different reasons. In the case of the older male, SAM, the pelvis (PELV) has much more fat than one would expect given the other data points for this animal in the scatterplot (Figure 5.9). This is true for SAF as well, suggesting the pelvis generally produces more fat per unit of bone volume than the other axial bones. With the small number of units represented in this analysis, the magnitude of this difference becomes very important. As is shown later, the fat content of the axial bones in SAM are comparable to those seen for mature female bison. The lack of significance in the relationship between grease fat weight and bone volume in the axial data of FYM, however, is not due to outliers, but probably occurs because this animal has not yet achieved full adult size. The fact that the regressions of the axial data were not significant for the males, but they were for the females, leads one to suspect that hemopoietic tissue volume may be relatively large yet in these males, as compared to the mature females.

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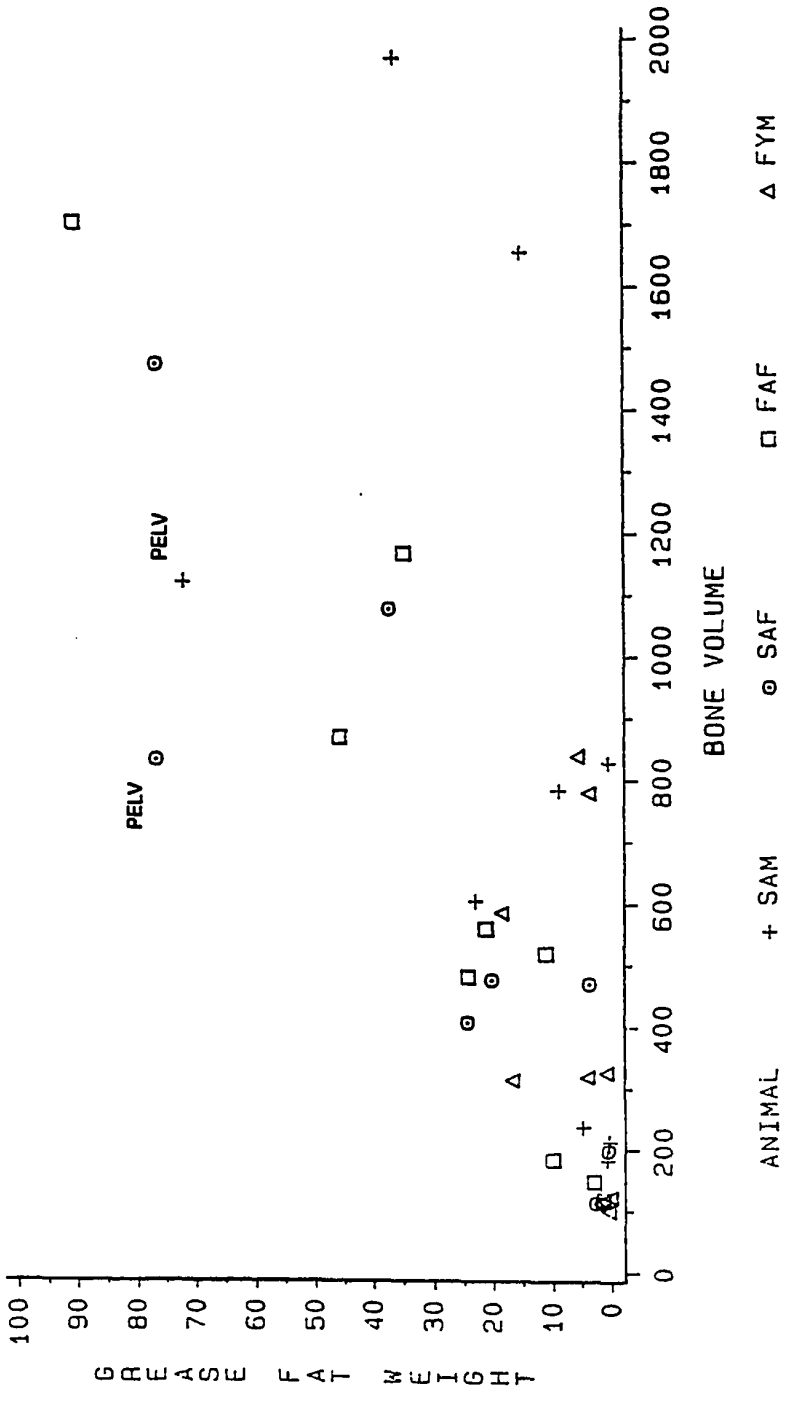

Figure 5.9. Regression of Grease Fat Weight on Bone Volume in Axial Units without Differentiation by Animal, Using Adjusted Axial-Appendicular Groups. Corresponds to regression No. 18 in Table 5.7.

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Three sets of data, (1) the low R^2 value for the regression of grease fat weight and dry bone weight for appendicular bones of FYM (No. 26, Table 5.7), (2) the much lower R^2 value in the regression of fat weight and bone volume (No. 34-37, Table 5.7) for FYM compared to the other three animals, and (3) the fact that several of the FYM proximal limb element fat weights are relatively much smaller than those of the more mature animals, all lead one to conclude that fat production in the appendicular units of FYM is not yet representative of a mature pattern. They also suggest that hemopoietic activity might still be active in the proximal limb elements of FYM.

Alternatively, the slower growth of the proximal limb elements compared to that of the more distal elements might account for the smaller grease fat weights of the proximal elements if the immature relationship differs from the mature pattern. Comparison of the regression scatterplots for appendicular bone volume for SAM and FYM overlayed on one graph (Figure 5.10), shows that between 1-1/2 and four years of age, the elements of the proximal limbs show the most growth and largest gains in grease fat weight. If the change in proportion of grease fat weight between the two animals is larger than that of the proportion of bone growth, then perhaps this might indicate that yellow marrow is replacing red marrow in those bone elements.

Figure 5.11 shows the changes in bone volume and fat weight for yellow marrow bones between the two males, FYM and SAM. The line on this graph represents the division between bones in which fat weight growth exceeds bone volume growth, and the reverse (i.e., $y = x$). As suspected, the increase in fat weight exceeds the increase in bone volume growth in the proximal limb elements between the age classes represented by these two animals. This might still merely indicate a difference in the relationship between fat content and bone volume between mature and immature animals, but

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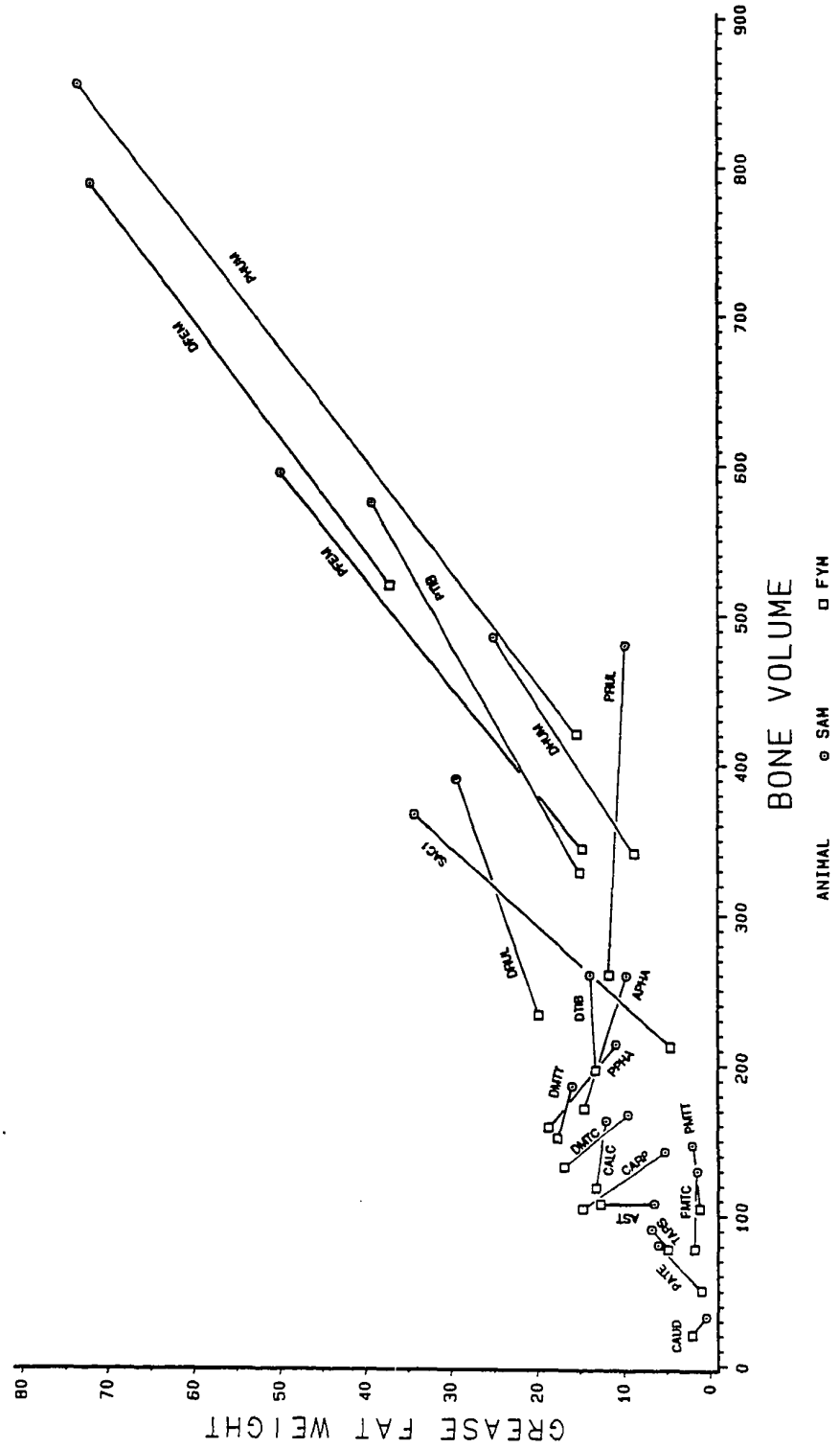

Figure 5.10. Regressions of Grease Fat Weight on Bone Volume in Appendicular Units from Male Bison. Like elements from the yearling, FYM, and the four year old, SAM, are connected to illustrate the magnitude of growth between these age groups for each skeletal element in the adjusted appendicular group.

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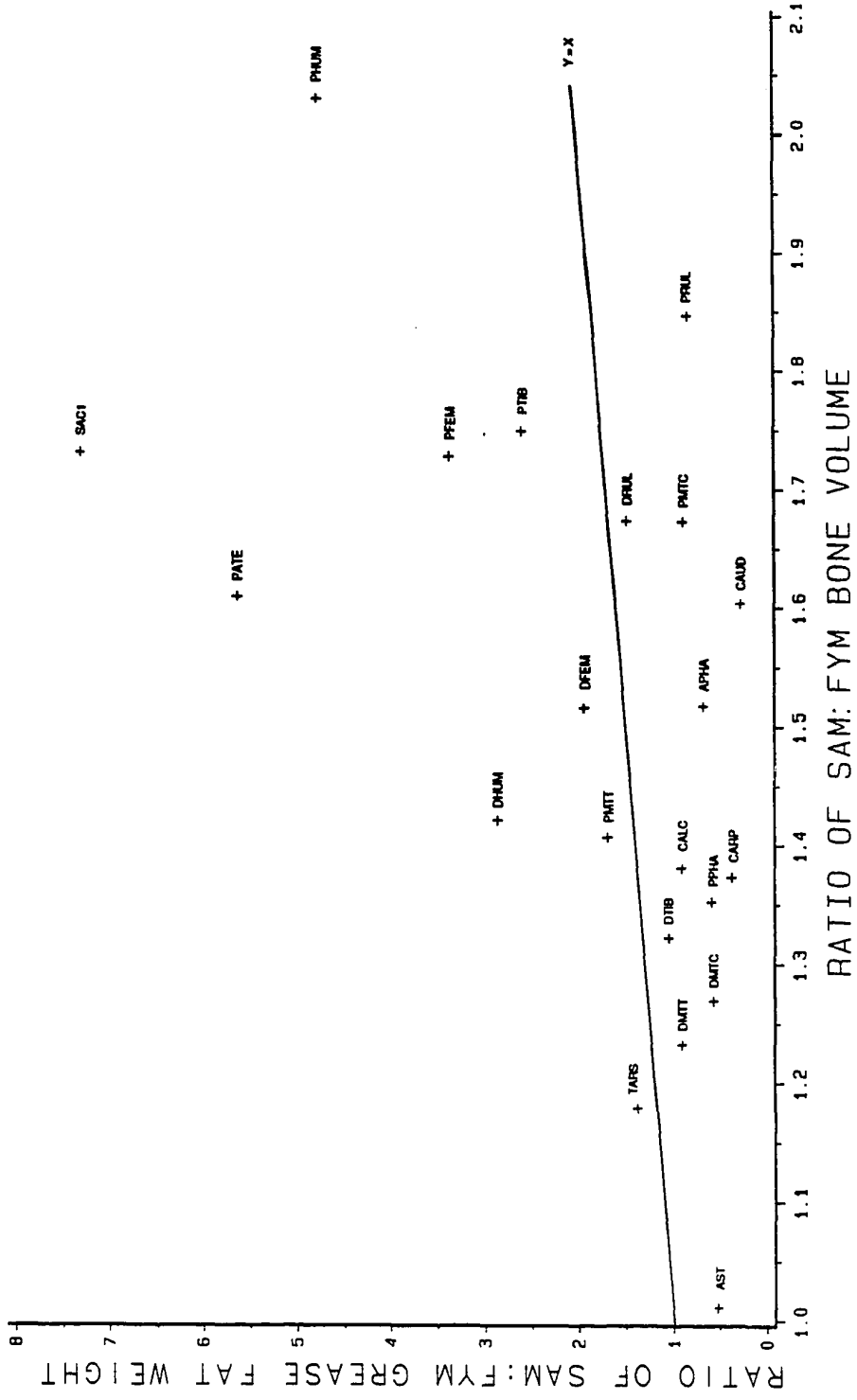

Figure 5.11. Comparison of Differences in Grease Fat Weight and Bone Volume Between Yearling and Four Year Old Male Bison. Units above the y = x line increase fat weight more than bone volume; units below the y = x line increase bone volume more than fat weight.

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it might also be related to the retreat of red marrow and expansion of yellow marrow in the limb bones of growing animals. These assessments would have to be verified by analyses of other bison, and determination of the ages and stages of the regression of hemopoietic tissue to axial elements. Assessment of the bone volume and fat content of bones of fully mature male bison would be particularly helpful in addressing this problem.

Lumping Versus Splitting the Data. The small R^2 values achieved when all bone and all animals were combined indicate that there are real differences in the relationship of grease fat weight and bone measurements between bone classes (axial and appendicular) and between animal classes as represented by the individual bison. This is in sharp contrast to the medullary marrow and cavity volume relationships discussed earlier, in which there were few apparent improvements made when the bones of individual animals were evaluated. For bones from the axial skeleton of mature females, the dry bone weight measures provide the easiest assessment of bone grease fat weight with only a minor drop in R^2 value from bone volume. For the appendicular skeleton of mature animals separated in groups by sex, regressions of bone volume measures provide the best fit to the data. These analyses point to the clear need for analyses of more individuals representing different age groups for each sex, and under circumstances where the conditions of the animals are clearly established.

Plotting the regression lines for the adjusted appendicular and axial units for grease fat weight and bone volume or dry bone weight respectively (Figures 5.12 and 5.13), illustrates relatively clearly the differences in the relationships of the independent and dependent variables between animals. These figures, in conjunction with the poorer R^2 values for grouped animal data and the slightly poorer results for sex class data,

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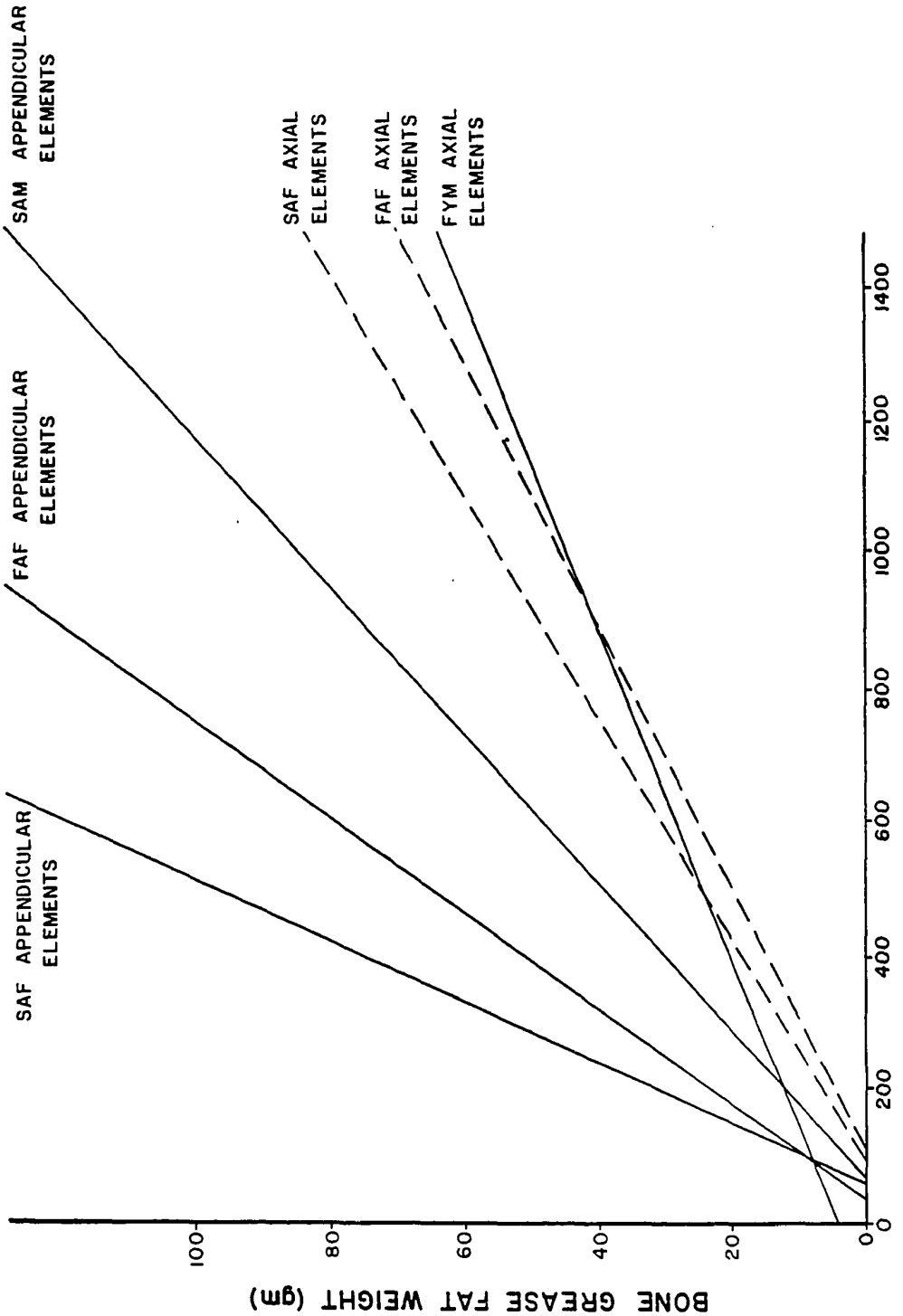

Figure 5.12. Summary Graph of Regression Lines for Bone Grease Fat Weight on Bone Volume for Individual Animals and Adjusted Axial-Appendicular Groups.

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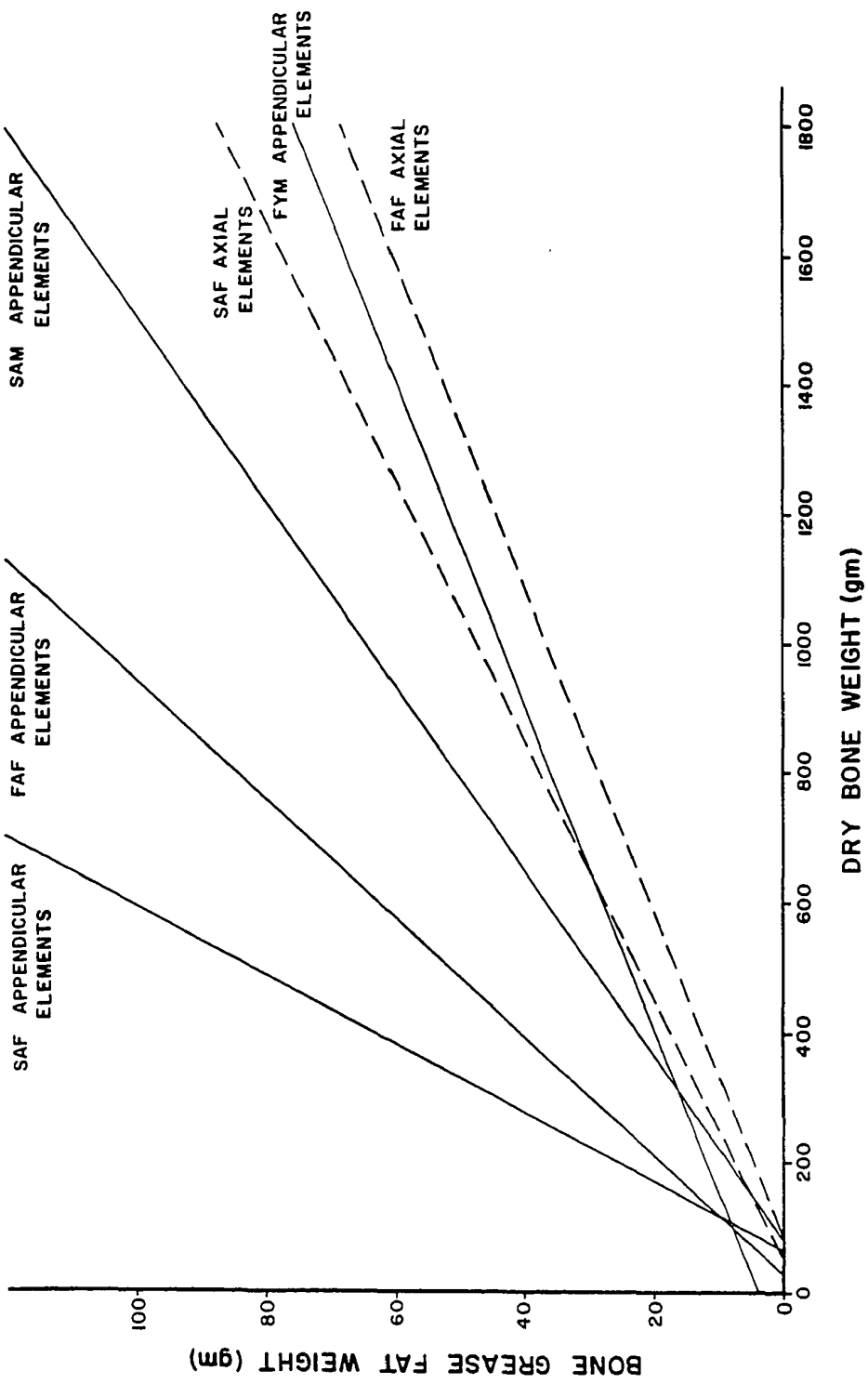

Figure 5.13. Summary Graph of Regression Lines for Bone Grease Fat Weight on Dry Bone Weight for Individual Animals and Adjusted Axial-Appendicular Groups.

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indicate that when possible, bone assemblages should be separated on the basis of animal sex and maturity. On the basis of the data presented here, a mature relationship between bone measurements and grease fat weight is not evident in yearling males. A significant relationship could not be established for the axial elements of the four year old male either, but this failure is attributed to a data point outlier, and not to lack of maturity in fat content in the bones of this animal. Appendicular elements of the four year old male, SAM, do show a significant relationship between bone volume and grease fat weight. Given the earlier achievement of maturity in females and the relationship between hemopoietic activity, growth, and marrow fat volume, one would expect that a mature relationship between bone volume and grease fat weight would be established sooner in females than males.

Finally, if information is available indicating that the animals represented by an assemblage of bones may have been in poor condition, then perhaps the regression data provided by the female, FAF, would provide better estimates of grease fat weight in females than the data from SAF. Where a small degree of variability exists between animals, as in the case of these bison, data grouped by sex class provide adequate estimates of grease fat weight. Studentized residuals of these regressions also indicate in which bones the fat weight is poorly estimated using bone measurements. These are listed for the grouped sex data in Table 5.8, Part B. The poor fit of these data points in these regression analyses may arise for two reasons. First, the bone measurement may be larger or smaller than one might anticipate, and second the grease fat weight may be larger or smaller than expected.

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Bone Production and Distribution

In this section, data from the four TRNP bison are examined for differences between animal classes in (1) the proportion that bone weight represents of carcass weight, including differences in fresh and dry bone weights; (2) the size of bones, determined by weight and volume; and (3) the distribution of bone weight and volume in the carcass. Similarities and differences in these factors are important to understanding how differences in bone might correlate with differences in marrow and bone grease availability, or perhaps with differences in associated muscle weight. By first defining how bone differs (or is the same) and then defining how the marrow, grease fat, and meat differ, one can determine where differences are pronounced and whether these are areas where bone products are most abundant, or of only minor importance.

Before beginning this discussion of bone production and distribution, however, a brief note should be made of the differences in how bone production and distribution are measured in the animal sciences and in anthropological studies. It is this difference combined with the need to compare the bison data with that of other animals (due to the small sample size here for bison) that makes it necessary to make comparisons between fresh and dry bone weights.

Measurement of Bone Weight in the Animal Sciences and Archaeology

In most studies of animal composition in the cattle industry, bone as a component of the carcass is considered in its fresh condition, sometimes including the weight of tendon, ligament, and cartilage. The lack of interest in a more refined measure of cattle bone and its products can be attributed to its status as a low valued carcass product. It is considered

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waste except for the price it brings as a component of wholesale or retail cuts. Due to the archaeologists' interest in the human use of marrow and bone grease, in anthropological studies of animal carcass composition, bone is usually considered in terms of its dry weight, indicating that it has been cleaned of connective tissues and cartilage, as well as of its marrow and grease products. The difference these two components represent of the total carcass weight varies to some degree. Dry bone weights represent relatively consistent proportions of the total carcass, because they reflect differences in animal age and sex that affect bone size. Fresh bone weights, which include marrow and bone grease weights, as well as nonfood products such as cartilage and some connective tissue, are affected by animal size, as well as by changing animal condition, and therefore, should show greater variability between animals than does dry bone weight. Both measures are considered in the following discussion.

Bone Weight as a Proportion of Carcass Weight

The first point to be considered concerning differences and similarities in bone weights is the total contribution of fresh and dry bone weight to the weight of the carcass. If dry bone weight as a percent of carcass weight does not differ between animals, this would indicate that bone size, as measured by weight, increases in proportion to increases in animal carcass size. If the percentages differ, then animal age or sex should be examined as potential factors affecting the contribution of bone to carcass weight. The same may be true for fresh bone weight as a percent of carcass weight, but as a combined weight of bone, marrow, bone grease fat, and other tissues, variability between animals might be masked by similar combined totals. Furthermore, because fat products are a component

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of fresh bone weight, the influence of animal condition on fresh bone weight must also be considered. Table 5.10 presents the bison bone weights and percentages they represent of the standard dressed carcass and of the nonstandard complete carcass used in anthropological studies.

Dry Bone Weight as a Percent of Carcass Weight. Dry bone weight percentages in Table 5.10 show very little variability between animals. The immature male, FYM, differs most from the other animals, though by only a few tenths of a percent. If this difference is significant, it is probably related to age rather than sex differences between the animals, given the intermediate placement of the older male, SAM, between the two females. As noted above, Berg and Butterfield (1976) found the bone component of carcass weight in cattle to be higher in calves and to decrease with age as the rate of muscle growth exceeds that of bone growth. This assessment was for fresh bone weight, however, so it is not known if it applies to dry bone weight as well. At 1-1/2 years of age, it appears that dry bone weight is at or near adult proportions of bison carcass weight.

Fresh Bone Weight as a Percent of Carcass Weight. Fresh bone weights in Table 5.10 show greater variability between animals than the dry bone weights. From these data, it is evident that the fresh bone weight percentages are comparable for the two bison females, and are lower than those reported for the two younger males. If the differences in values between these four animals are significant, one might expect that animal age, sex, condition, or a combination of these, is responsible. Although age differences appear important in the values of the two males, and possibly in the values of the males compared with those of the females, the lack of variability between the two females suggests that age differences are registered only until full maturity is reached. Sex differences may be

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Table 5.10. Fresh and Dry Bone Weight as a Percent of Standard and Non-Standard Carcass Weight

Part A. Bone Weight as a Percent of Standard[a] Carcass Weight

	FYM		SAM		SAF		FAF	
Bone Type	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass
Fresh	21,952.8	13.6	44,042.7	12.6	29,867.9	11.7	31,998.1	11.6
Dry	12,709.4	7.9	26,170.0	7.5	18,902.8	7.4	21,090.2	7.6
Carcass Weight (gm)	161,481.6		348,818.4		256,284.0		276,696.0	

Part B. Bone Weight as a Percent of Non-Standard[b] Carcass Weight

	FYM		SAM		SAF		FAF	
Bone Type	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass	Weight (gm)	% of Carcass
Fresh	28,143.3	15.6	56,623.8	14.7	38,594.8	13.7	41,084.9	13.4
Dry	17,886.6	9.9	37,422.4	9.7	26,671.4	9.5	29,434.6	9.6
Carcass Weight (gm)	180,391.1		385,942.7		281,862.8		305,627.2	

[a] Standard carcass excludes the weight of the blood, hide, head, tail, shanks and viscera.

[b] Non-standard carcass excludes the weight of the blood, hide and viscera.

registered in fresh bone weights, but the age structure of this sample makes it difficult to determine whether the variation between the male, SAM, and the females, is due to his having not reached full maturity, or is in fact a reflection of sex differences. To evaluate this one might examine the differences and similarities in the components of fresh bone weight.

Thus far, it has been shown that dry bone weight as a percentage of total carcass weight differs very little (except perhaps between immature and mature animals), whereas fresh bone weight percentages show much more marked differences in values between animals. Two questions that arise from this are, (1) from which component(s) of fresh bone weight do the differences originate, and (2) are animal age, sex, or condition influential in determining these values? In order to address these questions one must determine the weight of the components of fresh bone and the proportion they represent of the total bone weight in order to compensate for differences in animal and bone size.

Components of Fresh Bone Weight--Table 5. 11 presents the weights and proportions they represent of fresh bone weight for dry bone, marrow, and bone grease fat, as well as the combined weight of all other tissues plus water. This table also includes the percent these materials represent of carcass weight, illustrating that weight does not always adequately measure importance. Although dry bone weight is a relatively stable percent of standard carcass weight, it assumes a larger proportion of fresh bone weight with age, while at the same time fresh bone weight decreases as a percent of total carcass weight until full maturity is reached. Several factors are involved here. First, bones increase in weight and density until at some point in age, bone resorption at the endosteal surface (the surface of the marrow cavity) is faster than appositional bone growth beneath the

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Table 5.11. Components of Fresh Bone Weight

Part A. Bone or Component Weight (gm)

Component	FYM	SAM	SAF	FAF
fresh bone	21,952.8	44,042.7	29,867.9	31,998.1
dry bone	12,709.4	26,170.0	18,902.8	21,090.2
marrow	792.2	1,322.4	1,009.6	978.2
bone grease fat	478.9	1,091.5	1,752.9	1,339.1
other	7,967.3	15,458.8	8,202.6	8,590.6

Part B. Component as a Percent of Fresh Bone Weight

Component	FYM	SAM	SAF	FAF
fresh bone	100.0	100.0	100.0	100.0
dry bone	57.9	59.4	63.3	65.9
marrow	3.6	3.0	3.4	3.1
bone grease fat	2.2	2.5	5.9	4.2
other	36.3	35.1	27.5	26.8

Part C. Component as a Percent of Standard Carcass Weight[a]

Component	FYM	SAM	SAF	FAF
fresh bone	13.6	12.6	11.7	11.6
dry bone	7.9	7.5	7.4	7.6
marrow	0.5	0.4	0.4	0.4
bone grease fat	0.3	0.3	0.7	0.5
other	4.9	4.4	3.2	3.1

[a] See Table 5.10 for carcass weights.

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periosteum, and a net weight loss results (Garn 1970). It is unclear whether the older female, FAF, was experiencing bone loss when killed. Second, in order for dry bone weight to increase as a percent of fresh bone weight, the rate of bone growth must be larger than the increase in the weight of the other fresh bone components. Third, the decrease in fresh bone weight as a percent of carcass weight indicates that other carcass components increase in weight at a faster rate than fresh bone--a condition noted by Berg and Butterfield (1976).

Dry bone provides the largest weight component of fresh bone weight, ranging in value in these four bison from 57.9 to 65.9 percent of fresh bone weight. With animal age, dry bone weight increases as a percent of fresh bone weight. The decrease with age for fresh bone weight as a percent of carcass weight, therefore, cannot be attributed to dry bone weight. The other components of fresh bone weight have to be examined to determine from which component or combination of components the pattern for fresh bone weight as a percent of carcass weight is derived.

Table 5.11 shows that marrow is similar to dry bone weight as a component of the standard carcass, showing little variability between animals, but not as a component of fresh bone weight. Marrow represents a variable percent of fresh bone weight, and no trend in either sex or age is apparent. The fact that marrow represents only a small proportion of fresh bone weight suggests that it has little responsibility in producing the decrease with age that fresh bone weight represents of carcass weight. With the exception of the values for SAM, however, marrow also decreases as a proportion of fresh bone weight with age.

Bone grease fat weight is variable as both a percent of carcass weight and as a percent of fresh bone weight. The increase in percent of bone

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grease fat in fresh bone weight with age is minor between the immature male, FYM, and the older male, SAM. A larger increase is seen between the male, SAM, and the females. This difference might be related to the age differences or a combination of age and sex, as fat in cattle is found in larger amounts in older than younger animals, and in females than in males (Berg and Butterfield 1976). As both FYM and SAM are not fully mature, continued growth is associated with an increase in blood volume, which dictates proportionately larger amounts of red marrow and smaller amounts of yellow (or fatty) marrow, than in mature animals (Tavassoli and Yoffey 1983). The combined effect of age and sex is probably responsible for the percentages seen in Table 5.11 for bone grease fat as a percent of fresh bone weight. Like bone marrow, however, bone grease fat represents only a small proportion of fresh bone weight, and the pattern of change between animals of increasing age does not conform to that seen for the proportion that fresh bone weight is of carcass weight.

Changes in animal condition largely affect fat levels in animal carcass weight. Tavassoli and Yoffey (1983) indicate that the bone marrow that is mostly fat and is found in medullary cavities as well as in the epiphyses of the appendicular skeleton and tail is resistant, compared with other fat depots, to mobilization. Condition changes in animals would be delayed in their effect on marrow weight in these bones. These authors did find, however, that fat associated with the red marrow of the axial skeleton (in mature animals) responds to conditions of nutritional stress in much the same manner as body fat. Some condition differences might be evident in the value of bone grease fat as a percent of fresh bone weight, therefore. This component accounts for such a small percent of fresh bone weight, however, and varies in opposition to the pattern noted for fresh bone weight as a

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percent of carcass weight, that it is doubtful that it is influential here.

The final component of fresh bone weight is the combined weight of all other tissues plus water. These include connective tissue, cartilage, water, and a small amount of bone grease that could not be removed in the extraction process. As a percent of standard carcass weight, these values decrease with increasing age, and may show a difference in magnitude between the sexes as well. As a component of fresh bone weight, these combined materials decrease as a percent of total bone weight with increasing age, the pattern noted previously for fresh bone weight as a percent of carcass weight. It is this component of fresh bone weight that may account for the differences the fresh bone weight percentages represent of carcass weight totals. In addition to showing the same pattern of change between animals as the percentages that fresh bone weight is of carcass weight, the weight of these materials account for over one third of fresh bone weight in the males and a somewhat smaller percentage in the females. The size of this component, therefore, combined with the magnitude of the differences between the values for the animals, must be responsible for the changes seen in the weights of fresh bone and the percent it represents of carcass weight.

From the analysis of the components of fresh bone weight it was found that the principal factor influencing its variability is the combined weight of the components that are not dry bone, marrow, or bone grease fat. The next task is to determine whether it is age, sex, or animal condition that controls this aspect of fresh bone weight. Changes in animal condition are largely registered in changes in fat weight and corresponding changes in water weight. However, fat as a component of fresh bone weight is primarily limited to the bone marrow and bone grease components. Its influence on this component is through its effect on the moisture content of the bone

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grease. If bone grease behaves in a manner similar to bone marrow, losses in fat correspond to increases in moisture content. In the combined material component of fresh bone weight, changes in animal condition that result in loss of fat weight, might show up as an increase in the weight of this combined material component. As shown later, the female, FAF, appears to be in poorer condition than the female, SAF, so one would expect that if animal condition does affect the weight of the combined materials component of fresh bone weight, that it should be a higher percent of fresh bone weight in FAF than in SAF. Table 5.11 shows this is not true, indicating that animal condition has no influence on the weight of this component, or that its influence is so small that it is not registered in the variability between these two females. A larger sample and more refined determination of the weights of the elements of this component would be required to clarify this issue. It is possible that Brink (1986), in his analysis of bison appendicular bone grease might be able to address this issue, given the technique he used to derive the fat content, but the small size of his sample makes such an analysis subject to the same limitations as this study.

The importance of age and sex is obscured by the character of the bison sample. The magnitude of difference in the proportion this component represents of fresh bone weight between the females and males suggests that animal sex may be a factor in addition to animal age. The validity of such an assessment cannot be tested with this small sample, and literature for this or other species is non-existent. Therefore, in addition to not being able to suggest the cause of the variability in the weight of the combined materials component of fresh bone weight, no further definition of the cause of variability in the pro-portion that fresh bone weight represents of carcass weight could be determined.

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From this discussion of fresh and dry bone weights in bison carcasses, it appears that dry bone weight in animals at least four years of age is a relatively constant proportion of total carcass weight, with bone increasing in weight at a comparable rate to carcass weight increases. In immature animals, however, as suggested by Berg and Butterfield (1976), fresh, and possibly dry bone, represent a larger proportion of the carcass than in older individuals. Unlike dry bone, fresh bone shows some differences in the proportion it represents of the total carcass, which may reflect either age or sex differences or a combination of the two. One may suggest that age is important until full maturity is reached, with fresh bone weight decreasing as a proportion of carcass weight, and that sex may influence fresh bone weight as well, as suggested by differences in the magnitude of the values for males and females.

If the differences between these bison are representative, and if they are significant (neither of which can be demonstrated with such a small sample), then this suggests that, (1) dry bone weight in adult bison may show no difference between sexes in the percentage it represents of the total carcass, indicating that bone size increases in conjunction with body size; (2) immature age versus adult age may be the only significant factor in the differences registered for dry bone weight, with immature animals possibly having a greater proportion of carcass weight in bone; (3) if, as it appears, there are no sex differences in the dry bone component of mature animals, then the difference in fresh bone percentages must be attributed to non-bone components; (4) fresh bone weights increase in absolute values with age to maturity, but decrease as a proportion of carcass weight, indicating that other components of the carcass are increasing in weight at a faster

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rate; (5) the variability in fresh bone weight is largely influenced by the combined weight of water and tissue that is not bone, marrow, or bone grease fat; and (6) the influence of sex or age on the weight of this component of fresh bone weight, and therefore, of fresh bone weight as a component of carcass weight cannot be further defined with the data available, but I expect that both factors are responsible for the variability shown. Data from other species may help to clarify the importance of age and sex.

Implications of Studies of Bone in the Cattle Carcass. In the discussion above, possible age and sex differences were suggested for fresh bone, and for dry bone as a component of fresh bone. These interpretations, however, are based upon the results of a study on only four bison. If the range of variability for these values is wide, the interpretations of the existence of variability may be wrong. By examining the results of studies of cattle carcass composition where numerous animals were studied, one can assess whether the occurrence of the observed differences in bison bone weights are likely to be indicative of age differences, or simply representative of a wide range of variability in bone and other weights. Cattle studies provide good analyses of differences in fresh bone weight as influenced by animal age, as discussed below, but provide little information concerning sex differences in bone weight.

Bone is a tissue with early, high priority for growth in postnatal animals (Pfander 1969:296). Berg and Butterfield (1976:23) note that the early development of bone is due to the necessity for efficient functioning at birth. This results in a higher ratio of bone to muscle weight at birth than later in life. From this assessment, one can expect that young animals have higher percentages of their carcass weight in bone than do older animals. In this study, FYM, the youngest bison, does show the highest

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percent bone to carcass weight for both dry and fresh bone weights (Table 5.10). It is not clear, however, how long it takes to approach adult proportions of carcass composition, or whether at 1-1/2 years, the values for FYM are significantly higher. As previously noted, the older male, SAM, showed no difference in the proportion of carcass weight that is dry bone, but did differ from the females in fresh bone weight. As cattle industry studies focus on fresh, rather than dry bone weights, the fresh values for the male SAM appear to indicate that he has not yet reached full maturity.

Age and sex combine to produce differences in animal growth and the arrival of maturity. Females mature earlier than males (Berg and Butterfield 1976:8), so in studies of carcass composition, comparability in age does not assure comparability in maturity. Similarly, animals of like maturity may be of different ages, and this difference would have little or no affect on composition variability. For example, the age difference between the two fully mature bison females, SAF and FAF, was estimated to be approximately nine years. Despite this, these two animals showed similar bone composition for both fresh and dry bone weights.

SAM, on the other hand, is a male that has not reached full maturity, and FYM is an immature male. The immature bison shows consistently different values for bone weights than the mature females, and often from the older male. The male, SAM, however, is similar to the mature females in some cases and in others is more like the immature bison. His size and age suggest he is an adult, but not yet fully mature.

As previously noted, SAM appears to be comparable to the females in percent dry bone weight, but not in percent fresh bone weight. This male has a higher percent of its carcass weight in fresh bone than either of the older females. At four years of age and a little over 1411 lb (640 kg)

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liveweight, this male bison is not fully mature, but has probably attained approximately three quarters of his mature weight given the male bison growth curves (Figure 2.8). The question remains as to whether this animal has reached maturity in bone growth. The higher percentage value for fresh bone weight in the carcass would suggest he has not. Other information corroborates this assessment.

The incomplete fusion of the epiphyses of many of the long bones indicate that neither longitudinal nor appositional bone growth is yet complete in this adult male. It is not clear from fusion data, however, whether continued bone growth would result in any change in the proportion of bone weight to carcass weight. It could be possible that fusion has no effect on bone weight, and therefore, not serve well as an indicator of maturity when bone weight is the unit of measure. Consideration of whether the distribution of bone weight represents that of a mature animal offers additional evidence that age is a factor in the differential percentages of fresh bone weight in the carcasses of these animals. Dry bone weight is discussed later as well, because it helps to clarify the meaning of the fresh bone weight values. If the male, SAM, showed a mature animal bone weight distribution within the carcass, then age differences in fresh bone weight could be discussed and the differences might then be attributed to sex differences.

Jones et al. (1978) showed that the skeletal elements of the cattle carcass may be divided into three groups having different patterns of growth determined by whether they are early, intermediate, or late maturing bones. According to these authors, early maturing bone represents a large proportion of total bone weight in young animals, but as the animal matures the proportion of this type of bone declines. Late maturing bone begins as

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a small percent of total bone weight and increases with age. Intermediate maturing bone changes little in weight relative to total bone weight. In cattle, early maturing elements include bones of the limbs and the cervical vertebrae; intermediate maturing elements include the sternum, and the thoracic and lumbar vertebrae; and late maturing bones include the scapula, the sacrum-pelvis, and the ribs. Jones et al. (1978) found no significant sex differences in the rates of bone development and attributed all differences to problems arising from comparing animals of different maturity. I believe there are problems with that assessment, given the occurrence of sexual dimorphism and their failure to match animals of like maturity. Nevertheless, by dividing the bison bone weights into early, intermediate, and late maturing groups, and comparing the immature male, FYM, with the mature females, SAF and FAF, the maturity of SAM can be addressed.

Assuming that bison bone growth is like that shown for cattle, it appears that the male, SAM, is not fully mature in terms of either dry or fresh bone weight distributions (Table 5.12). In both dry and fresh bone weights, there is a decrease, with age, in the percent of early maturing bone with a concomitant increase in late maturing bone. The early and late maturing bone values for SAM lie between those of the immature bison, FYM, and the females, thus suggesting that SAM is not fully mature in bone weight distribution, but is more mature than the younger male, FYM. If lacking maturity in bone weight distribution correlates with lack of maturity in bone weight in general, then it is possible that age is a factor in the differences between the percent fresh bone weight reported for SAM and the other bison. If it does not, then lack of maturity in distribution might explain little or none of the variability seen.

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Table 5.12. Distribution of Bone Weight by Maturation Type

Part A. Percent of Dry Bone Weight

Maturation Class	FYM	SAM	SAF	FAF
early	53.9	51.0	48.3	47.2
intermediate	15.8	17.0	16.7	16.6
late	30.3	32.0	35.0	36.2

Part B. Percent of Fresh Bone Weight

Maturation Class	FYM	SAM	SAF	FAF
early	56.5	50.7	49.0	46.6
intermediate	16.9	18.1	18.0	18.6
late	26.6	31.2	33.0	34.8

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I am not convinced, however, that sex is not a factor in the distribution of bone weight. Jones et al. (1978) indicate that individual bones do show significant sex differences, but argue that these result from differences in maturity. The problem here lies in the fact that bone weights and distribution are compared at equal total bone weight, which fails to account for differences in animal size and maturity. To properly compare sex differences in bone growth, one would have to compare animals of like maturity, ignoring both age and total bone weight which vary between the sexes in different patterns influenced by the extent of growth and differences in when maturity is reached.

From these analyses, it appears that animal age and sex must both still be considered as possible factors leading to the variability that fresh bone weight represents of carcass weight. Further clarification of this factor seems doubtful given the lack of importance that bone carries as a product, and the difficulty in testing these relationships. For the purposes of this project, it is possibly sufficient to know that dry bone is a consistent proportion of carcass weight unaffected by sex and only minimally affected (if at all) by age. Variability in fresh bone weight does not appear to correspond directly to components that are of interest to archaeologists--bone marrow and bone grease fat--except possibly as bone and bone grease moisture weight might covary with bone grease fat weight. The significant inverse correlation that Marquez and Coblentz (1987) found between fat and water in deer marrow probably exists for grease fat and water, as well. The relationship between animal condition, bone grease fat weight, and bone grease moisture weight needs to be explored further, to identify the factors that influence variability in fresh bone weight.

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Age and Sex Differences in Bison Bone Size as Measured by Weight

Three factors may be considered when one discusses differences in bison bone size. These are differences in bone weight, volume, and density. It is these factors that might be measureable in archaeological bone, and therefore, should be studied for their relationships to the production of bone marrow and bone grease. Previously, it was shown that dry bone weight and bone volume are positively correlated with bone grease fat weight in axial and appendicular elements in individual animals and when grouped by sex. Bone density, however, did not show a significant relationship to axial bone grease fat weight, and the relationships in the appendicular units had much lower R^2 values than the regressions of bone volume. The improved fit of the regression lines to the scatterplots when the bones of each animal were analyzed, compared to the fit for grouped animal bone data, indicate that variability exists between animals in the size of their bones and their production of bone grease fat. As differences may exist in the size of bones or in the amount of fat associated with that bone, both must be examined for differences between animals or classes of animals. Bone size differences are considered here.

Increases in body size with animal growth necessitate concomitant growth in bone to support the weight of added tissue, and to provide space for adequate blood production to support this growth. As shown in Chapter 2, the extent of growth in bison is sexually dimorphic, with females achieving full maturity in growth earlier than males, and at smaller liveweights. Males have larger bodies and heavier bones than females (Table 5.13).

Aging, associated with growth, results in increases in bone size and weight. Although longitudinal bone growth ceases with the fusion of the

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Table 5.13. Carcass and Dry Bone Weights in Bison

Part A. Dry Bone Weight (gm)

Carcass Type[a]	FYM	SAM	SAF	FAF
standard carcass	12,709.4	26,170.0	18,902.8	21,090.2
non-standard carcass	17,886.6	37,422.4	26,671.4	29,434.6

Part B. Carcass Weight (gm)

Carcass Type[a]	FYM	SAM	SAF	FAF
standard carcass	161,481.6	348,818.4	256,284.0	276,696.0
non-standard carcass	180,391.1	385,942.7	281,862.8	305,627.2

[a] Standard carcass excludes head, shanks and tail; non-standard carcass includes the bones of the head, shanks and tail in addition to the bones of the standard carcass.

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epiphyseal plate, bone growth and increases in bone weight do not stop entirely. Appositional growth beneath the periosteum increases bone shaft width and cortical width until bone resorption at the endosteal surface in adults occurs as a faster rate than apposition and reduces cortical width (Garn 1970). The effect of this process is for bone to increase in weight with age, and then later in life, to decrease in weight. Decreases in bone weight might also occur with osteoporosis, a degenerative condition, just as arthritis results in abnormal bone accumulation. Without a large sample of bison bone from animals of different ages, it is not possible to determine whether the specimens used in this study are typical for their age and sex. The bison bone weight data are presented in Tables 5.14 through 5.16. In general, they suggest that bone weight increases with age and that males have heavier bones than females at younger ages. The bison bone volume data are presented in Table 5.17. These data show an increase in volume with increases in body size. The bones of the larger bodied, but younger animal, SAM, are larger in volume than those of both older females. Clearly, animal sex influences body size and thus, bone volume. With increasing animal age (up to maturity), body size and bone volume also increase. The importance of sex over age can be seen in the larger bone volumes of the carpals, tarsals, and metapodials of FYM over those of the currently larger, but eventually smaller females. Differences in animal condition are not evident in bone volume differences. Comparison of density measurements show that density increases with age, but its relationship to grease fat weight is weak, so it is not considered further here.

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Table 5.14. Fresh Bone Weight in the Standard Carcass

Carcass Unit	Fresh Bone Weight (gm)				Percent of Total Fresh Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
ATLAS	331.9	667.6	347.9	459.9	1.5	1.5	1.2	1.4
AXIS	275.3	565.2	352.4	376.7	1.3	1.3	1.2	1.2
C3C7	949.6	2,531.5	1,428.0	1,617.8	4.3	5.7	4.8	5.1
subtotal	(1,556.8)	(3,764.3)	(2,128.3)	(2,454.4)	(7.1)	(8.5)	(7.1)	(7.7)
THOR	2,307.8	4,884.7	3,395.2	3,773.1	10.5	11.1	11.4	11.8
LUMB	905.4	1,997.8	1,298.0	1,447.8	4.1	4.5	4.3	4.5
RIBS	2,560.7	5,911.0	4,381.3	5,456.9	11.7	13.4	14.7	17.1
STER	504.2	1,096.7	677.2	731.5	2.3	2.5	2.3	2.3
subtotal	(6,278.1)	(13,890.2)	(9,751.7)	(11,409.3)	(28.6)	(31.5)	(32.6)	(35.7)
SAC1	592.7	1,251.3	990.2	1,016.9	2.7	2.8	3.3	3.2
PELV	1,650.8	3,493.4	2,533.7	2,715.1	7.5	7.9	8.5	8.5
subtotal	(2,243.5)	(4,744.7)	(3,523.9)	(3,732.0)	(10.2)	(10.8)	(11.8)	(11.7)

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Table 5.14. (continued)

Carcass Unit	Fresh Bone Weight (gm)				Percent of Total Fresh Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	1,031.2	3,074.5	1,956.2	1,936.5	4.7	7.0	6.5	6.1
HUM	2,572.6	4,811.6	2,991.4	3,081.1	11.7	10.9	10.0	9.6
RUL	1,747.8	3,540.1	2,216.3	2,229.5	8.0	8.0	7.4	7.0
CARP	340.7	588.2	386.3	338.1	1.6	1.3	1.3	1.1
subtotal	(4,661.1)	(8,939.9)	(5,594.0)	(5,648.7)	(21.2)	(20.3)	(18.7)	(17.7)
FEM	2,938.8	4,819.7	3,286.3	3,326.5	13.4	10.9	11.0	10.4
PATE	149.5	276.1	193.3	204.4	0.7	0.6	0.6	0.6
TIB	2,052.4	3,212.1	2,371.1	2,264.6	9.3	7.3	7.9	7.1
TARM	1,041.4	1,321.2	1,063.1	1,021.7	4.7	3.0	3.6	3.2
subtotal	(6,182.1)	(9,629.1)	(6,913.8)	(6,817.2)	(28.2)	(21.9)	(23.1)	(21.3)
TOTAL (gm)	21,952.8	44,042.7	29,867.9	31,998.1				
(kg)	22.0	44.0	29.9	32.0				

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Table 5.15. Fresh Bone Weight in the Complete Non-Standard Carcass

Carcass Unit	Fresh Bone Weight (gm)				Percent of Total Fresh Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKULL	2,409.8	6,563.0	3,983.2	4,273.8	8.6	11.6	10.3	10.4
MAND	871.8	1,523.8	1,353.7	1,516.7	3.1	2.7	3.5	3.7
HYOID	12.0	76.7	48.8	41.7	T[a]	0.1	0.1	0.1
subtotal	(3,293.6)	(8,163.5)	(5,385.7)	(5,832.2)	(11.7)	(14.4)	(14.0)	(14.2)
ATLAS	331.9	667.6	347.9	459.9	1.2	1.2	0.9	1.1
AXIS	275.3	565.2	352.4	376.7	1.0	1.0	0.9	0.9
C3C7	949.6	2,531.5	1,428.0	1,617.8	3.3	4.5	3.7	3.9
subtotal	(1,556.8)	(3,764.3)	(2,128.3)	(2,454.4)	(5.5)	(6.6)	(5.5)	(6.0)
THOR	2,307.8	4,884.7	3,395.2	3,773.1	8.2	8.6	8.8	9.2
LUMB	905.4	1,997.8	1,298.0	1,447.8	3.2	3.5	3.4	3.5
RIBS	2,560.7	5,911.0	4,381.3	5,456.9	9.1	10.4	11.4	13.3
STER	504.2	1,096.7	677.2	731.5	1.8	1.9	1.8	1.8
subtotal	(6,278.1)	(13,890.2)	(9,751.7)	(11,409.3)	(22.3)	(24.5)	(25.3)	(27.8)

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Table 5.15. (continued)

Carcass Unit	Fresh Bone Weight (gm)				Percent of Total Fresh Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SAC1	592.7	1,251.3	990.2	1,016.9	2.1	2.2	2.6	2.5
PELV	1,650.8	3,493.4	2,533.7	2,715.1	5.9	6.2	6.6	6.6
subtotal	(2,243.5)	(4,744.7)	(3,523.9)	(3,732.0)	(8.0)	(8.4)	(9.1)	(9.1)
SCAP	1,031.2	3,074.5	1,956.2	1,936.5	3.7	5.4	5.1	4.7
HUM	2,572.6	4,811.6	2,991.4	3,081.1	9.1	8.5	7.8	7.5
RUL	1,747.8	3,540.1	2,216.3	2,229.5	6.2	6.3	5.7	5.4
CARP	340.7	588.2	386.3	338.1	1.2	1.0	1.0	0.8
MTC	740.3	1,139.0	836.8	800.3	2.6	2.0	2.2	1.9
APHS	602.6	1,065.9	772.0	745.3	2.1	1.9	2.0	1.8
subtotal	(6,004.0)	(11,144.8)	(7,202.8)	(7,194.3)	(21.3)	(19.7)	(18.7)	(17.5)

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Table 5.15. (continued)

Carcass Unit	Fresh Bone Weight (gm)				Percent of Total Fresh Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
FEM	2,938.8	4,819.7	3,286.3	3,326.5	10.4	8.5	8.5	8.1
PATE	149.5	276.1	193.3	204.4	0.5	0.5	0.5	0.5
TIB	2,052.4	3,212.1	2,371.1	2,264.6	7.3	5.7	6.1	5.5
TARM	1,041.4	1,321.2	1,063.1	1,021.7	3.7	2.3	2.8	2.5
MTT	908.6	1,235.0	975.9	910.8	3.2	2.2	2.5	2.2
PPHS	570.5	880.5	671.6	698.1	2.1	1.6	1.7	1.7
subtotal	(7,661.2)	(11,744.6)	(8,561.3)	(8,426.1)	(27.2)	(20.7)	(22.2)	(20.5)
CAUD	74.9	97.2	84.9	100.1	0.3	0.2	0.2	0.2
CARCASS TOTAL	28,143.3	56,623.8	38,594.8	41,084.9				

[a] T = trace (less than 0.1 percent)

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Table 5.16. Dry Bone Weight in the Complete Non-Standard Carcass

Carcass Unit	Dry Bone Weight (gm)				Percent of Total Dry Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKULL	2,409.8	6,563.0	3,983.2	4,273.8	13.5	17.5	14.9	14.5
MAND	915.6	1,561.8	1,400.2	1,557.0	5.1	4.2	5.2	5.3
HYOID	11.6	39.6	25.6	38.2	0.1	0.1	0.1	0.1
subtotal	(3,337.0)	(8,164.4)	(5,409.0)	(5,869.0)	(18.7)	(21.8)	(20.3)	(19.9)
ATLAS	192.4	432.8	229.0	310.0	1.1	1.2	0.9	1.1
AXIS	170.4	346.0	222.0	247.2	1.0	0.9	0.8	0.8
C3C7	579.2	1,639.2	953.0	1,096.8	3.2	4.4	3.6	3.7
subtotal	(942.0)	(2,418.0)	(1,404.0)	(1,654.0)	(5.3)	(6.5)	(5.3)	(5.6)
THOR	1,299.8	3,004.0	2,056.2	2,341.2	7.3	8.0	7.7	8.0
LUMB	549.4	1,194.2	855.2	944.2	3.1	3.2	3.2	3.2
RIBS	1,719.6	4,096.4	3,315.2	3,857.8	9.6	10.9	12.4	13.1
STER	157.2	245.0	240.0	216.0	0.9	0.7	0.9	0.7
subtotal	(3,726.0)	(8,539.6)	(6,466.6)	(7,359.2)	(20.8)	(22.8)	(24.2)	(25.0)

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Table 5.16. (continued)

Carcass Unit	Dry Bone Weight (gm)				Percent of Total Dry Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SAC1	340.8	595.6	517.0	562.6	1.9	1.6	1.9	1.9
PELV	1,072.0	1,909.0	1,564.2	1,710.4	6.0	5.1	5.9	5.8
subtotal	(1,412.8)	(2,504.6)	(2,081.2)	(2,273.0)	(7.9)	(6.7)	(7.8)	(7.7)
SCAP	719.8	1,779.0	1,224.4	1,499.4	4.0	4.8	4.6	5.1
HUM	1,295.8	2,626.4	1,704.0	1,937.4	7.2	7.0	6.4	6.6
RUL	1,031.4	2,098.0	1,458.0	1,614.0	5.8	5.6	5.5	5.5
CARP	197.4	339.0	255.4	278.6	1.1	0.9	1.0	0.9
MTC	488.6	846.2	606.2	619.0	2.7	2.2	2.3	2.1
APHS	345.0	658.6	512.0	566.0	1.9	1.8	1.9	1.9
subtotal	(3,358.2)	(6,568.2)	(4,535.6)	(5,015.0)	(18.8)	(17.6)	(17.0)	(17.0)

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Table 5.16. (continued)

Carcass Unit	Dry Bone Weight (gm)				Percent of Total Dry Bone Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
FEM	1,465.0	2,698.6	1,881.8	1,988.4	8.2	7.2	7.1	6.8
PATE	74.8	137.2	104.4	121.6	0.4	0.4	0.4	0.4
TIB	1,181.2	2,069.2	1,537.0	1,543.0	6.6	5.5	5.8	5.2
TARM	663.2	960.4	786.0	821.6	3.7	2.6	2.9	2.8
MTT	621.8	951.6	735.0	709.0	3.5	2.5	2.8	2.4
PPHS	354.8	577.0	462.2	516.4	2.0	1.5	1.7	1.8
subtotal	(4,360.8)	(7,394.0)	(5,506.4)	(5,700.0)	(24.4)	(19.8)	(20.6)	(19.4)
CAUD	30.0	54.6	44.2	65.0	0.2	0.1	0.2	0.2
CARCASS TOTAL	17,886.6	37,422.4	26,671.4	29,434.6				
(kg)	17.9	37.4	26.7	29.4				

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Table 5.17. Bone Volume in the Bison Side, Non-Standard Carcass

Carcass Unit	Bone Volume (cm^3)				Percent of Side Bone Volume			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
MAND	321.4	527.9	440.1	478.5	4.0	3.6	4.3	4.5
ATLAS	116.9	213.1	114.9	147.1	1.5	1.5	1.1	1.4
AXIS	99.5	182.9	115.7	117.7	1.3	1.2	1.1	1.1
C3C7	325.7	828.7	471.4	518.4	4.1	5.7	4.7	4.8
THOR	780.5	1,651.9	1,077.8	1,166.2	9.8	11.3	10.6	10.9
LUMB	313.4	603.4	409.6	479.8	3.9	4.1	4.0	4.5
SAC1	212.4	367.6	302.4	330.7	2.7	2.5	3.0	3.1
PELV	584.7	1,118.7	834.1	868.6	7.3	7.6	8.2	8.1
CAUD	20.7	33.2	27.9	32.3	0.3	0.2	0.3	0.3
RIBS	839.6	1,966.7	1,472.6	1,697.2	10.5	13.4	14.5	15.8
STER	122.6	236.7	201.3	183.6	1.5	1.6	2.0	1.7
AXIAL TOTAL	(3,737.4)	(7,730.8)	(5,467.8)	(6,020.1)	(47.0)	(52.8)	(54.0)	(56.1)

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Table 5.17. (continued)

Carcass Unit	Bone Volume (cm^3)				Percent of Side Bone Volume			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	318.5	782.7	477.0	558.8	4.0	5.3	4.7	5.2
PHUM	420.8	854.0	472.1	508.3	5.3	5.8	4.7	4.7
DHUM	341.7	485.6	334.3	359.2	4.3	3.3	3.3	3.3
(HUM)	(762.5)	(1,339.6)	(806.4)	(867.5)	(9.6)	(9.1)	(8.0)	(8.1)
PRUL	260.4	480.8	304.7	337.4	3.3	3.3	3.0	3.1
DRUL	233.5	390.8	260.9	233.0	2.9	2.7	2.6	2.2
(RUL)	(493.9)	(871.6)	(565.6)	(570.4)	(6.2)	(6.0)	(5.6)	(5.3)
CARP	104.4	143.4	100.5	94.4	1.3	1.0	1.0	0.9
PMTC	78.0	130.5	89.5	92.1	1.0	0.9	0.9	0.9
DMTC	132.5	168.2	120.6	110.8	1.7	1.1	1.2	1.0
(MTC)	(210.5)	(298.7)	(210.1)	(202.9)	(2.6)	(2.0)	(2.1)	(1.9)
APHS	171.6	260.4	200.3	206.3	2.2	1.8	2.0	1.9
FORELIMB TOTAL	(2,061.4)	(3,696.4)	(2,359.9)	(2,500.3)	(25.9)	(25.2)	(23.3)	(23.3)

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Table 5.17. (continued)

Carcass Unit	Bone Volume (cm^3)				Percent of Side Bone Volume			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
PFEM	344.4	594.9	398.7	419.1	4.3	4.1	3.9	3.9
DFEM	519.7	787.9	553.9	522.7	6.5	5.4	5.5	4.9
(FEM)	(864.1)	(1,382.8)	(952.6)	(941.8)	(10.9)	(9.4)	(9.4)	(8.8)
PATE	50.4	81.1	56.5	59.2	0.6	0.6	0.6	0.6
PTIB	328.8	575.1	375.3	347.6	4.1	3.9	3.7	3.2
DTIB	197.1	260.7	201.8	192.0	2.5	1.8	2.0	1.8
(TIB)	(525.9)	(835.8)	(577.1)	(539.6)	(6.6)	(5.7)	(5.7)	(5.0)
TARS	303.9	364.2	297.1	272.1	3.8	2.5	2.9	2.5
PMTT	104.9	147.6	111.2	103.0	1.3	1.0	1.1	1.0
DMTT	151.7	187.0	140.0	122.0	1.9	1.3	1.4	1.1
(MTT)	(256.6)	(334.6)	(251.2)	(225.0)	(3.2)	(2.3)	(2.5)	(2.1)
PPHS	158.8	214.8	170.1	175.8	2.0	1.5	1.7	1.6
HINDLIMB TOTAL	(2,159.7)	(3,213.3)	(2,304.6)	(2,213.5)	(27.1)	(21.9)	(22.7)	(20.6)
SIDE TOTAL	7,958.5	14,640.5	10,132.3	10,733.9				

Differences in Bone Weight Distribution

Differences in animal size make it difficult to directly compare the size of bison bones between animals of different age or sex. By examining the size of one bone compared to the summed weight or volume of all bones, it is possible to make cross-animal comparisons and identify where a particular bone is proportionately smaller or larger in that animal than in the others. In this section I examine differences in bison bone weight distribution, because bone weight is most easily measured. In the following section I examine distribution differences in bone volume, because it was previously shown that this measurement is a better predictor of grease fat weight than dry bone weight.

Sex and age differences can be identified for individual bones and groups of bones by considering the distribution of bone weight throughout the skeleton. These bone weight distribution differences are not important unless these differences correspond to areas of high productivity of marrow and bone grease. The purpose of this section, therefore, is to identify distribution differences and similarities and determine their relationship to fat production which is used to construct models of carcass utility. Age and then sex differences are discussed.

Age Differences in Bone Weight Distribution. Age differences in individual bone weight are evaluated by comparing the percent individual bone weight to total bone weight for FYM with those of the older and more mature animals, SAM, SAF, and FAF. Tables 5.14 and 5.15 present the data for fresh bone weight for the standard and complete carcass, and Table 5.16 lists the dry bone weight data for the complete carcass. Where the percentages for FYM differ from those of the other animals, age-related distribution differences may be responsible. Bones showing no appreciable

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differences in the percentages of bone to total bone weight are judged not to be influenced by age or sex. These include the atlas, axis, sternum, patella, and tail for fresh bone weight distributions. Review of the dry bone weight distributions in the total carcass show no clear age or sex-related differences in these bones, nor in the hyoid, lumbar vertebrae, and possibly the anterior phalanges and sesamoids. Table 5.18 summarizes the findings of potential age-related differences in individual dry bone weight distribution and the direction of the difference of the values for the immature animal, FYM, from those of the older animals.

These bison data may be compared with early, intermediate, and late maturing bone in cattle, although differences and similarities are not necessarily diagnostic for bison. As in cattle, the limb elements are early maturing and represent a larger proportion of dry bone weight than in the three older animals. The third through the seventh cervical vertebrae, which in cattle are early maturing, and therefore, a larger proportion of the immature skeleton, are a smaller proportion of bone in FYM, thus indicating a possible age influence for this difference in these animals, and possibly indicating late maturity of this bone group in bison. The FYM pelvis differs very little from the mature females in the percent of total dry bone weight it represents (Table 5.16), but shows a bigger difference from the male, SAM, suggesting that age and sex are factors in the different percentages seen between these bison. In cattle, this bone is late maturing.

The ribs and scapula are both small in the proportion they represent of bone weight (Table 5.16), as expected for late maturing bone. In both FYM and SAM, these represent a smaller proportion of total bone weight than in the mature females. Like the pelvis, the sacrum, another late maturing bone

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Table 5.18. Possible Age-Related Differences in Dry Bone Weight Distribution

Unit	Bone[a] Maturation Class	FYM > SAM	FYM < SAM	FYM = SAM	FYM > Females	FYM < Females	FYM = Females	No Difference
SKULL	---		x			x		
MAND	---	x				x		
ATLAS	early			x			x	x
AXIS	early			x			x	x
C3C7	early		x			x		
THOR	intermed.		x			x		
LUMB	intermed.			x			x	x
SAC1	late	x					x	
PELV	late	x			x			
CAUD	---							x
RIBS	late		x			x		
STER	intermed.							x
SCAP	late		x			x		
HUM	early	x			x			
RUL	early	x			x			
CARP	early	x			x			
MTC	early	x			x			
APHA	early			x			x	x
FEM	early	x			x			
PATE	early			x			x	x
TIB	early	x			x			
TARS	early	x			x			
MTT	early	x			x			
PPHA	early	x			x			

[a] Source: Jones et al. (1978)

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in cattle, was proportionately heavier than in the older male, but of similar proportion to that found in the older females. Once again, this suggests age-related differences only within the male sex of this sample and suggests sex as the controlling factor. The thoracic vertebrae, which in cattle are intermediate in maturation, are smaller relative to the total bone weight in this young bison than in all of the older animals. This is the only bone group in the intermediate maturation bone class for cattle that showed potential age-related differences in bison. The skull and mandible, not being part of the standard carcass in cattle, were not classified to maturation class in cattle. In this set of data, the skull does not appear to be an early maturing bone, and is smaller in this young bison than in all the older animals. The mandible is comparable to the females, but is a larger percentage than in the older male, suggesting another element with sex-related age differences.

The importance of age-related differences in bone weight distribution must be evaluated in terms of their productivity in marrow and bone grease. Clearly age is important to total carcass composition, because the bones of the limbs assume a greater proportion of the carcass weight in young than in older animals. This is important because these are the bones that provide marrow and the higher valued white bone grease in ungulates (Binford 1978:34,73). These factors must be considered for their effect upon construction and application of utility indices.

Sex Differences in Bone Weight Distribution. In cattle, Jones et al. (1978) found no sex differences in the pattern of individual bone growth with increases in total side bone weight. Their study covered a wide range of carcass weights, and therefore, probably a wide range of animal ages and stages of maturity. Comparing the weights of individual bones to total bone

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in animals of varied ages should result in great variability between animals. The authors noted this variability, but failed to consider the consequences on their tests of sex difference. By failing to control for differences in maturity and thus, failing to reduce the range of variability in bone weights, not surprisingly, sex differences were found not to be significant. This does not demonstrate, however, that there are no sex-related differences in bone weight. It demonstrates only that in a population including mature and immature individuals, sex differences cannot be statistically shown. Based upon this small sample of bison, I believe that such differences would be identified if animal maturity were controlled. Jones et al. (1978) did find both breed and sex differences when adjustments were made to equalize total side bone weight. They attributed this to differences in the stage of maturity of the animals studied, however, and did not believe them to be economically important. However, in their study, by equalizing total side bone weight, the authors were comparing animals more closely matched in maturity than when they compared the population as a whole. Admittedly, males and females at equal bone weight are not equally mature, but it is possible that another test in which maturity was matched would result in significant sex differences in individual bone weight to total bone weight.

The animals used in this study of bison carcass composition are different ages and at different stages of maturity, and no two of them can be matched for total bone weight. The bones of the standard carcass that Jones et al. (1978) found to differ in the rate of growth at similar total bone weight between sexes in cattle include: the femur, patella, radius-ulna, humerus, thoracic vertebrae, sacrum-pelvis, scapula, and ribs. To identify sex differences in this sample of bison, one must note the trend in

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values from immature to mature animals and examine the values of the older male, SAM, and the females, SAF and FAF, in this light.

If one assumes that the bone weight distributions of FYM and the two females represent the trend from immaturity to maturity, then values for SAM that are not within or close to the range of the values for FYM and the females, or comparable to those of the females, may indicate areas of possible sex differentiation in bone weight distribution. This does not mean that those bones whose values fall between FYM and the females are not significantly different due to sex. Some bones may represent a significantly smaller portion of the total bone weight in males than in females. If this is already in effect at a young age, it would not be evident in this partially mature male. With a larger sample of animals in which sex and age were controlled, these elements could be identified. Where the value for SAM is smaller than those of both females, regardless of the value of FYM, note of the difference and the direction of the size difference is made (Table 5.19).

Some of the bone elements that show sex differences in distribution in relation to total fresh bone weight in the standard carcass in cattle, when animals are matched for total bone weight, do not show differences in bison that are unmatched for total fresh bone weight (Table 5.14). Sex differences were not evident in the lumbar vertebrae, femur, or patella as they were in cattle. Several bones, however, appear to show sex differences that were not identified in cattle. These include the cervical vertebrae (third through seventh), ribs, tarsals, and possibly the posterior phalanges (Table 5.19). If the entire carcass is evaluated, rather than limiting the investigation to the standard carcass (Table 5.15), then the skull and mandible, could be added to this list of potentially sex-influenced

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Table 5.19. Possible Sex-Related Differences in Bison Fresh and Dry Bone Weight Distributions

Unit	Bone[a] Maturation Class	Fresh Bone Weight Distribution			Dry Bone Weight Distribution	
		Cattle[a]	Male > Females	Male < Females	Male > Females	Male < Females
SKULL	---		x		x	
MAND	---			x		x
ATLAS	early					
AXIS	early					
C3C7	early		x		x	
THOR	intermed.	x		x		
LUMB	intermed.	x				
SAC1	late	x		x		x
PELV	late	x		x		x
CAUD	---					
RIBS	late			x		x
STER	intermed.					

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Table 5.19. (continued)

Unit	Bone[a] Maturation Class	Fresh Bone Weight Distribution			Dry Bone Weight Distribution	
		Cattle[a]	Male > Females	Male < Females	Male > Females	Male < Females
SCAP	late	x	x			
HUM	early	x	x		x	
RUL	early	x	x			
CARP	early					
MTC	early					
APHA	early					
FEM	early	x				
PATE	early	x				
TIB	early					
TARS	early			x		x
MTT	early					
PPHA	early			x		x

[a] Source: Jones et al. (1978)

differences in fresh bone weight distribution. In bison therefore, bones that appear to show sex differences in fresh bone weight include the skull and mandible, cervical and thoracic vertebrae, sacrum, pelvis, ribs, scapula, humerus, radius-ulna, and possibly the tarsals and posterior phalanges. The radius-ulna, posterior phalanges and sesamoids all lie outside the range of proportions noted for the immature male and the mature females, but are only one tenth of a percentage point outside that range. These may be different in males and females, but their proximity to the percentage range defined by the immature male and mature females makes it unclear. Again, as before, I must emphasize that the trends identified from these differences are not statistically testable with the current sample.

Fresh bison bone weight data were examined to see how they compare to cattle data in order to assess where problems related to sample size might be involved. Nevertheless, it is dry bone weight that must be examined, because it is this measure that is tied to grease fat weight. Table 5.16 presents the dry bone weight data, thus excluding all non-bone differences in bone weight distribution. From these data, it appears that the sex difference noted for the scapula was due to non-bone weight, because in this table the value for SAM falls within the range of values for the two females. The skull, mandible, cervical vertebrae, sacrum, pelvis, ribs, humerus, and possibly the tarsals and posterior phalanges all continue to register potential sex differences in weight distribution. Specifically, these data indicate that the skull, cervical vertebrae, and humerus are a larger proportion of the skeleton in males than in females, and that the mandible, sacrum-pelvis, ribs, tarsals, and possibly the posterior phalanges are a larger portion in females. Table 5.19 presents the results of these analyses of individual bone weight distribution.

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Of the bones that show possible sex-related differences in fresh bone weight distribution, only the humerus is an important marrow producing bone (Table 5.14). The difference here is quite small, however, and does not affect the ranking of bones by weight. Therefore, if bone weight distribution can be used as an indicator of marrow weight distribution, one would not expect selection of marrow bones within the carcass to differ in males and females--that is, a good marrow producing bone in a male should probably be a good marrow producing bone in a female. The abundance and distribution of marrow in males and females, and in mature and immature animals are examined in the next section.

The importance of the differences in bone weight distribution may lie in their influence on bone grease distribution, or as structural supports for sex-related differences in muscle development. It is doubtful that most of these sex differences in bone size would influence animal use for selection in bone grease processing. Most of the bones noted above as showing potential sex differences in their weight distribution in the carcass, produce what Binford (1978:34,73) calls yellow grease. Only the humerus, tarsals, and posterior phalanges exhibit potential sex differences in white grease fat producing bones. The humerus is larger in males, and the tarsals and posterior phalanges may be larger in females. These bones should be evaluated for sex differences in white grease fat production. In Binford's (1978) compilation of carcass utility models incorporating the meat, marrow, and grease products of the caribou and sheep, white grease is given greater value than yellow grease. One would expect that sex differences in bone weight distribution in the carcass may be somewhat influential in bone grease processing decisions related to both yellow and white grease processing. The differences in white grease fat bones are

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often relatively minor, however, and may not affect processing decisions in these bones.

Summary of Age and Sex Differences in Bone Weight Distribution. From this analysis of bison bone weight distribution in these four animals, I found that there are both age and sex differences evident that should be investigated further to confirm their statistical significance. In dry bone weight distributions, the atlas, axis, lumbar vertebrae, sternum, posterior phalanges, patella, and tail showed neither age nor sex differences. Possible age-related differences were found for most limb elements, the skull, mandible, third through seventh cervical vertebrae, thoracic vertebrae, sacrum, pelvis, and ribs. In young animals, the limbs represent a larger proportion of dry bone weight than in older animals. The other elements with age-related differences represent smaller proportions of total bone weight. Of these bones, the skull, cervical vertebrae, sacrum, pelvis, ribs, humerus, tarsals, and possibly the posterior phalanges showed sex differences in addition to age differences in the proportion they represent of dry bone weight. The elements in this group found in the hindquarter are larger in females than in males, and the elements of the head and neck (except for the mandible) are larger in males, than in females. The humerus is larger in males and the ribs are larger in females.

From this analysis it appears that sex differences are of only minor importance in bone weight distributions for bones that yield marrow or white bone grease. Increasing age, however, results in a decrease in the importance of marrow yielding bones in bone weight distribution.

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Differences in Bone Volume Distribution

Differences in bone grease fat weight are more closely tied to differences in bone volume than dry bone weight. Although bone volume is more difficult to measure than dry weight, the improvement in the R^2 values using bone volume to predict grease fat weight makes it a potentially more valuable measure. In this section, I examine the bison data for differences in bone volume distribution between the animals. I know of no other data from livestock studies that examine age and sex differences in bone volume.

Table 5.17 above, presents the bone volume and the percent of total bone volume for each skeletal element. Age differences appear to exist in the distribution of bone volume between the immature male, FYM, and the older male, SAM, with elements sometimes representing a larger or smaller proportion of total volume in the younger than older animal. Bones that represent a smaller percentage of total carcass bone volume in FYM than in SAM include the mandible, cervical vertebrae, thoracic vertebrae, pelvis, ribs, and scapula (Table 5.20). Bones that represent a larger proportion of total bone volume in the immature bison, FYM, than in the more mature male, SAM, include elements from the limbs, as would be expected given the normal pattern of animal growth. The larger proportions of total volume in FYM are most pronounced in the hindlimb bones, where each element from the femur to the phalanges represents a substantial difference in percent of total volume. The age difference is less well pronounced in the forelimb elements, being most evident in the humerus and metacarpal, and less evident in the radius-ulna, carpals, and phalanges. This difference between the hind- and forelimb elements suggests that in addition to showing a distal to proximal direction of growth, a hindlimb to forelimb gradient may also exist with earlier growth registered in the hindlimb.

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Table 5.20. Possible Age-Related Differences in Bone Volume Distribution

Unit	Maturation[a] Class	FYM > SAM	FYM < SAM	FYM = SAM
MAND	---		x	
ATLAS	early			x
AXIS	early			x
C3C7	early		x	
THOR	intermediate		x	
LUMB	intermediate			x
SAC1	late	x		
PELV	late		x	
CAUD	---			x
RIBS	late		x	
STER	intermediate			x
SCAP	late		x	
HUM	early	x		
RUL	early	x		
CARP	early	x		
MTC	early	x		
APHA	early	x		
FEM	early	x		
PATE	early			x
TIB	early	x		
TARS	early	x		
MTT	early	x		
PPHA	early	x		

[a] Source: Jones et al. (1978)

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Age differences may be responsible for the percent of total bone volume differences seen between the seven year old female, SAF, and the 16-1/2 year old female, FAF, as well (Table 5.17). Many of the leg bones show a smaller percent of total bone volume in the older female, FAF, while the axial elements show higher percentages than SAF. This might represent random variability between sample specimens, or it might be related to changes that sometimes occur with increasingly advanced age. I cannot evaluate this with the currently available data.

Sex differences in bone volume distribution are also evident in the bison data presented in Table 5.17 and are summarized in Table 5.21. The proportion that a bone or bone group represents of total bone volume is larger in the male, SAM, than in the two females in the cervical and thoracic vertebrae, the humerus, and possibly the radius. The male appears smaller than the females in the percent of total bone volume in the mandible, sacrum, pelvis and ribs. These bone volume distribution differences complement those for dry bone weight for the most part. The tarsals and phalanges no longer show sex differences when bone volume is the measure, and the radius-ulna, which showed no dry bone weight distribution difference between sexes, does in bone volume, with the male being larger than the females.

Age and sex differences in bone volume distribution occur in bones that are both important and unimportant in the production of highly valued bone grease fat. Age differences from immature to mature animals show growth occurring most markedly in bones that become most valued for their production of white bone grease--the limb bones. As noted previously, however, distribution differences do not indicate the presence of animal

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Table 5.21. Possible Sex-Related Differences in Bone Volume Distribution

Unit	Maturation[a] Class	Male > Females	Male < Females	No Difference
MAND	---		x	
ATLAS	early			x
AXIS	early			x
C3C7	early	x		
THOR	intermed.	x		
LUMB	intermed.			x
SAC1	late		x	
PELV	late		x	
CAUD	---			x
RIBS	late		x	
STER	intermed.			x
SCAP	late			x
HUM	early	x		
RUL	early	x		
CARP	early			x
MTC	early			x
APHA	early			x
FEM	early			x
PATE	early			x
TIB	early			x
TARS	early			x
MTT	early			x
PPHA	early			x

[a] Source: Jones et al. (1978)

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production differences. Although immature animals have higher percentages of total bone volume in the limbs than do adults, their bone volumes are also smaller.

Sex differences occur most frequently in bones of the axial skeleton (except for the humerus and possibly the radius-ulna). With the exception of these appendicular elements, the sex differences occur in bones that are not as highly valued for their grease fat as reported by Binford (1978) among the Nunamiut hunters. The differences in the humerus and possibly the radius-ulna, might be important, however, if sex differences in grease fat production between the sexes do not override the differences in bone volume. These differences are examined in the section on grease fat production and distribution.

Bone Marrow Production and Distribution

The possibility that age and sex differences exist in marrow production and distribution must be considered in several respects. First, are there differences in the production of marrow relative to the weight of the carcass? Second, are there age, sex, or animal condition differences in the distribution of marrow cavity volume, marrow weight, percent marrow fat, or marrow fat weight relative to the totals for each of these variables? Ideally, it would be important to evaluate the fatty acid composition of the marrow as well, but this aspect of the research project was omitted due to time and budget constraints.

Total Marrow Production Differences

The way in which marrow production is considered determines whether age, sex, and condition differences are evident in bison. When production

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is considered in terms of the proportion it represents of total carcass or standard carcass weight, there appear to be no differences in production. When production is considered in the quantity of product available from a given animal, there are marked differences between animals.

In the previous section, bone marrow was found to represent 0.4 percent of standard carcass weight (excluding the head and distal limbs) in all but the immature bison, FYM. Marrow in this animal was 0.5 percent of standard carcass weight. Adding the marrow of the mandible, metapodials, and first phalanges provides the total weight of marrow from the medullary cavities in the complete bison carcass (referred to in this dissertation as the nonstandard carcass to differentiate it from the standard carcass of the livestock industry). Table 5.22 shows that the addition of these elements does not alter the percent that marrow represents of the carcass. This suggests that neither sex nor age greatly affect total marrow production relative to carcass weight as measured by marrow weight. It is doubtful that the difference noted for the immature male, FYM, is significant. If so, however, it indicates that marrow represents a slightly higher proportion of the animal carcass in immature individuals than in mature adults.

Marrow fat weight, like marrow weight, represents a minor proportion of the total carcass, and its proportion does not appear to be affected by animal age or sex (Table 5.23). The proportion that marrow fat weight represents of the bison carcass is similar for all four animals, ranging from 0.3 percent to 0.4 percent of carcass weight.

Despite the equality in the proportion that marrow weight represents of the total carcass weight, there are clear differences in the relative production of marrow between these four individual bison. The marrow

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Table 5.22. Comparative Weights and Proportions of Marrow in Complete Bison Carcasses

	FYM		SAM		SAF		FAF	
Carcass Type[a]	Weight (gm)	Percent of Carcass	Weight (gm)	Percent of Carcass	Weight (gm)	Percent of Carcass	Weight (gm)	Percent of Carcass
Standard	797.2	0.5	1,322.4	0.4	1,009.6	0.4	978.2	0.4
Non-standard	949.6	0.5	1,539.2	0.4	1,204.0	0.4	1,189.6	0.4

[a] Standard carcass excludes the head, shanks and tail; non-standard carcass includes the standard carcass and the head, shanks and tail.

Table 5.23. Comparative Marrow Measurements in the Side Non-Standard Carcass of Bison

Part A. Marrow Measurements and Percent Contribution to Side Weight

Marrow Measurement	Weight or Volume				Percent of Side Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Marrow Cavity Volume (ml)	546.5	910.5	743.0	731.0	---	---	---	---
Marrow Weight (gm)	474.8	769.6	602.0	594.8	0.5	0.4	0.4	0.4
Marrow Fat Weight (gm)	385.5	618.1	514.1	451.8	0.4	0.3	0.4	0.3

Part B. Comparative Carcass Yields

Marrow Cavity Volume[a]

	FYM	SAM	SAF	FAF
FYM	---	60.02	73.55	74.76
SAM		---	122.54	124.56
SAF			---	101.64
FAF				---

Marrow Weight[a]

	FYM	SAM	SAF	FAF
FYM	---	61.69	78.87	79.83
SAM		---	127.84	129.39
SAF			---	101.21
FAF				---

Marrow Fat Weight[a]

	FYM	SAM	SAF	FAF
FYM	---	62.37	74.99	85.32
SAM		___	120.23	136.81
SAF			---	113.79
FAF				---

[a] cell values equal the vertical animal's weight or volume as a percent of the horizontal animal's weight or volume.

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weights recorded in Part A of Table 5.23 indicate that adult males (as represented by SAM) produce more marrow than adult females (as represented by SAF and FAF) and that immature animals (as represented by FYM) produce less marrow than adults. At some point between 1-1/2 and 4 years of age, male bison surpass female bison in the production of marrow, due to their greater size. This pattern is repeated for total marrow cavity volume, and marrow fat weight as well (Table 5.23, Part A).

The fact that marrow production is similar for all animals, when measured as a proportion of carcass weight, is important to the construction of utility indices. It indicates that the relative production of marrow in the bison carcass does not change with changing animal size. When any animal is killed, therefore, approximately 0.4 percent of the carcass should be marrow. Prehistorically, if marrow were an important component of the diet, however, a hunter would not overlook the fact that real differences exist in the absolute quantity of this resource available in animals of different age and sex. Under conditions where selection is possible due to the size of the kill, one might see variable use of marrow bones both between sexes and between components of the carcass that produce greater quantities of preferred marrow. One would expect as well, that age, sex, and condition differences might affect distribution of this product in the animal carcass. This aspect of marrow production is considered below.

Assessment of Animal Condition from Marrow Fat Content

In order to assess differences in marrow production and distribution in bison, one must determine whether the four individual animals are in comparable nutritional condition, and whether, as a group, they are representative of a healthy bison population. If this group is in poor

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condition, and if that condition affects distribution of marrow or marrow fat, then use of these results to construct utility models might lead to inappropriate conclusions when applied to an assemblage from a population of healthy animals. Additionally, if the animals are in variable condition, the assessment of age and sex differences as represented by these four animals might differ.

Differences in animal condition may be the result of long-term or short-term causes. Long-term causes affecting entire herds might include extended periods of poor forage quality and availability due to the compounded effects of climatic conditions over multiple seasons. Long-term causes for poor animal condition might also result from chronic conditions specific to individual animals. For example, an injury or a progressive condition that affects an animal's ability to consume and digest available food may have long-term effects on the amount of fat that may be stored in body tissues, and thus on an animal's ability to survive periods of low food availability. Short-term causes of relative differences in animal condition might occur due to differences in how animals of different age and sex classes are affected by normal seasonal fluctuations in food availability and quality, changes in energy requirements (e.g., increased energy demands of pregnancy or seasonal responses to environmental changes), or fluctuations in food intake (e.g., rut-related reductions in time spent feeding). Another factor of importance is how different measures of animal condition differentially register declines in the progression from good health to starvation.

Prior to discussing the conditions of the TRNP herd and the individual bison used in this study, an assessment should be made of the kinds of condition differences and causes that may be registered in bone marrow fat

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production. There is some disagreement in marrow fat/animal condition studies concerning whether short-term, seasonal changes in forage quality, quantity or intake are evident in reduced marrow content levels. In a description of the symptoms of malnutrition in deer, Harris (1945) indicated that bone marrow is the last fat depot to be utilized for energy production. Cederlund et al. (1986:723), however, indicate that fat mobilization is not sequentially exclusive--that is, not all body fat is used before marrow fat use begins. Cederlund et al. (1989:591) hypothesize that initially, fat mobilization may occur simultaneously in the fat depots, but differences in mobilization rates ultimately result in sequential patterns of depletion or deposition. Suttie (1983:563) found that red deer kidney fat is depleted in parallel to marrow fat when kidney fat levels are below 40 percent, showing the faster rate of early use of other fat depots. The question remains, therefore, whether short-term periods of submaintenance nutrition that occur on a seasonal basis (e.g., during the rut or in late pregnancy) would be evident in reduced fat levels in marrow.

In a study of 56 pronghorn antelope (Antilocapra americana) carcasses, Bear (1971:586) found no significant seasonal changes in the fat content of femur or tibia marrow fat for either males or females during the period of their study. Fong (1981:545) similarly found no evidence of seasonal variation in metatarsal marrow fat in moose (Alces alces) over two years of age, but fat depletion at this location would be relatively late compared to more proximal elements, so seasonal changes in condition might not be evident. Cederlund et al. (1989:590) also note that Fong's study area has relatively mild winters and good winter food supplies. The drop in moose mandible marrow fat content between adult male samples prior to and following the rut (Cederlund et al. 1989) suggests short-term changes in

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animal condition may be reflected in changes in marrow fat content as well.

Based upon these studies, it is possible that marrow fat content of the adult TRNP bison may reflect both long- and short-term responses to changes in their ability to meet energy requirements. Long-term causes of marrow fat reduction might include reduced quantity or quality of forage due to changes in weather patterns or chronic pathologies specific to individual animals. Short-term causes of submaintenance nutrition might be expected to have a higher impact on marrow fat levels when occuring in conjunction with other long- or short-term changes. In Chapter 3, the possibility of a long-term decline in forage quantity or quality was suggested for TRNP based upon a prolonged pattern of suboptimum climatic conditions. It is possible that short-term causes of suboptimum nutrition might also be evident in lowered marrow fat content in the TRNP bison. The animals SAF and SAM, collected in early spring, may exhibit lowered marrow fat levels in response to over-winter declines in forage quality and quantity. The female SAF, was pregnant when shot and may have lowered fat levels in response to greater energy requirements associated with reproduction. The female FAF, was killed in the fall when forage conditions are normally good. Cederlund et al. (1989) report that female moose do not respond like males with lowered marrow fat content to rut-related activities. Lowered marrow fat content in the adult female FAF, might be related to the long-term effects of lowered forage quality or quantity, or to a chronic abnormality evident in the left mandible and dental wear of this bison.

In a study of mandible marrow fat levels in moose, Cederlund et al. (1986:725) found that it was normal for calves to use marrow fat as a source of energy during the first seasons of low food availability and quality, because body fat had not yet accumulated to the point where these other fat

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reserves could sustain energy production during low food availability. Ballard and Whitman (1987:67) report rapid mobilization of marrow when moose calves are separated from cows. Similarly, Bjarghov et al. (1977:337) found metatarsal marrow fat content in reindeer calves dropped 50 percent during the winter, whereas fat content remained unchanged in adults during the period of their study. Short-term or seasonal fluctuations in marrow fat content might be evident in young animals, therefore, following a winter and spring of low food availability. The season of capture becomes important then in comparing the conditions of groups of young animals. Cederlund et al. (1986) also argue that low marrow fat content in young animals should not be used to assess the nutritional condition of adult populations. Seasonal tracking of the condition of young animals, however, should be similar to that of adults during periods of abundant food. It is doubtful that the young male, FYM (collected in the fall), would register exceptionally low marrow fat levels, unless the long-term availability and quality of food had been suppressed prior to his collection. Low fat levels in this yearling, therefore, should be related primarily to age and sex differences.

Assessment of Group Condition. Bone marrow fat content has often been studied as an indicator of an animal's or a herd's physiological condition (e.g., Riney 1955, Bear 1971, Anderson et al. 1972, Nichols 1975, Franzmann and Arneson 1976, Bjarghov et al. 1977, Fong 1981, Reich 1981, Suttie 1983, Cederlund et al. 1986, 1989, and Adamczewski et al. 1987b). In his study of antelope, Bear (1971:586) found no significant difference in the fat content of the tibia and femur. Reich (1981) and Nichols (1975), however, found that fat content can vary between bone marrow sites when animals are in variable or declining condition. Reich (1981) for example, found that in

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impala, fat mobilized faster in the hindlimb than in the forelimb elements. In assessing group condition, therefore, it is apparently important to analyze more than one bone marrow location. Marrow samples were collected from all available locations from the Theodore Roosevelt National Park (TRNP) bison, with the exception of the mandibles of the two fall collected animals.

Table 5.24 presents the percent fat for each of the bison marrow samples and Figure 5.14 illustrates these data for the major long bones. From these data it is apparent that marrow fat content is high in all four TRNP bison, but lower than that reported by Brink (1986) for bison from the Edmonton region of Alberta, Canada. The lower values of the TRNP bison may indicate normal patterns of population variability, or possibly a degree of nutritional stress in the TRNP specimens. Studies of winter-killed moose in Alaska (Franzmann and Arneson 1976) and impala in Africa (Reich 1981), however, indicate these TRNP animals are still comparably healthy. The femur marrow of the winter-starved moose nearly always showed less than 10 percent fat (Franzmann and Arneson 1976:339). The impala study (Reich 1981:417), which included a sample of both healthy and sick animals, included specimens with fat levels in the different limb bones that ranged from zero to over 90 percent. Generally, animals with marrow fat levels above 80 percent are considered to be in good condition, and Cederlund et al. (1986:724) disagree with the suggestion that levels below 80 percent in adult moose are indicative of fat mobilization. They suggest that adult moose with marrow fat levels above 70 percent were not experiencing serious nutritional stress.

Marrow fat content (Figure 5.14) in the TRNP sample ranged from 76 to 92 percent (in the major long bones), whereas, the corresponding range in

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Table 5.24. Fat Content of Bison Bone Marrow Determined by Ether Extraction

Anatomical Unit	Portion	Percent Fat			
		FYM	SAM	SAF	FAF
mandible	complete	---	46.51	53.82	---
scapula	complete	---	80.90	82.45	---
humerus	proximal	85.86	85.06	92.69	76.30
	distal	83.43	83.19	90.62	78.54
	complete	84.80	84.30	91.50	77.40
radius	proximal	84.22	82.22	88.86	82.61
	distal	87.80	86.73	91.17	82.67
	complete	85.70	84.10	89.50	82.60
ulna	complete	84.41	79.84	89.46	82.14
metacarpal	proximal	85.24	89.70	91.40	84.60
	distal	87.58	88.46	91.28	83.70
	complete	85.90	89.30	91.10	84.40
first phalanges	complete	88.99	81.00	85.93	82.58

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Table 5.24. (continued)

Anatomical Unit	Portion	Percent Fat			
		FYM	SAM	SAF	FAF
pelvis	complete	78.96	81.49	92.62	77.27
femur	proximal	84.01	81.79	91.13	80.53
	distal	88.23	86.95	90.41	75.73
	complete	85.70	83.60	90.90	78.90
tibia	proximal	85.19	86.52	91.07	78.54
	distal	88.07	83.75	89.15	84.93
	complete	86.40	85.50	90.20	81.10
metatarsal	proximal	90.19	85.98	90.68	83.37
	distal	88.67	86.73	91.04	80.73
	complete	89.80	86.20	90.70	82.50
first phalanges	complete	89.06	86.38	89.72	83.07

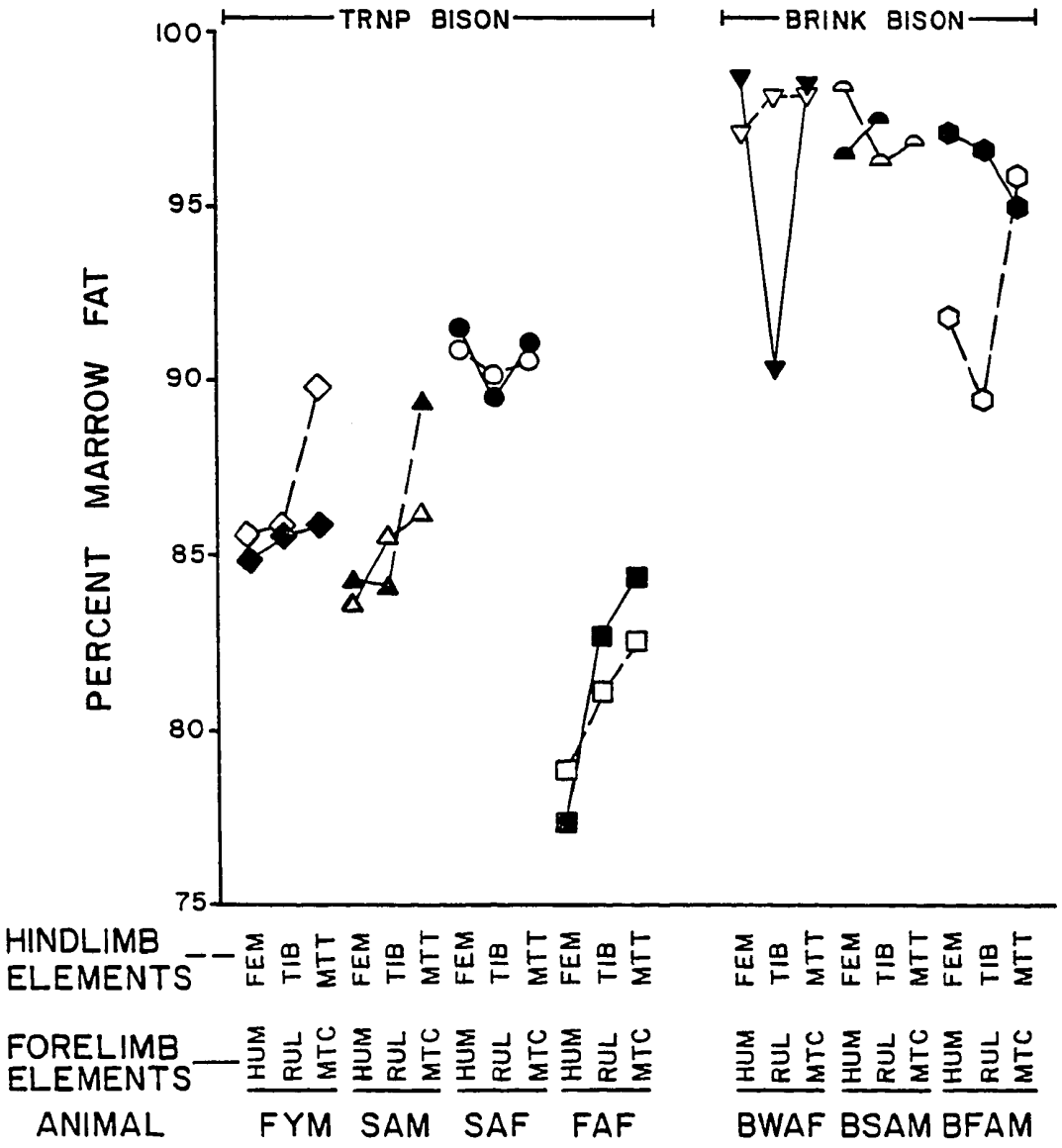

Figure 5.14. Fat Content of Marrow in Major Long Bones of TRNP and Brink Sample Bison. Brink data source: Brink (1986)

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the Brink (1986) sample was 89 to 99 percent. It appears that marrow fat values may show possible nutritional differences even at high levels of fat content. Mandible marrow fat levels were determined for two bison, SAM and SAF. The low value for SAM (46.5 percent) might be normal given the assessment of Cederlund et al. (1986) that male moose marrow fat content declines with age. The low fat value (53.82 percent) for the SAF mandible marrow, however, is much lower than the normal ranges recorded for female moose (76-78 percent) in Sweden. Mandible marrow is early to begin mobilization, but one of the last locations to be depleted. Davis et al. (1987:370) found a positive correlation in the percent marrow fat from mandibles and femurs of caribou (Rangifer tarandus granti). If generalizations between caribou, moose and bison are not out of order, then the low fat content in the bison samples may be indicative of poor condition. It should be noted, however, that the bison samples contained high percentages of non-marrow tissue (e.g., nerve tissue) which suggests that the low fat content might be due to this factor as well. The differences illustrated here, along with the data on winter starvation and disease, suggest that the TRNP bison are not in peak condition, but neither are they showing signs of serious nutritional stress. The expected declines in animal condition suggested in Chapter 3 by changes in weather data and assumed changes in forage quality may be in evidence here.

Assessment of Individual Animal Condition. The assessment of the condition of the four individual bison is important in order to avoid identifying possible sex and age differences in marrow production and distribution that instead might be due to differences in animal condition. To identify differences in the condition of the four bison, one must first have some expectation of their relationships to one another, based upon

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marrow studies in other game animals. The assumption of comparability between these ungulate species and bison, and between one specific marrow source and others, is necessary in order to clarify which bison, if any, are showing abnormal marrow fat levels. The identification of these differences, however, is tied to the recognition of age and sex differences in these other ungulates, and to the sequence of fat mobilization when marrow fat is used as a source of energy. To avoid circularity in the idenficiation of age and sex differences tied to condition differences, one must be careful not to use overall marrow fat levels alone to decide upon the relative condition of a particular animal. In this argument, therefore, the relative fat levels of the marrow between limb elements are used to assess whether fat mobilization may have been occurring when the bison were killed. The relative position of the percent fat curves (Figure 5.14) of the different animals are used to assess which animals are in better or poorer condition than normal. Before discussing the bison data, however, I briefly review some of the literature pertaining to marrow fat levels in ungulates.

In a study of impala, Reich (1981) found that a sequence of fat mobilization could be demonstrated for the limb bones. Reich found that when marrow fat is used for energy, mobilization began with the proximal limb bones and proceeded distally. If nutritional stress is severe and the animal is approaching starvation, the fat content of the distal, as well as the proximal limb bones, may be low. Initially, however, it is the fat of the proximal elements, and of the hindlimb before the forelimb (Reich 1981), that is used at a more rapid rate as a source for energy production when the diet is below maintenance.

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Reich's (1981) work suggests that one might expect, (1) comparable levels of fat in the limb bones in healthly animals; (2) lower fat levels in the femur and humerus in animals in the initial stages of prolonged nutritional stress; (3) lower fat levels in the proximal and medial elements in animals in intermediate stages of stress; and (4) low fat levels in all limb bones in animals in serious nutritional stress. Reported fat levels from impala killed by wild dogs (Reich 1981:417) show a great amount of variability in the ranking of bones by fat level within individual animals (Figure 5.15). Generally, however, when one or two elements are exceptionally lower in fat content than the others, it is the proximal elements that are lowest. One may expect, therefore, that bison with fat levels that are high, and clustered, are in relatively good condition, and if fat mobilization has begun, it should be evident first in the humerus and femur.

In addition to the sequence of fat mobilization and corresponding marrow fat percentages, normal patterns of marrow fat levels have been studied for individual bones between animals of different age and sex that were collected at different seasons of the year. Anderson et al. (1972:584) found that femur marrow fat levels in mule deer (Odocoileus hemionus) were significantly higher in females than in males, and in mature females than in immature females. Cederlund et al. (1989), however, found no sex differences in moose (Alces alces) mandible marrow fat between the sexes in the winter-spring period of their study. In an earlier study of mandible marrow fat in moose, Cederlund et al. (1986) found that females had high fat levels throughout life, while males showed lower marrow fat content with age. Moose calves had the lowest mandible marrow fat levels (58-60 percent), yearlings had intermediate fat levels (70 percent) and adults over two years of age had the highest marrow fat content (77-81 percent) during

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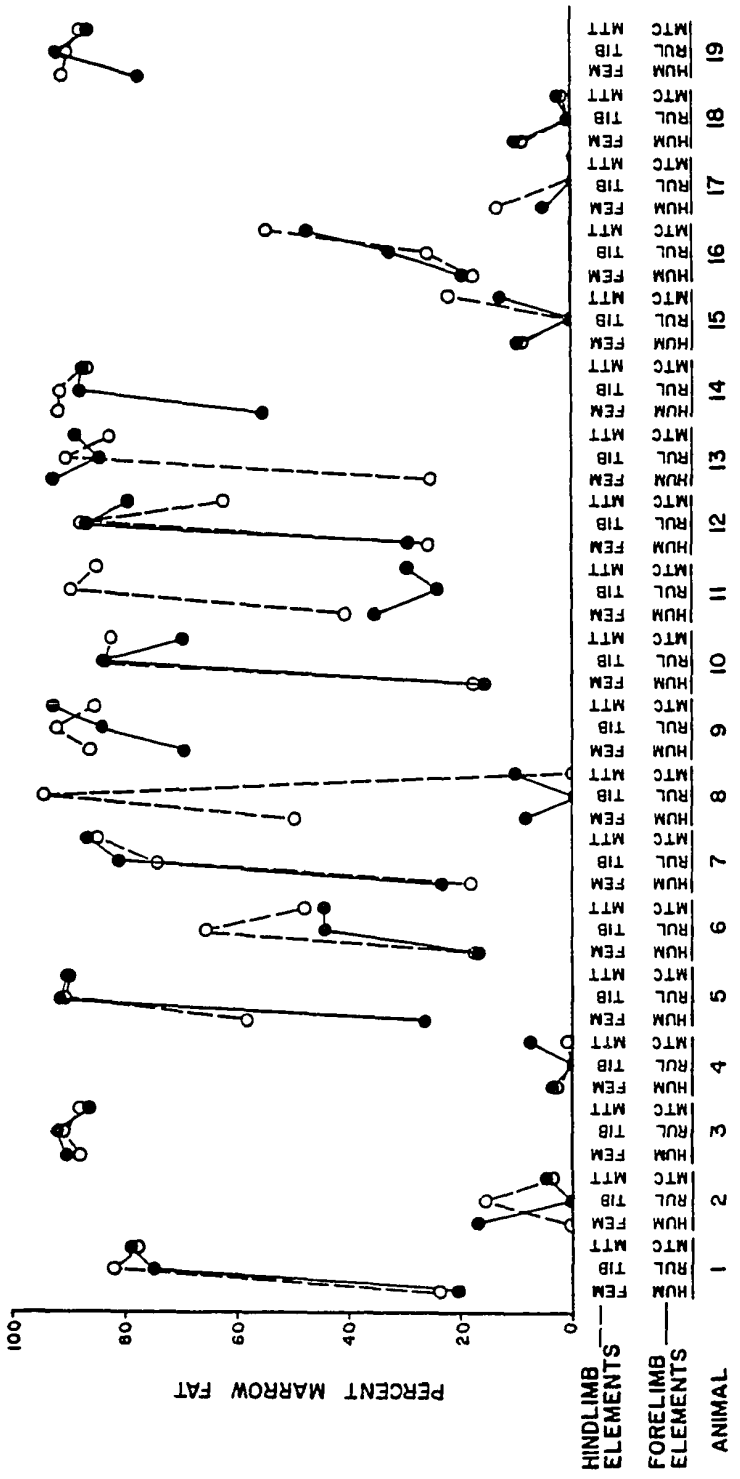

Figure 5.15. Fat Content of Marrow in Major Long Bones of Nineteen Impala. Source: Reich (1981:417)

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the pre-rut perod, while post-rut males 10 years old or older had the lowest fat levels (56 percent (Cederlund et al. 1989)). Female moose generally do not show substantial seasonal variations in mandible marrow fat content in autumn and winter, but female calves often must mobilize mandible marrow fat, while adult males generally accumulate fat in autumn and have high fat levels in winter (Cederlund et al. 1986:724).

For the TRNP bison, several expectations may be outlined. First, the two females, SAF and FAF, should have higher levels of marrow fat, because they are both mature adults; as they are both fully mature, there should be little difference between them. If there is a difference in fat levels between SAF and FAF, the fall-killed animal should have the higher levels of fat, because nutritional stress is not normally a factor in this season. If the relationship is reversed, the advanced age or abnormal dentition of the fall-killed female may be an important factor in her condition. Second, these reports also suggest that the fat levels of the yearling bison, FYM, may be higher than those of the older male, SAM, if the assumed, lowered spring season fat levels in SAM are large enough to compensate for the expected higher fat levels in four year olds than yearlings when the animals are not in a submaintenance regime. Given these expectations, the bison data are examined, first for evidence of fat mobilization indicating some degree of nutritional stress, and second, for differences from the expected relationships in fat levels between males and females and between younger and older males.

In Figure 5.14 and Table 5.24 it is evident that the femur and humerus of FAF and FYM have relatively lower fat percentages than the more distal bones. This is true as well for the hindlimb elements of SAM, but the humerus and radius-ulna have nearly the same fat content. Lower fat content

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in the proximal bones is not evident in the spring-killed female, SAF. Furthermore, the fat percentages of the medial and distal limb bones in FAF are lower than those in the other three bison, although these values are still above 80 percent. It appears, therefore, that early signs of nutritional stress are evident in the males and in the older female, FAF, and that it is most pronounced in this female. The younger female, SAF, does not appear to have mobilized marrow fat as a source of energy in the major marrow producing bones for a long enough period to demonstrate differential fat levels. The fact that the values for SAF are lower than those recorded for the apparently healthy bison in Brink's (1986) study, however, suggests that this animal may be showing some degree of stress, but not to the extent shown in the other three study specimens.

The evidence for differences in animal condition from the graphs of marrow fat content for each of the bison (Figure 5.14) correlates well with the relationships suggested by the sequencing of marrow fat mobilization noted by Reich (1981). Generally, for most bones, the percent fat is highest in the female, SAF, intermediate in the males, FYM and SAM, and lowest in the female, FAF.

The fact that the marrow fat levels for FAF are below those listed for both the young male, FYM, and the male, SAM, however, suggests that this female is exhibiting some degree of nutritional stress. Both the immature male, FYM, and FAF should have been approaching the seasonal peak in the levels of their marrow fat content, when they were collected in the fall. The lower values of FAF, therefore, in conjunction with SAF values that show the expected relationship between younger males and older females, and male values that show the expected relationship between seasonal collections, all suggest that FAF was experiencing some degree of nutritional stress. The

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fact that the values for FYM and SAM exceed the values for FAF is unusual.

Lower body fat in males (especially in young males) should make them more susceptible than females to changes in condition associated with energy intake. Despite the slightly lowered femur and humerus fat levels in the two males, which suggest the possible mobilization of marrow fat, the lower fat levels in the older female, FAF, are markedly lower than those of the more distal elements and indicate uneven susceptibility between animals to conditions that produce such effects.

The poorer condition of FAF is apparently not yet indicative of serious nutritional stress, nor could it have been in effect for a particularly prolonged period of time. This is evident in the fact that her marrow fat levels were well above the percentages shown for starving animals, and more directly by the fact that she had calved the spring prior to her fall collection. Her poorer condition may be due to the effects of advanced age, to a pathological abnormality of her jaw and teeth, or possibly to the combined effects of these factors and the normal energy demands of her most recent pregnancy, under the presumed conditions of poorer forage quality and/or quantity.

From the data presented above, which shows lower proximal limb marrow fat content, and lower between-animal fat content, it appears that FAF differs somewhat from the normal pattern of marrow fat levels for females, and that FAF, FYM, and SAM all have lower fat content in the femur and humerus than expected for animals in peak condition. Given these assessments, when the values for individual bones are compared for identification of sex-related differences, consideration should be given to the fact that the FAF value may be atypical of the normal healthy female value, and the femur and humerus values for these three bison may be lower than normal.

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It is apparent, however, from the values in Table 5.23 that these considerations of differences in animal condition apply only to marrow fat weight. They apply to neither marrow cavity volume, nor to marrow weight--at least, for animals in conditions comparable to the animals in this sample. If animal condition deteriorates to a much lower level, however, one might see differences registered in the marrow weight of different animals as well, as marrow fat is depleted and marrow water content increases. The bison in this sample, however, are not greatly different in their condition, and therefore, the difference in SAF and FAF for total marrow weight is not large (Table 5.23). The total cavity volume for SAF is 101.6 percent of that for FAF, indicating comparable size, and the marrow weight is 101.2 percent of the FAF marrow weight. Marrow fat weight in SAF, however, is 113.8 percent of that in FAF (Table 5.23, Part B). These condition factors should be taken into account when evaluating the age and sex differences in production and distribution in the marrow fat weight data.

The absence of major differences in the relationship of FYM to SAM (Table 5.23, Part B) in total marrow cavity volume, marrow weight, and marrow fat weight suggests that the differences that are observed in individual bone production and distribution between these two males are related to animal size and age, and not to their relative conditions. A similar lack of marked variability was noted for these two males in the percent fat in the marrow samples (Table 5.24). These data both suggest that the two males were in similar condition and that any differences observed between them in the production and distribution of bone marrow products may be attributed instead to age differences.

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Analysis of Individual Bone Marrow Production and Distribution Differences

In this section, I consider the amount of marrow, marrow fat, and marrow cavity volume produced for each bone element and the distribution of these products throughout the skeleton. The purpose here is to identify areas where age and sex influence marrow productivity, and therefore, may influence human use of this product.

For each marrow characteristic (i.e., medullary cavity volume, marrow weight, and marrow fat weight), there is a table indicating the volume of the cavity or weight of the product for each bone, as well as the percent of the total volume or product weight asssociated with each bone in each animal carcass (Tables 5.25, 5.26, and 5.27). Illustrations of the values derived in these tables for distribution and actual output per animal, are presented in Figures 5.16 through 5.21. The data in Table 5.24 and Figure 5.14 are mean percent fat values determined for marrow samples analyzed by ether extraction. These data were used to determine the marrow fat weight for each bone or bone half by multiplying the marrow sample weight by the percent extractable fat.

Based upon the data for the four bison presented in these tables and figures, the possibility of the occurrence of age or sex differences in production or distribution is evaluated. Summaries of the evaluations of the presence and direction of age or sex differences are presented in Tables 5.28 and 5.29. These two tables indicate whether immature animals (represented by FYM) show greater production or relative distribution of marrow cavity volume, marrow weight, or marrow fat weight than the more mature male, SAM. They also indicate where the male, SAM, shows differences in production or relative distribution of these products and volume than the females (as represented by SAF and FAF, or by SAF alone).

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Table 5.25. Comparative Marrow Cavity Volume and Distribution in the Bison Side

	Marrow Cavity Volume (ml)				Percent of Total Cavity Volume			
Unit	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
MAND	29.0	52.0	45.0	61.0	5.3	5.7	5.8	8.3
SCAP	1.0	8.0	5.0	0.0	0.2	0.9	0.7	0.0
PHUM	60.0	136.0	73.5	75.5	11.0	14.9	9.9	10.3
DHUM	45.5	73.0	80.5	67.0	8.3	8.0	10.8	9.2
HUM	(105.5)	(209.0)	(154.0)	(142.5)	(19.3)	(23.0)	(20.7)	(19.5)
PRAD	43.5	55.0	64.0	49.5	8.0	6.0	8.6	6.8
DRAD	29.0	46.0	28.0	30.0	5.3	5.1	3.8	4.1
ULNA	12.0	12.5	16.5	14.5	2.2	1.4	2.2	2.0
RUL	(84.5)	(113.5)	(108.5)	(94.0)	(15.5)	(12.5)	(14.6)	(12.9)
PMTC	17.0	23.0	19.5	28.0	3.1	2.5	2.6	3.8
DMTC	8.0	11.0	7.0	7.5	1.5	1.2	0.9	1.0
MTC	(25.0)	(34.0)	(26.5)	(35.5)	(4.6)	(3.7)	(3.6)	(4.9)
APHA	2.5	7.0	3.0	5.0	0.5	0.8	0.4	0.7
PELV	11.5	13.0	9.0	14.0	2.1	1.4	1.2	1.9
PFEM	64.5	149.0	119.0	109.0	11.8	16.4	16.0	14.9
DFEM	48.5	78.5	55.0	53.0	8.9	8.6	7.4	7.3
FEM	(113.0)	(227.5)	(174.0)	(162.0)	(20.7)	(25.0)	(23.4)	(22.2)
PTIB	85.0	126.5	95.0	97.5	15.6	13.9	12.8	13.3
DTIB	55.5	77.0	76.5	67.0	10.2	8.5	10.3	9.2
TIB	(140.5)	(203.5)	(171.5)	(164.5)	(25.7)	(22.4)	(23.1)	(22.5)
PMTT	21.5	24.0	30.0	29.5	3.9	2.6	4.0	4.0
DMTT	8.5	10.5	10.0	15.5	1.6	1.2	1.3	2.1
MTT	(30.0)	(34.5)	(40.0)	(45.0)	(5.5)	(3.8)	(5.4)	(6.2)
PPHA	4.0	8.5	6.5	7.5	0.7	0.9	0.9	1.0

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Table 5.26. Comparative Marrow Weight and Distribution in the Bison Side

	Marrow Weight (gm)				Percent of Total Marrow Weight[a]			
Unit	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	0.6	5.6	3.4	0.0	0.1	0.8	0.6	0.0
PHUM	53.9	106.9	48.3	57.0	12.0	14.6	8.5	10.1
DHUM	39.3	69.4	65.5	59.6	8.7	9.5	11.5	10.6
HUM	(93.2)	(176.3)	(113.8)	(116.6)	(20.7)	(24.1)	(20.0)	(20.7)
PRAD	39.6	53.0	58.0	46.0	8.8	7.3	10.2	8.2
DRAD	26.6	39.6	24.3	25.6	5.9	5.4	4.3	4.5
ULNA	10.1	10.0	13.7	12.1	2.2	1.4	2.4	2.1
RUL	(76.3)	(102.6)	(96.0)	(83.7)	(16.9)	(14.1)	(16.9)	(14.8)
PMTC	14.7	19.5	20.0	23.0	3.3	2.7	3.5	4.1
DMTC	6.2	9.1	4.6	5.2	1.4	1.2	0.8	0.9
MTC	(20.9)	(28.6)	(24.6)	(28.2)	(4.7)	(3.9)	(4.3)	(5.0)
APHA	2.2	2.2	1.4	2.3	0.5	0.3	0.2	0.4
PELV	7.2	6.4	3.7	7.4	1.6	0.9	0.7	1.3
PFEM	54.9	118.1	95.4	90.7	12.2	16.2	16.8	16.1
DFEM	37.5	66.4	44.0	45.3	8.3	9.1	7.8	8.0
FEM	(92.4)	(184.5)	(139.4)	(136.0)	(20.6)	(25.3)	(24.6)	(24.2)
PTIB	77.8	116.3	81.9	87.1	17.3	15.9	14.4	15.5
DTIB	51.1	69.5	66.6	58.3	11.4	9.5	11.7	10.4
TIB	(128.9)	(185.8)	(148.5)	(145.4)	(28.7)	(25.4)	(26.2)	(25.8)
PMTT	17.6	22.5	25.3	25.2	3.9	3.1	4.5	4.5
DMTT	6.3	8.5	7.2	12.4	1.4	1.2	1.3	2.2
MTT	(23.9)	(31.0)	(32.5)	(37.6)	(5.3)	(4.2)	(5.7)	(6.7)
PPHA	3.6	7.6	4.4	5.6	0.8	1.0	0.8	1.0

[a] Total marrow weight excludes mandible marrow for these calculations.

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Table 5.27. Comparative Marrow Fat Weight and Distribution in the Bison Side

	Marrow Fat Weight (gm)				Percent of Total Marrow Fat Weight[a]			
Unit	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	0.41	4.53	2.80	0.0	0.1	0.7	0.5	0.0
PHUM	46.28	90.93	44.77	43.49	12.0	14.7	8.7	9.6
DHUM	32.79	57.73	59.36	46.81	8.5	9.3	11.5	10.4
HUM	(79.07)	(148.66)	(104.13)	(90.30)	(20.5)	(24.1)	(20.3)	(20.0)
PRAD	33.35	43.58	51.54	38.00	8.7	7.1	10.0	8.4
DRAD	23.35	34.35	22.15	21.16	6.1	5.6	4.3	4.7
ULNA	8.53	7.98	12.26	9.94	2.2	1.3	2.4	2.2
RUL	(65.23)	(85.91)	(85.95)	(69.10)	(16.9)	(13.9)	(16.7)	(15.3)
PMTC	12.53	17.49	18.28	19.46	3.3	2.8	3.6	4.3
DMTC	5.43	8.05	4.20	4.35	1.4	1.3	0.8	1.0
MTC	(17.96)	(25.54)	(22.48)	(23.81)	(4.7)	(4.1)	(4.4)	(5.3)
APHA	1.96	1.78	1.20	1.90	0.5	0.3	0.2	0.4
PELV	5.69	5.22	3.43	5.72	1.5	0.8	0.7	1.3
PFEM	46.12	96.59	86.94	73.04	12.0	15.6	16.9	16.2
DFEM	33.09	57.74	39.78	34.31	8.6	9.3	7.7	7.6
FEM	(79.21)	(154.33)	(126.72)	(107.35)	(20.5)	(25.0)	(24.6)	(23.8)
PTIB	66.28	100.62	74.59	68.41	17.2	16.3	14.5	15.1
DTIB	45.00	58.21	59.37	49.51	11.7	9.4	11.5	11.0
TIB	(111.28)	(158.83)	(133.96)	(117.92)	(28.9)	(25.7)	(26.1)	(26.1)
PMTT	15.87	19.35	22.94	21.01	4.1	3.1	4.5	4.7
DMTT	5.59	7.37	6.55	10.01	1.5	1.2	1.3	2.2
MTT	(21.46)	(26.72)	(29.49)	(31.02)	(5.6)	(4.3)	(5.7)	(6.9)
PPHA	3.21	6.57	3.95	4.65	0.8	1.1	0.8	1.0

[a] Total excludes mandible marrow.

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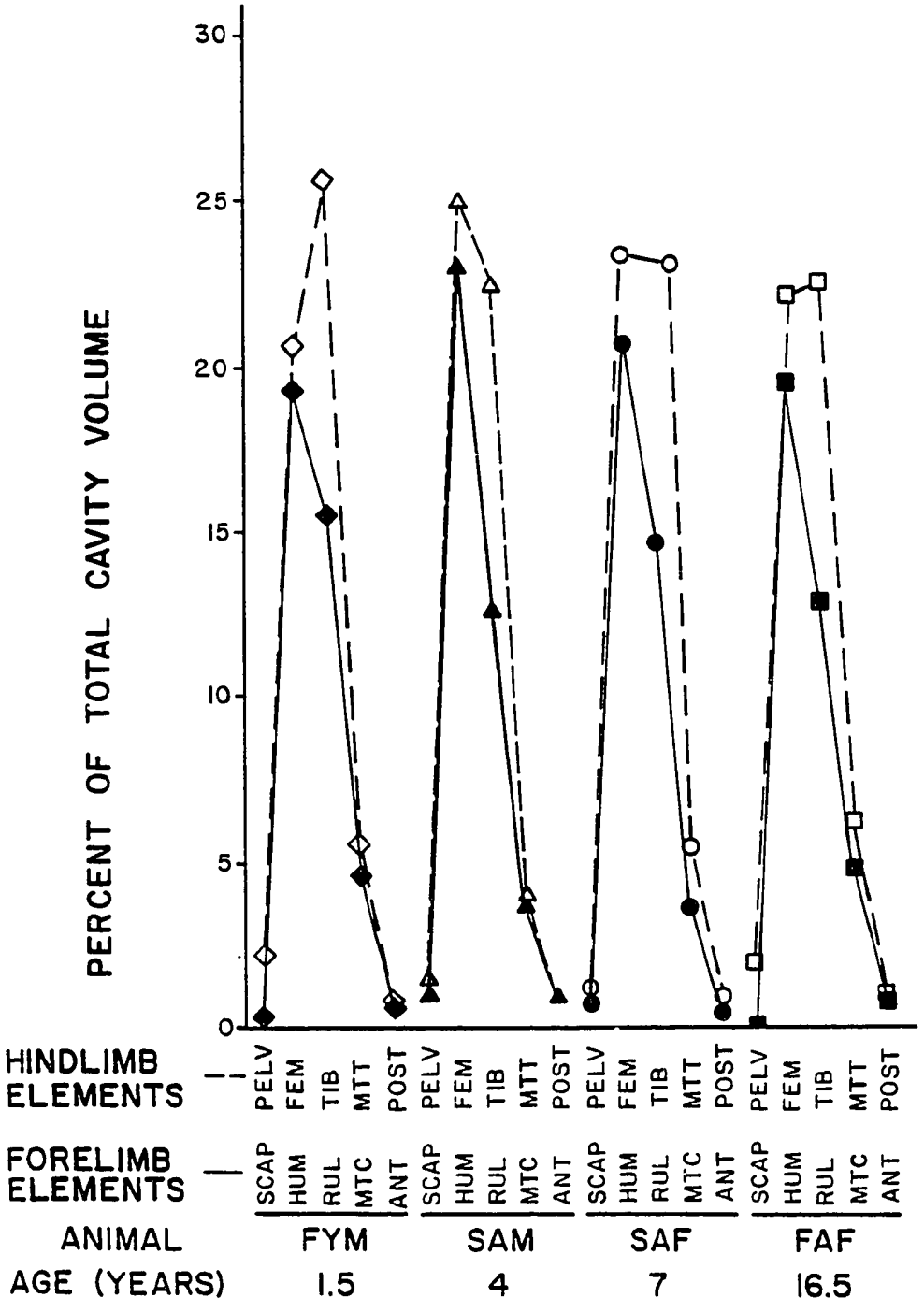

Figure 5.16. Comparative Distribution of Marrow Cavity Volume in the Bison Carcass.

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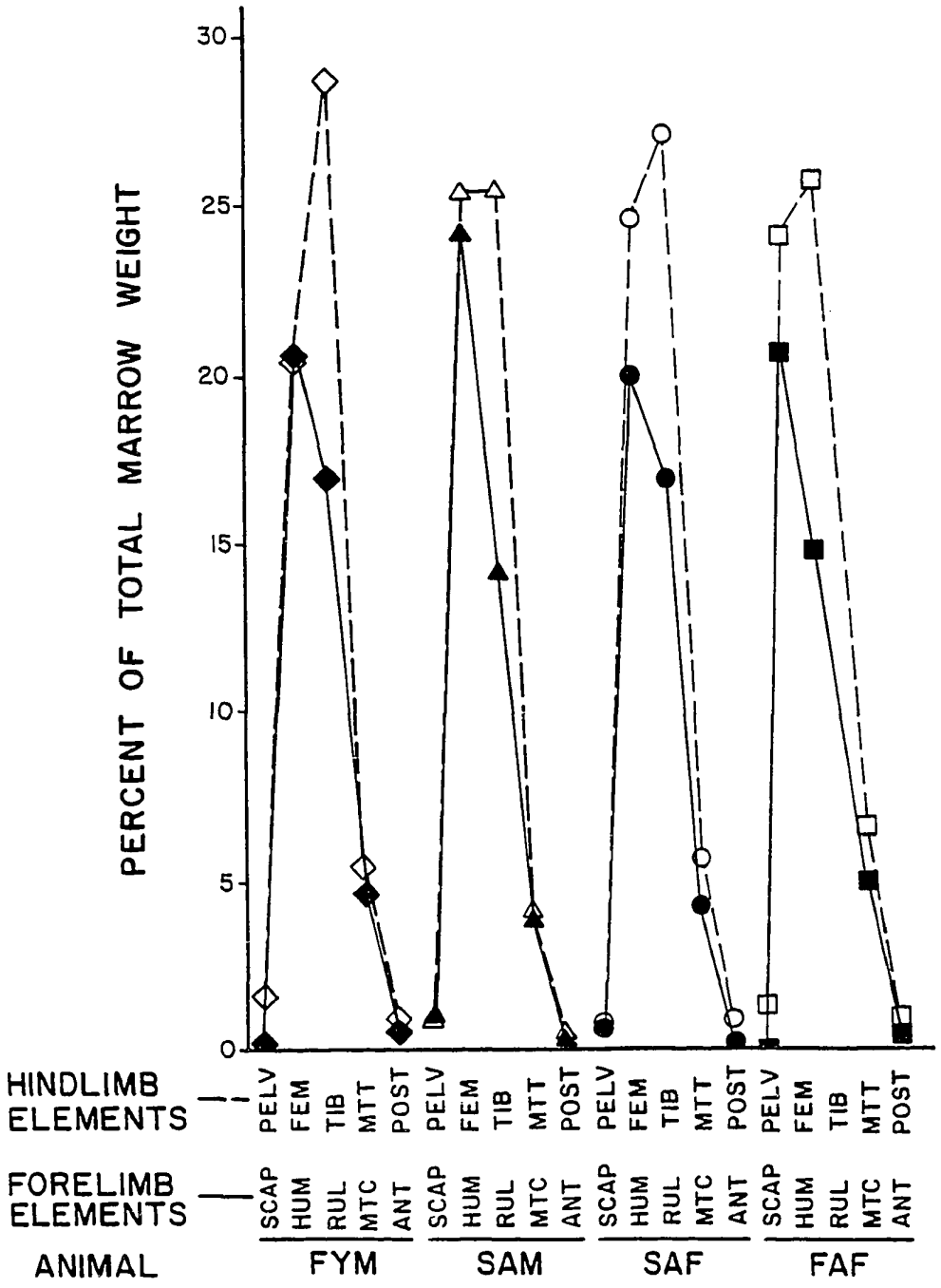

Figure 5.17. Comparative Distribution of Marrow Weight in the Bison Carcass.

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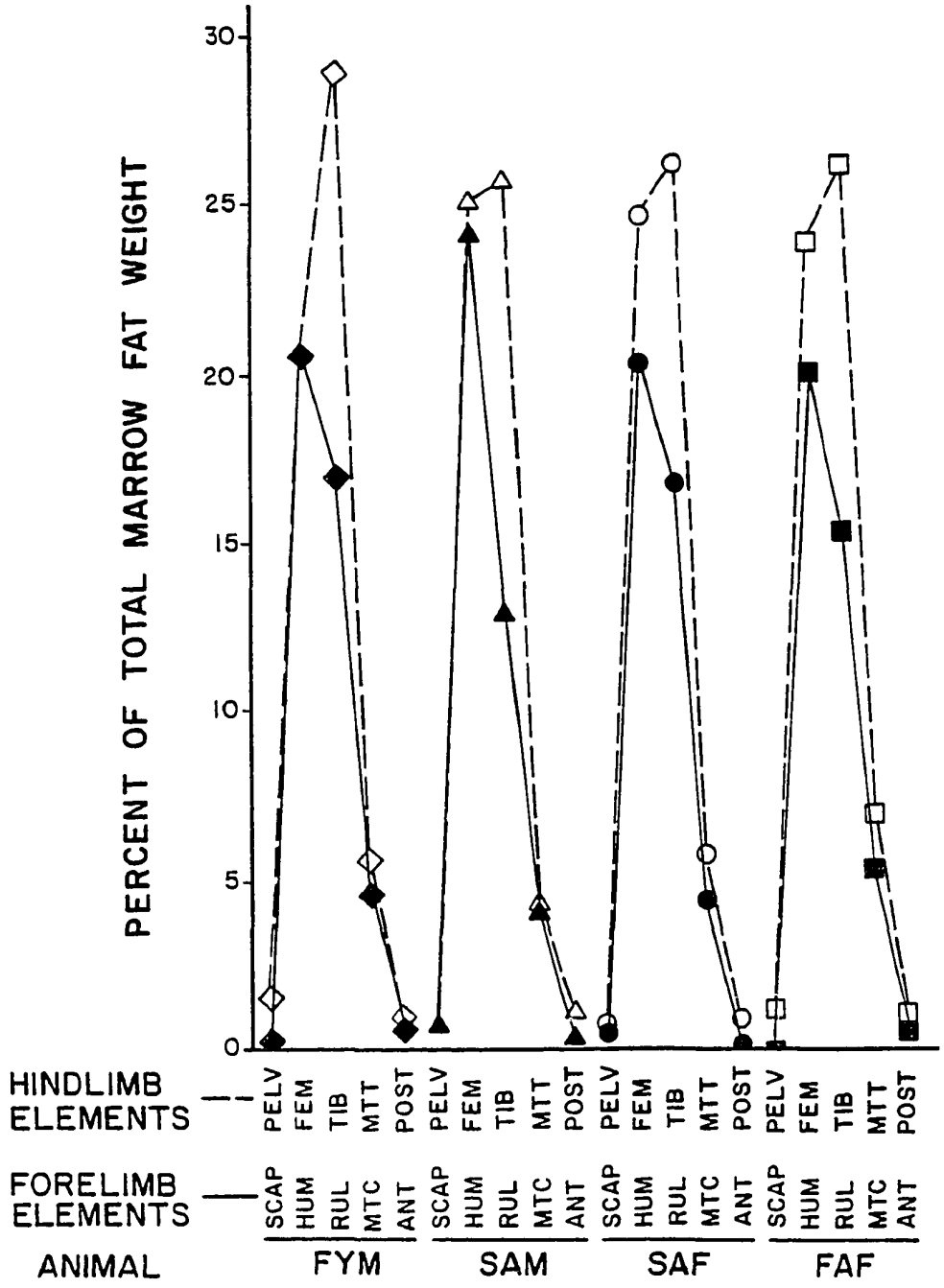

Figure 5.18. Comparative Distribution of Marrow Fat Weight in the Bison Carcass.

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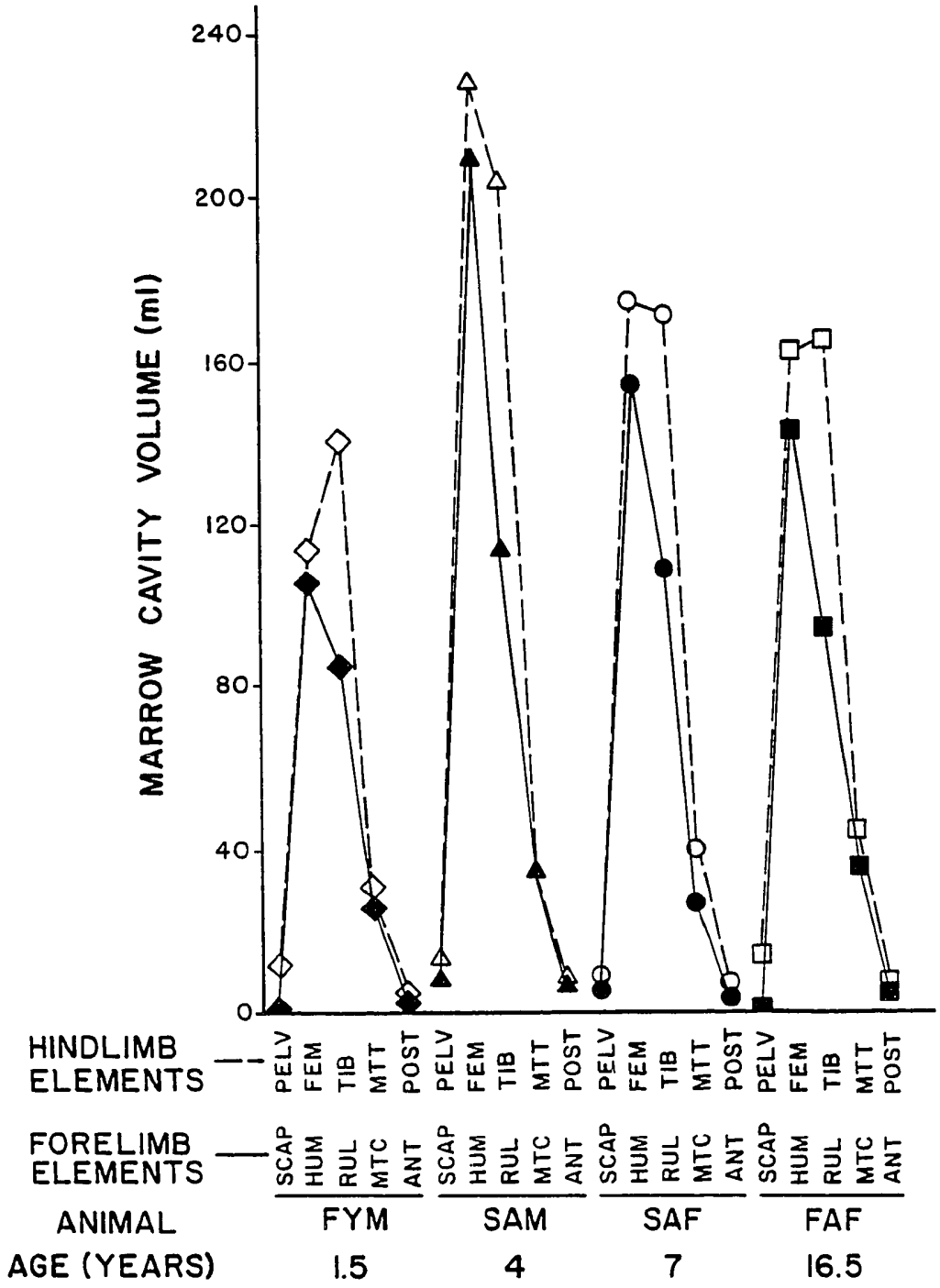

Figure 5.19. Comparative Volumes of Marrow Cavities of Bone in the Bison Side Carcass.

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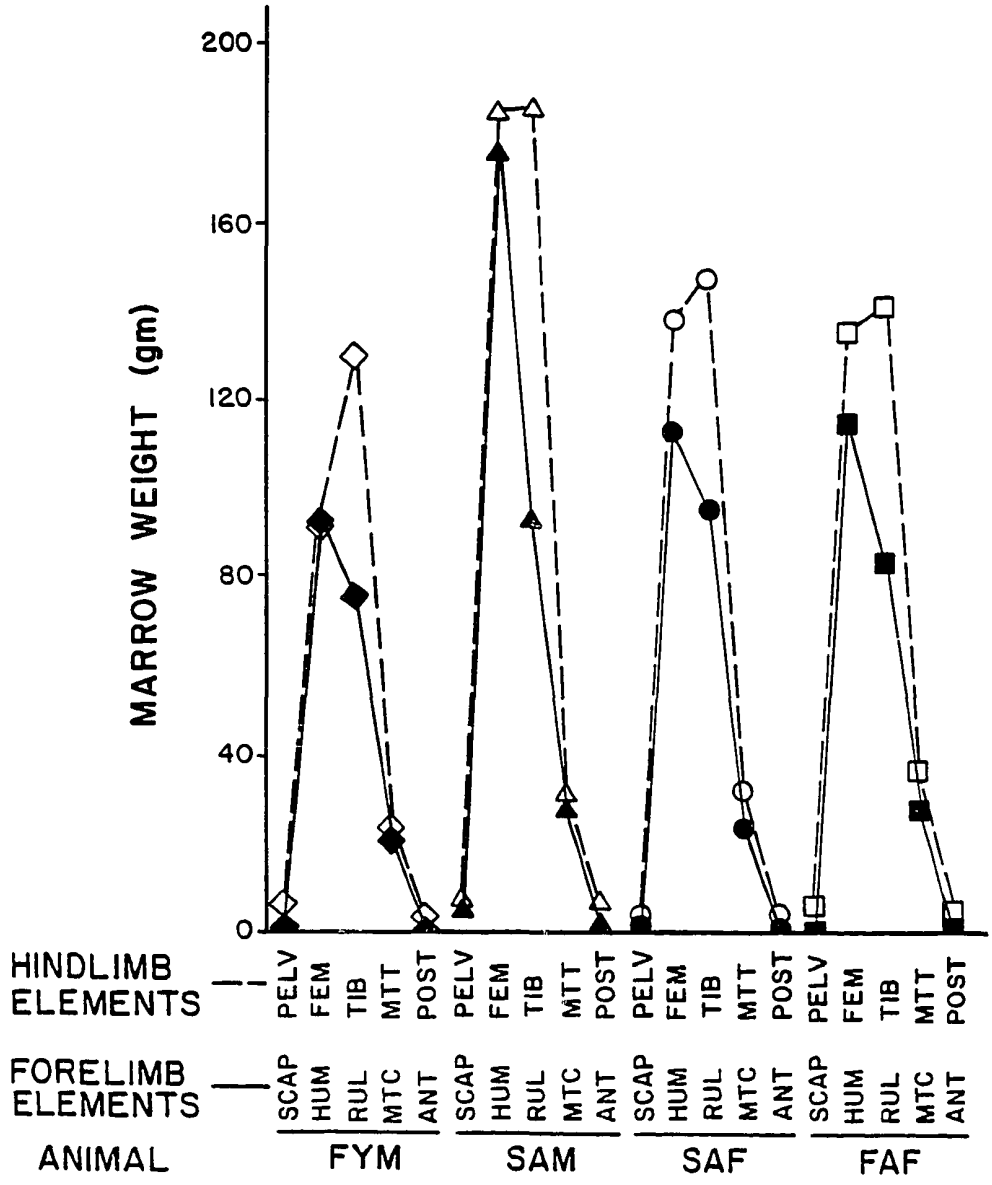

Figure 5.20. Comparative Production of Marrow in the Bison Side Carcass.

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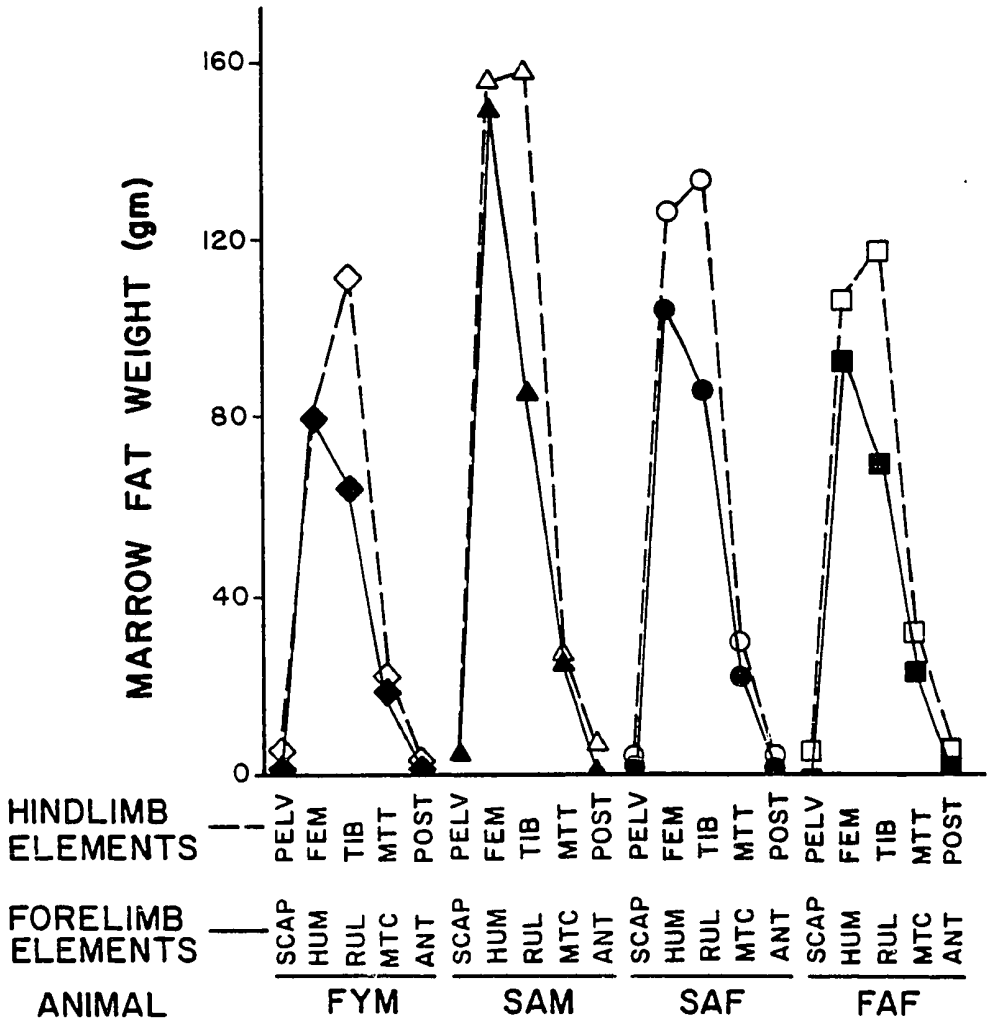

Figure 5.21. Comparative Production of Marrow Fat in the Bison Side Carcass.

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Table 5.28. Summary of Age and Sex Differences in Carcass Distribution of Marrow and Cavity Volume

	Cavity Volume Distribution				Marrow Weight Distribution				Marrow Fat Weight Distribution			
	Bison Age		Bison Sex		Bison Age		Bison Sex		Bison Age		Bison Sex	
Unit	I > M	I < M	M > F	M < F	I > M	I < M	M > F	M < F	I > M	I < M	M > F	M < F
MAND								x	---	---	---	---
SCAP		x				x			---	---	---	---
HUM		x	x			x	x			x	x	
RUL	x								x			x
MTC	x				x			x	x			x
APHA												
PELV	x				x				x			
FEM		x	x			x	x			x	x	
TIB	x				x				x			x
MTT	x			x	x			x	x			x
PPHA												

Bison Age: I = immature, M = mature; Bison Sex: F = Female, M = Male; x possible age or sex difference in distribution; --- data are not available

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Table 5.29. Summary of Age and Sex Differences in Carcass Yield of Marrow Weight and Cavity Volume

	Cavity Volume Distribution				Marrow Weight Distribution				Marrow Fat Weight Distribution			
	Bison Age		Bison Sex		Bison Age		Bison Sex		Bison Age		Bison Sex	
Unit	I > M	I < M	M > F	M < F	I > M	I < M	M > F	M < F	I > M	I < M	M > F	M < F
MAND		x				x			---	---	---	---
SCAP												
HUM		x	x			x	x			x	x	
RUL		x				x				x		
MTC						x	x			x	x	
APHA												
PELV												
FEM		x	x			x	x			x	x	
TIB		x	x			x	x			x	x	
MTT		x		x		x				x		x
PPHA		x	x			x	x			x	x	

Bison Age: I = immature, M = mature; Bison Sex: F = Female, M = Male; x data suggest possible age or sex difference in distribution; --- data are not available.

Distribution of Marrow Cavity Volume, Marrow and Marrow Fat Weight. Marrow fat weight, as a component of bone marrow weight, is directly correlated with the volume of the marrow cavity. Therefore, differences in the carcass distribution of marrow weight or cavity volume that are related to differences in animal age, sex, or condition, might also be evident in differences in marrow fat distribution. In the following paragraphs, possible differences in the distribution of total volume, marrow weight, and marrow fat weight are considered. This is followed by consideration of the importance of the differences as reflected by changes in bone rank for production of marrow fat weight. This analysis indicates where distribution differences might have significance in hunter selection of bones for marrow recovery.

Cavity Volume--The distribution of total marrow cavity volume for each animal is presented in Table 5.25 and Figure 5.16. Age and sex differences are present in these data, but condition differences between animals should not affect marrow cavity volumes. Age differences in volume distribution appear to be evident in several bones. The radius and tibia in FYM both represent a larger proportion of total volume than they do in the other bison. The humerus and femur conversely, represent smaller proportions than in the other animals, with the differences most pronounced between FYM and SAM. The metatarsal volume is a larger proportion of the total in FYM than SAM, but is comparable to that seen in the females. Other bones in FYM also show differences in proportions of total cavity volume from the other animals, but these bones have quite small volumes and appear to vary between the adults as well.

Sex differences in cavity volume distribution appear to be evident in the humerus, femur, and possibly in the metatarsal. The humerus and femur

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both are larger proportions of total cavity volume in SAM than in the females, and metatarsal volume is a smaller proportion of the total in this male. Given that the values for these bones in FYM are similar to those seen in the females, and that the values for SAM are not intermediate between the values for FYM and the females, sex differences, rather than age differences probably account for the variability, if in fact, the differences are significant.

The importance of the differences in the distributions of total marrow cavity volume between the marrow producing bones, in terms of how they might be perceived by hunters processing a bison kill, are clarified somewhat by Figure 5.22. In this figure, the bones are ranked by decreasing marrow cavity volume in each animal, with the corresponding volumes listed. Comparison of the ranks of bones between animals indicates where differences in volume distribution affect rank, and inspection of the volume differences between adjacently ranked units indicates where these rank differences may, or may not be particularly important. For example, a difference in rank between two bones of similar cavity volume, might be statistically significant, and yet probably would not be an important factor in selection decisions if the actual difference between that unit and the adjacently ranked unit are not substantial.

The age differences in the proportions of total cavity volume noted above, vary in their affect on the rank order of bones between animals. Apparently, the magnitude of the differences in the radius are too small to change the rank of this unit between animals. The differences in the tibia, humerus and femur, however, are large enough to affect the order of bones ranked by cavity volume. The femur and humerus are a smaller proportion of total cavity volume in FYM than in the more mature bison, SAM. Hunter

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Figure 5.22. Rank Order of Carcass Units by Marrow Cavity Volume in the Half Carcass

Unit Rank Order				Unit Cavity Volume (cm^3)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
TIB	FEM	FEM	TIB	140.5	227.5	174.0	164.5
FEM	HUM	TIB	FEM	113.0	209.0	171.5	162.0
HUM	TIB	HUM	HUM	105.5	203.5	154.0	142.5
RAD	RAD	RAD	RAD	72.5	101.0	92.0	79.5
MTT	MAND	MAND	MAND	30.0	52.0	45.0	61.0
MAND	MTT	MTT	MTT	29.0	34.5	40.0	45.0
MTC	MTC	MTC	MTC	25.0	34.0	26.5	35.5
ULNA	PELV	ULNA	ULNA	12.0	13.0	16.5	14.5
PELV	ULNA	PELV	PELV	11.5	12.5	9.0	14.0
PPHA	PPHA	PPHA	PPHA	4.0	8.5	6.5	7.5
APHA	SCAP	SCAP	APHA	2.5	8.0	5.0	5.0
SCAP	APHA	APHA	SCAP	1.0	7.0	3.0	0.0

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selection of bones, based on animal age and marrow cavity volume, however, probably would not be influenced by these differences due to their high positions in the rank order. Although the femur and humerus are proportionately smaller in the young bison, the cavity volumes are relatively high for this animal, and so if bones from this animal were used, these would probably be among those selected. The differences apparent in the ranks of bones in the lower part of the orders probably would not be particularly important either. In each case, where age affects volume distribution, and the rank of a bone changes between the orders for FYM and SAM, the volume of the adjacent unit within each order is similar and probably would not be perceived as being substantially different. Age differences in marrow cavity volume distribution, therefore, are unlikely to influence the order of carcass unit selection for marrow recovery.

The sex differences in marrow cavity volume distribution probably would not affect hunter selection of marrow bones either. The differences in the proportion of total cavity volume in the metatarsal was no effect on bone rank (Figure 5.22). The greater proportion of volume in the humerus of SAM than in the females is evident in a rank order change, but the differences in cavity volume between the humerus and tibia in SAM is not large, suggesting the rank difference may not be important. Perhaps in a more mature male, this difference would be more pronounced between the sexes. The differences in the femur do not appear to be substantial. In each animal, this bone is ranked first or second in cavity volume. Although no difference is noted in the proportions of total cavity volume in the tibia between the sexes, it appears in Figure 5.22, that the possible rank difference in the humerus forces an inverse shift in the rank of the tibia. If the humerus difference is unimportant, as suggested, then the difference

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in tibia volume rank might also be incidental. Given that the femur, humerus, and tibia are the three bones with the largest volume, however, any distribution differences that affect bone rank to such a limited extent, are probably of little importance to hunter selection of marrow bones within individual carcasses. One may conclude, therefore, that bone selection based upon marrow cavity volume, probably does not differ between the carcasses of male and female bison.

Marrow Weight--As with marrow cavity volume, differences in marrow weight distribution between animals, in bones that have small cavities, are varied, and here, are considered unimportant in their influence on hunter selection of marrow bones. Bones that appear to show age differences in the weight distribution of marrow (Table 5.26 and 5.28, Figure 5.17), and that produce more than minor amounts of this material, include the humerus, femur, and tibia, and possibly the radius, metacarpal, and metatarsal. The immature bison, FYM, has proportionately more of total marrow weight than the older male SAM in the smaller bones (i.e., the radius and metapodials), and SAM has larger proportions of the total in the humerus, femur and tibia. Given the distal to proximal growth gradient, this is not surprising.

Sex differences in the distribution of marrow weight in the larger producing bones, are potentially evident in the humerus, metacarpal and metatarsal, and possibly in the femur. The clearest difference is in the proportion of marrow weight in the humerus, which is larger in the male, SAM, than in the females.

Condition differences in the distribution of marrow weight between animals, specifically between FAF and SAF, are difficult to evaluate. Despite differences in the fat content of the marrow samples, the differences between SAF and FAF in the distribution of marrow weight appear

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to be slight. In Figure 5.17, the most apparent difference is in the radius-ulna, with the poorer conditioned female, FAF, having a smaller proportion of total marrow weight in this bone. This might be a reflection of smaller marrow cavity volume, however. When fat is mobilized from marrow, however, the rate of change has been shown to generally be fastest in the proximal limb elements, although in individual animals the pattern may differ. The proximal elements still show similar proportions of total weight between these two females, suggesting two things. First, if the differences seen in the humerus and femur are not significant, then the difference in the radius-ulna may be insignificant as well. Second, a loss of fat due to mobilization may not show up in substantial changes in marrow weight, due to the replacement of the fat by water (Marquez and Coblentz 1987). It seems doubtful, therefore, that with the existing differences in animal condition, that the distribution of marrow is altered. Inspection of the cavity volume distribution data (Table 5.25, Figure 5.16) also indicates a difference between these females in the size of the radius-ulna. The marrow weight difference, therefore, is potentially attributed to that factor, rather than to condition differences between the animals.

The importance of the age and sex differences in marrow weight distribution must be evaluated by how they affect the relative rank of a bone in the order of bones for marrow production. This analysis is clarified by the ordering of data and bones in Figure 5.23. Very few bones in this figure change rank order between animals. The differences evident in the lower portions of the orders occur in bones that are small marrow producers and that show some degree of variability between animals. It seems doubtful that these differences are particularly important. Their low productivity might result in their common classification as relatively

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Figure 5.23. Rank Order of Carcass Units by Marrow Weight in the Half Carcass

Unit Rank Order				Unit Marrow Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
TIB	TIB	TIB	TIB	128.9	185.8	148.5	145.4
HUM	FEM	FEM	FEM	93.2	184.5	139.4	136.0
FEM	HUM	HUM	HUM	92.4	176.3	113.8	116.6
RAD	RAD	RAD	RAD	66.2	92.6	82.3	71.6
MTT	MTT	MTT	MTT	23.9	31.0	32.5	37.6
MTC	MTC	MTC	MTC	20.9	28.6	24.6	28.2
ULNA	ULNA	ULNA	ULNA	10.1	10.0	13.7	12.1
PELV	PPHA	PPHA	PELV	7.2	7.6	4.4	7.4
PPHA	PELV	PELV	PPHA	3.6	6.4	3.7	5.6
APHA	SCAP	SCAP	APHA	2.2	5.6	3.4	2.3
SCAP	APHA	APHA	SCAP	0.6	2.2	1.4	0.0

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unimportant sources of marrow, except during periods of food stress in hunter populations (e.g., Binford 1978:43). The scapula and pelvis in caribou, for example, are not recognized as marrow yielding bones among Binford's Nunamiut informants, and the phalanges, though accepted as marrow yielding, commonly are not classified with the other more productive bones.

Other than the rank differences in low marrow producing bones, the only rank change occurs between the humerus and femur units in FYM and SAM. In SAM, the femur is ranked higher and in FYM the humerus is ranked higher. However, the actual marrow weights of the humerus and femur in FYM differ by only 0.8 gm, indicating these two units are essentially of equal rank in this young animal. The difference in rank between SAM and FYM, therefore, must be considered insignificant. One may reasonably assume, therefore, that based on marrow weight, the same order of bone selection for marrow recovery would be used in the processing of individual animals, regardless of age or sex. If differences occur, therefore, one may anticipate that differences in fat content and thus, marrow fat weight are responsible. This is evaluated next.

Marrow Fat Weight--The weights and distribution of extractable marrow fat are presented in Table 5.27. The percent each bone produces of the total marrow fat weight is illustrated in Figure 5.18. Comparison of the values of FYM and SAM, with consideration of the values in the adult females, suggests that age differences do affect the distribution of marrow fat in the bones of bison, but these differences are largely a reflection of changes in bone size. The humerus and femur produce smaller proportions of total marrow fat weight in FYM than in SAM, and the radius-ulna, metacarpal, pelvis, tibia and metatarsal produce larger proportions of this total in the younger animal. With the exception of the differences noted in the femur

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and tibia, the percent of total fat values in FYM are comparable to those in the two females. The tibia has a larger percent of marrow fat weight than in the adult females, and the femur is a smaller percent of this total. The distal to proximal growth gradient in the limbs is evident in the earlier development of the more distal limb elements and the smaller proportions of the total found in the proximal elements.

Sex differences in marrow fat weight distributions are also apparent in the data in Table 5.27 and Figure 5.18, and as with the age differences noted above, mostly reflect differences in bone size and marrow weight (Table 5.28). The four year old male, SAM, has a greater proportion of total marrow fat weight in the humerus and possibly in the femur than that found in the females. The proportion of total fat weight is smaller in SAM in the radius-ulna, metatarsal, and possibly in the metacarpal and tibia. The larger proportions of fat weight in the proximal limb elements in SAM than in the females cannot be attributed to age difference for two reasons. First, if differences in the growth gradient were responsible, the females would have the larger percentages in these units. Second, the differences between FYM and the females indicate the direction of immature to mature changes in weight distribution, and in neither case do the values for SAM fall within the range noted for these two groups. The differences noted in the radius-ulna were not evident in cavity volume or marrow weight, and therefore, seem problematic. The differences in the tibia, however, are so slight, that their significance is questionable.

The differences in animal condition noted above may be evident in differences in fat weight distribution in SAF and FAF. Fat mobilization in marrow, though variable, is most rapid in the more proximal elements (Reich 1981, Brooks et al. 1977), and therefore, mobilization should result in a

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shift in the distribution of marrow fat weight in the bones. Specifically, one should see a reduction in the fat weight and possibly in the proportion of total fat weight in the proximal units, and a corresponding increase in the proportion of the total found in the distal elements. This pattern is evident in the values of SAF and FAF, although the magnitude of the differences are generally quite small.

Although marrow fat weight distribution appears to change with age, sex, and condition differences between animals, the importance of these differences must be evaluated in terms of whether they would affect hunter selection of marrow bones. The marrow fat weight data has been ordered by most to least productive whole bones in Figure 5.24, and the corresponding fat weights listed. The lack of rank order changes between animals, except in the four least productive bones, indicates that the order of bone selection for recovery of marrow fat should not differ in animals of different age or sex. The close comparability with orders based upon cavity volume and marrow weight, suggest that bone size differences are largely responsible for the age and sex differences noted for marrow fat weight. The lack of rank order differences in marrow fat weight production in Figure 5.24 also indicates that a decline in condition, comparable to that seen in FAF, is not of a large enough magnitude to affect selection. One might anticipate, however, that with a continued decline in condition, the more proximal limb elements might eventually be less productive, drop in rank, and presumably in selection order in the processing of individual carcasses.

Production of Marrow and Marrow Fat. Although it was shown above that these bison have similar rankings of bones for the production of bone marrow and marrow fat in their carcasses despite differences in age, sex, and condition, there are clear differences evident in the amount of marrow and

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Figure 5.24. Rank Order of Carcass Units by Marrow Fat Weight in the Half Carcass

Unit Rank Order				Unit Marrow Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
TIB	TIB	TIB	TIB	111.3	158.8	134.0	117.9
FEM	FEM	FEM	FEM	79.2	154.3	126.7	107.4
HUM	HUM	HUM	HUM	79.1	148.7	104.1	90.3
RUL	RUL	RUL	RUL	65.2	85.9	86.0	69.1
MTT	MTT	MTT	MTT	21.5	26.7	29.5	31.0
MTC	MTC	MTC	MTC	18.0	25.5	22.5	23.8
PELV	PPHA	PPHA	PELV	5.7	6.6	4.0	5.7
PPHA	PELV	PELV	PPHA	3.2	5.2	3.4	4.7
APHA	SCAP	SCAP	APHA	2.0	4.5	2.8	1.9
SCAP	APHA	APHA	SCAP	0.4	1.8	1.2	0.0

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marrow fat produced between animals (Tables 5.26 and 27). For example, although the tibia is ranked highest in each of the four animals for marrow and marrow fat production (Figures 5.23 and 5.24), the amount of material produced varies by as much as 56 gm for marrow weight and 47 gm for marrow fat weight between the largest and smallest producers, SAM and FYM (Tables 5.26 and 5.27). When multiple groups of bones are considered, the high yielding bones of a low marrow fat producing animal often fall below the more intermediate producing bones of high marrow fat producing animals. Whereas, the distribution and rank order analyses above indicate where differences may occur in the selection order of the bones within individual carcasses, examination of the raw weights of the marrow and marrow fat indicates (1) where differences in animal age, sex, or condition result in appreciable differences in material weight for the same bone between individuals, and (2) where the differences in bone product weight might influence hunter selections between the parts of multiple carcasses, as might happen at a kill or processing site.

Differences in Single Bone Productivity Between Animal Carcasses--Age, sex, and condition differences are evident in the marrow and marrow cavity volume data from the four TRNP bison. Possible age differences in cavity volume, marrow and marrow fat weights by bone, are summarized in Table 5.29 from the data in Tables 5.25-5.27. It is evident here that with age, bone size increases, as does the weight of the associated marrow. Marrow fat weight also increases with age, but as a result of larger marrow plug size, rather than as a result of increased per unit weight fat content. For example, although the marrow fat content of eight of ten of the bones studied (Table 5.24), is somewhat higher in the younger animal, FYM, than in SAM, the greater size of the marrow plug in the older animal, results in

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greater marrow fat weights (Table 5.27). The size effect of age is also evident between the females and FYM. The fat content of the marrow of each bone (Table 5.24) was higher in both females than in FYM, although the female, FAF, is judged to have been in poor condition. In most cases, the greater size of the marrow cavity and its associated marrow plug, results in a greater total fat weight in the marrow of the adult animals than in the yearling, FYM (Table 5.27). The exceptions to this are in bones that produce only small amounts of marrow, such as the scapula, pelvis, and anterior phalanges.

Possible sex differences in cavity volume, marrow and marrow fat weight are also summarized in Table 5.29, based on the data in Tables 5.25-5.27. The possible occurrence of sex differences in fat production are determined by comparing the data for the male, SAM, with both females for analyses of marrow cavity volume and marrow weight, and with the female, SAF, for marrow fat weight. Only SAF is used in the sex comparison of marrow fat weight, because the female, FAF, was in poor condition when killed and differences between this animal and SAM could not be attributed to the sex factor alone. Data from FAF are included in the marrow and cavity volume analyses because poor condition does not appear to affect marrow weight. As expected, with fat mobilization, marrow fat is replaced by water, so comparable values are evident for marrow weight in the two females. Another complicating factor in this analysis of sex differences in marrow characteristics is the lack of full maturity in the male, SAM. It is not expected that further growth in this animal would have altered the relationship for cavity volume or marrow weight compared to the females. Any age-related decreases in marrow fat content in males compared to the females probably would not be large enough to overcome the effects of the sex differences in the size of the marrow

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plug. Due to their larger size, older males, therefore, probably continue to have larger marrow fat weights than females.

Examination of the data in Tables 5.25-5.27, indicates that the values for the male, SAM, appear to be larger for the humerus, metacarpal, femur, tibia, and possibly the posterior phalanges, while the females are larger only in the metatarsal. In most cases, the pattern is repeated for cavity volume, marrow weight, and marrow fat weight, suggesting that the sex differences in marrow and fat weights are largely due to differences in animal size. This is especially evident, when one notes that fat weights are higher in the male, SAM, than in the female, SAF (Table 5.27, Figure 5.21), despite the fact that the fat content per unit of weight is smaller in the male (Table 5.24). The greater marrow and fat weights in the male than in the females, in three of the four major long bones, suggests that hunters wanting to maximize marrow fat recovery, would choose adult males over females, despite differences in the per unit weight fat content, which is slightly more concentrated in females. The sex differences in the metatarsal data are probably unimportant, given the relatively small magnitude of difference, the fact that it is not a large marrow producing bone, and the expectation that data from a fully mature male might exceed the females as well.

Condition differences are evident in the fat content values (Table 5.24) of these bison. The values for marrow cavity volume and marrow weight (Tables 5.25 and 5.26) for the two females are roughly comparable, but the fat content by bone differs. In all marrow samples studied from these two females, the fat content per unit of weight was higher in SAF than in FAF. Computed marrow fat weights (Table 5.27) in the proximal and medial limb bones are lower in FAF than in SAF, but are higher in the more distal

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metapodials and phalanges. Part of this difference may be attributed to the greater marrow plug weights in the distal bones of FAF and the larger size of the marrow plug in all but one of the more proximal bones in SAF. Differences in marrow plug size and fat content combine to produce a proximal to distal variability in fat weight that conforms to the expected gradient of fat depletion during mobilization. The potential importance of the differences in marrow weight between animals for proximal and distal bones should not be overlooked, although the consistently smaller per unit weight fat content does indicate poorer condition in FAF.

Earlier hindlimb than forelimb mobilization of marrow fat has been suggested by Reich (1981) for impala. Table 5.30 lists the marrow fat content of the two female bison, as well as the differences in the percentages. These data indicate that FAF was in poorer condition than SAF, and that with the exception of the humerus and femur, the differences in fat content were larger in the hindlimb than forelimb elements. This suggests that fat mobilization is more rapid in the hindlimb, except in the proximal units where the humerus marrow fat appears to have mobilized more rapidly in this individual. It should be noted that the forelimb to hindlimb differences between SAF and FAF are relatively small. This is contrary to the pattern suggested by Ratcliffe (c.f., Speth 1983:103-104) for roe deer. This and the fact that Davis et al. (1987) failed to find a significant difference in marrow fat content of forelimb to hindlimb pairs in caribou, indicates that more studies of forelimb-hindlimb fat mobility patterns are needed. If limb differences in fat mobility do occur and are expressed as was evident in the bison from this study, the effect on hunter selection might be exhibited through greater abandonment of intermediate and distal hindlimb than forelimb elements at kill sites.

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Table 5.30. Marrow Fat Content as an Indicator of Marrow Fat Mobility

Forelimb				Hindlimb			
	Fat Content		Difference		Fat Content		Difference
Unit	SAF	FAF	SAF - FAF	Unit	SAF	FAF	SAF - FAF
HUM	91.5	77.4	14.1	FEM	90.9	78.9	12.0
RAD	89.5	82.6	6.9	TIB	90.2	81.1	9.1
MTC	91.1	84.4	6.7	MTT	90.7	82.5	8.2
APHA	85.9	82.6	3.3	PPHA	89.7	83.1	6.6
		forelimb total	31.0			hindlimb total	35.9

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Animals of the same sex that are in different condition may or may not be exploited differently when marrow fat recovery is the goal, depending upon the extent that fat from the carcass and skeleton has been mobilized. If fat mobilization has progressed to the point that marrow fat has been used appreciably as an energy source, then hunters might be expected to treat these carcasses differently than those of less fat-depleted animals of the same sex.

The effect of condition differences on the comparative use of carcasses of animals of other ages or sex must also be considered. For example, at this point in the mobilization of fat in FAF, the marrow fat weights remain higher than those seen in the immature male, FYM, in all marrow yielding bones. The fat weights of the tibia and radius-ulna are not widely different (Table 5.27), however. A female in poorer condition than FAF might have marrow fat weights smaller than those of this yearling male. This relationship would not exist, however, if the cause of the poor condition in the adult extended to other members of the herd as well.

Based on this assessment of the effects of condition differences, one might expect that hunter selections of animals from a cow/calf herd, for recovery of marrow and marrow fat, would focus first on healthy adult females, but might also include females showing some degree of marrow fat depletion (perhaps even somewhat more severe than that seen here in FAF), before young animals are selected. This selection order should be used as well, if the circumstances leading to fat mobilization affect the entire herd, rather than influencing the conditions of a limited number of individual animals. The maintenance of this selection order is dictated by the fact that young animals, that have smaller fat reserves in the carcass depots, would be expected to show earlier mobilization of the marrow fat

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reserves than adult females experiencing similar levels of submaintenance nutrition.

Animal selection by hunters for marrow fat recovery, based on age, sex, and condition differences in the animals, therefore, should focus first on adult males, followed by adult females, and finally by immature animals. Condition differences leading to the mobilization of marrow fat in females, and possibly in males, should not dramatically affect this selection priority of adults in relation to young animals, unless the conditions of restriction are limited to the adult(s) and are prolonged enough to severely reduce their fat reserves. It is not possible to use this bison sample to discuss how fat depletion in males would affect the relationship of male to female productivity for marrow fat recovery.

Influence of Productivity When Multiple Carcasses Are Available--As suggested above, a bison kill of multiple animals results in the possibility of selecting individual high ranking bones from multiple animals, permitting incomplete use of carcass portions of low productivity. Arrangement of the marrow fat weight data by descending order of production (Table 5.31), helps to illustrate why not all available bones from a particular carcass location are used, when animals of variable age, sex, and condition are included in the kill population. In this example, all four of the bison from this study are included in the table, and represent a composition that is not particularly typical of a kill population, in terms of the numbers of animals of various age and sex classes, but which illustrates the possible relationships in productivity that might be seen in a mixed herd (such as occurs during the breeding season). In Table 5.31, no division of marrow fat is made between proximal and distal ends of the bones, as suggested by Binford (1978) in his calculations of carcass utility indices. Although

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Table 5.31. Cumulative Production of Marrow Fat in the Side Carcass

Animal	Carcass Unit	Marrow Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Marrow Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
SAM	TIB	158.8	158.8	8.1	FAF	RUL	69.1	1,652.8	83.9
SAM	FEM	154.3	313.1	15.9	FYM	RUL	65.2	1,718.0	87.2
SAM	HUM	148.7	461.8	23.4	FAF	MTT	31.0	1,749.0	88.8
SAF	TIB	134.0	595.8	30.2	SAF	MTT	29.5	1,778.5	90.3
SAF	FEM	126.7	722.5	36.7	SAM	MTT	26.7	1,805.2	91.7
FAF	TIB	117.9	840.4	42.7	SAM	MTC	25.5	1,830.7	92.9
FYM	TIB	111.3	951.7	48.3	FAF	MTC	23.8	1,854.5	94.2
FAF	FEM	107.4	1,059.1	53.8	SAF	MTC	22.5	1,877.0	95.3
SAF	HUM	104.1	1,163.2	59.1	FYM	MTT	21.5	1,898.5	96.4
FAF	HUM	90.3	1,253.5	63.6	FYM	MTC	18.0	1,916.5	97.3
SAF	RUL	86.0	1,339.5	68.0	SAM	PPHA	6.6	1,923.1	97.6
SAM	RUL	85.9	1,425.4	72.4	FAF	PELV	5.7	1,928.8	97.9
FYM	FEM	79.2	1,504.6	76.4	FYM	PELV	5.7	1,934.5	98.2
FYM	HUM	79.1	1,583.7	80.4	SAM	PELV	5.2	1,939.7	98.5

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Table 5.31. (continued)

Animal	Carcass Unit	Marrow Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Marrow Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
FAF	PPHA	4.7	1,944.4	98.7	FYM	APHA	2.0	1,964.3	99.7
SAM	SCAP	4.5	1,948.9	98.9	FAF	APHA	1.9	1,966.2	99.8
SAF	PPHA	4.0	1,952.9	99.2	SAM	APHA	1.8	1,968.0	99.9
SAF	PELV	3.4	1,956.3	99.3	SAF	APHA	1.2	1,969.2	100.0
FYM	PPHA	3.2	1,959.5	99.5	FYM	SCAP	0.4	1,969.6	100.0
SAF	SCAP	2.8	1,962.3	99.6	FAF	SCAP	0.0	1,969.6	100.0

Note: table excludes mandible marrow fat.

differences do exist between the ends of bones in their marrow and marrow fat productivity (Tables 5.26 and 5.27), it seems unlikely that a portion of the marrow plug would be abandoned or used at different times once the cavity is opened, unless perhaps the bones are frozen and used as halves.

One might expect that ordinarily, rules concerning the relative productivity of whole carcasses and the distribution of material within the carcass would dictate the order of bone collection. It is not expected that hunters would process carcasses strictly by the order of marrow fat productivity, but differences in productivity between the units of multiple carcasses, might affect the order of bone selection in marrow processing once the meat is stripped from the bones.

The cumulative marrow fat weight data (Table 5.31) illustrates the importance of several relationships in the general pattern of relative animal and bone productivity that were discussed above. First, the pelvis, scapula, and phalanges do not appear in the cumulative fat weight list until over 97 percent of the total available marrow fat has been accounted for by other marrow producing bones. Given their small fat weights, it is not difficult to understand their general lack of importance as marrow bones (assuming similar Plains hunter perceptions of bison carcasses as reported by Binford (1978) for the Nunamiut caribou hunters). Their potential importance during periods when fat is an important component of diet comes from the fact that these bones in these four bison produced 53.1 gm of fat. In a large kill, during periods of nutritional stress in the human population, the effort of processing large numbers of these marginally producing bones may be sufficiently rewarding to encourage their use.

Second, in a kill of numerous animals, the bones of young individuals are probably selected later for marrow recovery than the same bones of

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adults, unless the individual adult animals exhibit severe fat depletion that is not characteristic of the herd as a whole. To illustrate the potential low value of the marrow bones in young animals in a healthy herd, one may note that in Table 5.31, the tibia of FYM lies relatively high in the cumulative order, but nearly 43 percent of the available marrow fat is accounted for by higher producing bones of other animals that come before it. The next highest fat producing bone from FYM (the femur) does not appear in this table until 72 percent of the total marrow fat of these four bison is accounted for. A processing pattern that focuses on adult animals first, would thus be more productive.

Third, in a kill of a healthy herd, the bones of adult males, being larger than those of the females, should be selected first, unless the presence of some other resource (e.g. bone grease, meat fat, etc.) acts to increase the relative value of the female carcass units. Where there are no time or labor constraints for processing the available marrow, one might expect that marrow processing would be similar for bones from males and females, but if some major marrow producing bones are abandoned, more of these should be from females than from males.

Fourth, as adults decline in condition due to individual occurrences of submaintenance nutrition, the frequency with which the proximal limb units are processed for marrow recovery should eventually decrease, approaching, and in extreme fat depletion, falling below the frequency of use in animals that are normally less productive due to either their age or sex. A male in poor condition might eventually be less productive than healthy females, and a female might be less productive than an immature animal. Due to the gradient of mobilization, the differences should be evident earliest in the more proximal elements.

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Fifth, poor condition might be reflected in differences in the use of forelimb and hindlimb elements. If the more rapid mobilization of fat in the hindlimb than the forelimb elements (except for the humerus and femur) is typical of bison, as seen here and as reported by Reich (1981) for impala.

Sixth, age and conditon effects may combine to influence selection decisions. When conditions exist that result in submaintenance nutrition in all members of a herd, differences between animals in their metabolism and the availability of carcass fat to mobilize for energy needs, should result in young, functioning ruminants showing marrow fat depletion earliest, and adults latest. The non-functioning ruminant (nursing calf) which is dependent upon its mother for its nutrition and growth, may continue to receive adequate nutrition for growth when the cow is in early stages of submaintenance nutrition and her body fat reserves are used to supply energy for her own and her calf's maintenance. This would probably have little effect on hunter selection, however, because marrow fat in calves is available only in small quantities due to both small cavity volume size and the greater relative volume of marrow (medullary cavity and cancellous tissue marrow) that serves to fulfil hemopoietic needs. If there is an effect on hunter selection involving young animals, it seems logical that the shift in selection would be between these calves and the older, yet immature animals that are functioning ruminants. Young ruminants that are growing, have relatively small fat reserves, and thus are early to show the effects of submaintenance nutrition. In this case, calves that indirectly are living off their mothers' fat reserves might be more useful than other immature animals.

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The seventh relationship between animal class and marrow productivity concerns the reproductive status of the individual as it relates to condition. Non-pregnant, non-lactating cows may show later marrow fat depletion than any other group due to a higher carcass fat content that results from the absence of reproductive energy requirements. This assessment assumes, however, that the barren state of the cow is not a reflection of continued poor condition. If poor condition is responsible, then the fat reserves might or might not have been re-established to a level comparable to that of reproducing females. In the early stages of gestation, pregnant cows might be in better condition than barren cows. At some point, however, one might expect that their marrow fat weights would be nearly comparable as this depot is the earliest to be replenished to normal levels when nutrition conditions improve. In the winter and spring when pregnant and lactating cows have maintenance costs associated with reproductive functions added to the normal cyclical winter and spring season energy demands, non-pregnant cows might be more productive than pregnant or lactating cows. This would occur if seasonal conditions are poor enough to affect fat weights to the extent that marrow fat is mobilized in the cows with higher energy demands.

It is unclear whether male reproductive energy expenditures and fat weight losses would be evident in their marrow fat weights during or immediately following the breeding season. Although sexually active bulls reportedly lose as much as two hundred pounds during the rut, it is not clear what the total fat weight of a fully mature bull would be, and whether it is high enough to prevent marrow fat weight loss through mobilization. The work of Cederlund et al. (1989:589) on moose, suggests that rut-related behavior and energy expenditure may indeed be evident through lower marrow fat levels in males two years old and older. In moose older than 10 years

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of age, marrow fat levels dropped 27 percent. A similar drop in marrow fat levels in male bison would result in fat weights comparable to or lower than those found in healthy females (using SAF and SAM as representatives). If a fully mature male, with larger bone and marrow plug size were used as the representative, however, I suspect that males might continue to have comparable weights of marrow fat as females. It is suggested that in all seasons, possibly with the exception of the post-rut period, a greater frequency of the available male than female marrow bones would probably be processed.

Summary--These analyses of marrow productivity illustrate one reason why differential use of marrow bones is sometimes evident in archaeological assemblages of bone from kill and processing sites, despite the fact that marrow is similarly distributed in the carcasses of animals of different age and sex. Clearly, the differences in productivity in classes of animals and between the different marrow producing bones operates to make the larger, major fat producing bones of larger animals the most preferred. As time and labor permit, the smaller, less productive bones of young animals are probably included in the processing, possibly followed by small marrow bones (e.g., the phalanges, pelvis, etc.) of animals of every age and sex. Bones from animals in poor condition may also show evidence of marrow recovery, because submaintenance nutrition must be prolonged before fat mobilization in the marrow is substantial enough to affect the relative productivity of adult animals compared to smaller or younger bison.

Bone Grease Production and Distribution

In this section, four aspects of bone grease production are considered: (1) the quantity of total bone grease fat available in the four bison; (2)

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differences in production within different parts of the carcass; (3) differences in the distribution of this fat in the carcasses of these bison; and (4) the importance of the magnitude of the production differences. For the purpose of these discussions, the bone grease data are organized into two categories, white and yellow grease, which reflect the differences in quality that Binford (1978) suggested are evident in human selection of sheep and caribou bone, for use in bone grease production. In these discussions, white bone grease is the fat found in the cancellous tissue of the appendicular skeleton, and yellow grease is that found in the axial skeleton. Although it was shown above that the quantity of grease fat in the scapula is more typical of yellow grease bones, and that of the sacrum and caudal vertebrae units are more like white grease bones, these units are evaluated here in terms of their locational designations of grease fat.

Bone grease fat weight, determined by multiplying bone grease sample weight by the percent total fatty acids (determined by ether extraction), is used in the following discussions as the measure of product availability. Neither bone grease sample weight, nor percent extractable fat is considered directly in this discussion, because they vary depending upon how much water was recovered with the sample in the collection process. The calculated value of extractable fat weight, therefore, is the only measure of actual bone grease production that is discussed here.

Total Bone Grease Fat Production

Bone grease fat production is evaluated through examination of total grease fat weight, and its components, total white and yellow grease fat weights. Of these, white grease fat production would probably be of greatest interest to hunters, because it is more unsaturated. The need for

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maximum fat recovery, however, might improve the selective priority of yellow grease fat.

Total Grease Fat Production. Unlike bone marrow, the production of bone grease fat does not appear to be closely associated with animal size. In this sample of four bison, the largest animal with the biggest bones (SAM) did not have the largest bone grease fat production. It is possible that within each sex, grease fat weight might correlate positively with bone volume when animal condition is good, but it cannot be demonstrated with this bison sample due to differences in animal age, and among the females, due to differences in animal condition.

Table 5.32, lists the total bone volume in the half carcasses of the four study bison, and also indicates how the animals compare in size when using total bone volume as the measure of size. Total bone volume decreases in the following order: SAM, FAF, SAF, and FYM. Relative comparisons of total bone volume shows the adult male, SAM, is larger than the two females (145 and 136 percent larger than SAF and FAF) and the younger male (176 percent larger); the females are roughly comparable in size, with the older female, FAF, having a slightly larger total bone volume; and the yearling male, FYM, is approximately 77 to 82 percent of the size of the females.

Total bone grease production (Table 5.33), however, follows a different order of ranking, from largest to smallest yield: SAF, FAF, SAM, FYM. Variability in bone grease production between animals appears to reflect age, condition, and probably sex differences. A comparison of fat production per unit of bone volume (Table 5.34) illustrates these differences. For example, both FYM and SAM have substantially lower fat weights per unit of bone volume than the females. These differences may be due to either age or sex influences. The similarity in the values for FYM

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Table 5.32. Comparative Animal Size as Measured by Bone Volume in the Half Carcass

Part A. Bone Volume of the Vertical Set as a Percent of Bone Volume of the Horizontal Set

	FYM	SAM	SAF	FAF
FYM	---	58.71	81.89	77.23
SAM		---	144.54	136.31
SAF			---	94.31
FAF				---

Part B. Animal Rank Based Upon Bone Volume

	FYM	SAM	SAF	FAF
Bone Volume (cm^3)	9,298.4	14,646.1	10,133.0	10,744.7
Rank	4	1	3	2

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Table 5.33. Comparative Animal Size as Measured by Bone Grease Fat Production in the Half Carcass

Part A. Bone Grease Fat Weight of the Vertical Set as a Percent of Bone Grease Fat Weight of the Horizontal Set

	FYM	SAM	SAF	FAF
FYM	---	52.37	31.62	40.15
SAM		---	60.37	76.66
SAF			---	126.98
FAF				---

Part B. Animal Rank Based Upon Bone Grease Fat Weight

	FYM	SAM	SAF	FAF
Grease Fat Weight (gm)	312.6	596.9	988.7	778.6
Rank	4	3	1	2

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Table 5.34. Total Bone Grease Fat Production Per Unit Bone Volume in the Half Carcass[a]

	FYM	SAM	SAF	FAF
Grease Fat Weight (gm)	312.6	596.9	988.7	778.6
Bone Volume (cm^3)	8298.4	14646.1	10133.0	10744.7
Weight (gm) Per Unit Volume (cm^3)	0.038	0.041	0.098	0.072

[a] data excludes the skull, mandible, and hyoid units

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and SAM indicate that the differences between these animals in total bone grease production is related primarily to differences in animal size, and indicates there is no substantial change in the rate of fat production between 1-1/2 and four years of age in males.

A difference in volume unit production is evident between the two females. The relatively poorer condition of FAF than SAF, is reflected in the lower per unit volume fat weight (0.072 compared to 0.098 gm per cm^3). With only minor differences between these females in the total volume of bone (Tables 5.30, 34), this decrease represents a substantial loss in total bone grease fat production.

In these four bison, the females produce proportionately larger quantities of bone grease fat than the males, neither of which was fully mature. This occurs despite the smaller body and bone volume size in the females (Tables 5.32 and 5.33). This was evident above in the scatterplot of grease fat weight and bone volume (Figure 5.12).

Based upon these totals of bone volume and bone grease fat alone, one would expect that animal selection for recovery of bone grease would focus first on females, then on adult males, and finally upon immature males. The relationship between immature females or fully mature males and these other age and sex classes is not known. As young animals, however, immature females may be expected to have less bone grease fat than adult females.

Total White and Yellow Grease Fat Production. As noted above, preferences for bone grease from some bone elements over others (as sources for white versus yellow bone grease) was expressed in Binford's (1978) study of Nunamiut carcass processing practices. Division of this product into white and yellow grease categories does not change the relative ranking of animals for fat productivity (Table 5.35). That is, the rank order of most

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Table 5.35. Relative Production of Bone Grease Fat in the Half Carcass

Part A. Grease Fat Weight (gm)

	FYM	SAM	SAF	FAF
Total Grease Fat Weight	312.6	596.9	988.7	778.6
White Grease Fat Weight	258.0	409.6	690.5	511.3
Yellow Grease Fat Weight	54.6	187.3	298.2	267.3

Part B. Animal Rank for Fat Production

	FYM	SAM	SAF	FAF
Total Grease Fat	4	3	1	2
White Grease Fat	4	3	1	2
Yellow Grease Fat	4	3	1	2

Part C. Percent of Total Grease Fat Weight

	FYM	SAM	SAF	FAF
White Grease Fat	82.5	68.6	69.8	65.7
Yellow Grease Fat	17.5	31.4	30.2	34.3

Note: excludes data from the skull, mandible, and hyoid

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to least white or yellow grease production is the same as for total grease: SAF, FAF, SAM, and FYM. Selection of animal carcasses for bone grease fat recovery should be as outlined above, focusing first on adult females, then on adult males, and finally, if at all, on immature animals. It appears that fat mobilization in FAF is not advanced enough in this skeletal fat depot for total fat production to fall below that seen in the male, SAM.

Closer examination of the productivity of these grease types in the four study specimens shows that while animal ranking by quantity of grease produced does not change, there are differences in the proportions of total grease that these two fat types represent (Table 5.35). When the proportions that white and yellow bone grease represent of total bone grease are evaluated, it appears that animal maturity has the greatest effect on productivity. White grease fat production, as a percent of total grease fat production, is larger in the immature animal, FYM, representing 82.5 percent of the total compared to 65.7 to 69.8 percent of the total for the other three animals (Table 5.35). This division of bone grease reflects the higher impetus for growth in the limbs compared to the bones of the axial skeleton that Berg and Butterfield (1976) report for young animals, as well as the probable proportionately larger volume of the red marrow fraction in the immature male. The larger percent of white grease fat to total grease fat would not be expected to improve the value of immature animals as a source for bone grease, however, because they produce less bone grease, of either type, than adult animals. If yellow grease is the desired product, however, young males might not produce enough grease to warrant the cost of its recovery.

Considering the other three study animals, there appears to be no clear difference in the proportions that yellow and white grease represent of

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total bone grease, as measured by fat weight (Table 5.35). White grease ranges from 65.7 to 69.8 percent in these three bison, and yellow grease ranges from 30.2 to 34.4 percent.

The similarity in the percent yellow and white grease fat values as proportions of total grease fat weight in the male, SAM, and the females (Table 5.35) is interesting in light of the earlier contrast between this male and the females in the per unit bone volume grease fat production (Table 5.34). Table 5.36 lists the proportion of yellow grease fat to total grease fat grouped by bone maturation classes (e.g., Jones et al. 1978), and shows that the male, SAM, produced comparable values to those of the mature females. These data indicate that the male, SAM, was mature, at least in the division of bone grease fat between white and yellow grease fat types. It also suggests that the per unit bone volume production value differences for total grease fat between the male, SAM, and the females, may be due to a sex difference in grease fat production, rather than due to the lack of full maturity in SAM. Proof of this relationship, however, would require knowledge of the production value for fully mature males.

Summarizing the differences in bone grease production for the four bison studied, it appears that (1) that females produce more bone grease fat both literally and in proportion to their carcass size than males (at least in males up to four years of age), despite their smaller bone size; (2) the immature male produces smaller absolute quantities of bone grease than the four year old male, but in similar proportion to bone volume; and (3) that bone grease is partitioned differently between white and yellow grease in immature and mature animals, with the immature animal having a larger proportion of the total grease fat weight represented by white grease (i.e., by grease from appendicular bones). The effects of the difference in

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Table 5.36. Comparative Yield and Distribution of White and Yellow Grease Fat Grouped by Bone Maturation Class

Bone[a] Maturation Class	Division or Carcass Unit	Fat Type	Grease Fat Weight (gm)				Percent of Total Grease Fat			
			FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Early	CERV	Yellow	2.96	1.46	8.98	15.41	1.2	0.3	1.0	2.3
	Other	White	182.93	350.39	564.65	385.64	76.4	64.2	64.4	57.6
	Total		185.89	351.85	573.63	401.05	77.6	64.5	65.4	59.9
Intermediate	STER	Yellow	0.22	4.85	0.79	9.87	0.1	0.9	0.1	1.5
	THOR	Yellow	3.79	15.13	37.22	34.57	1.6	2.8	4.2	5.2
	LUMB	Yellow	16.74	22.77	24.37	24.13	7.0	4.2	2.8	3.6
	Total	Yellow	20.75	42.75	62.38	68.57	8.7	7.8	7.1	10.2
Late	SACl	Yellow	4.67	34.29	67.05	42.93	2.0	6.3	7.7	6.4
	PELV	Yellow	18.47	71.83	76.50	45.47	7.7	13.2	8.7	6.8
	RIBS	Yellow	5.60	36.26	76.62	90.31	2.3	6.6	8.7	13.5
	Total	Yellow	28.74	142.38	220.17	178.71	12.0	26.1	25.1	26.7
	Other	White	4.07	8.77	20.29	21.20	1.7	1.6	23.1	3.2
	Total		32.81	151.15	240.46	199.91	13.7	27.7	27.4	29.9
All	Total		239.45	545.75	876.47	669.53				

[a] Source: Jones et al. (1978)

partitioning of the grease fat between the mature animals and the immature male, FYM, extends to the level of individual bones as well, as illustrated in Figure 5.25. Here, the values for the percent of total bone volume are matched with the percent of total grease fat weight in appendicular bones. Removal of the FYM data points improves the R^2 value of the regression from 0.7347 to 0.8507.

Production and Distribution of White Bone Grease Fat

At large bison kills where both time and the size of the work force are adequate, one would expect that selection for grease bones might occur at the level of individual bones or parts of bones, rather than at the level of the complete animal carcass. For this reason, it is important to understand how bone grease production and distribution varies in smaller divisions of the bison carcass, and it is this aspect of bison carcass composition that is examined in the following paragraphs.

Partitioning of White Grease Fat Between the Limbs. Table 5.37 presents the weight of extractable bone grease fat determined for the samples recovered from the bones or halves of bones of each of the four bison. Before discussing the production and distribution differences for these elements, I first examine whether age, sex, or condition differences are evident in the division of the white grease fat production of the fore- and hindlimbs, as has been reported for cattle muscle tissue by Berg and Butterfield (1976).

Table 5.38 summarizes the weights of extractable fat recovered from the forelimb and hindlimb of the bison carcasses, and presents the proportions that these groups of bones produce of the total white grease fat weight. The similarity of the proportional values for FYM, SAM, and SAF, and the

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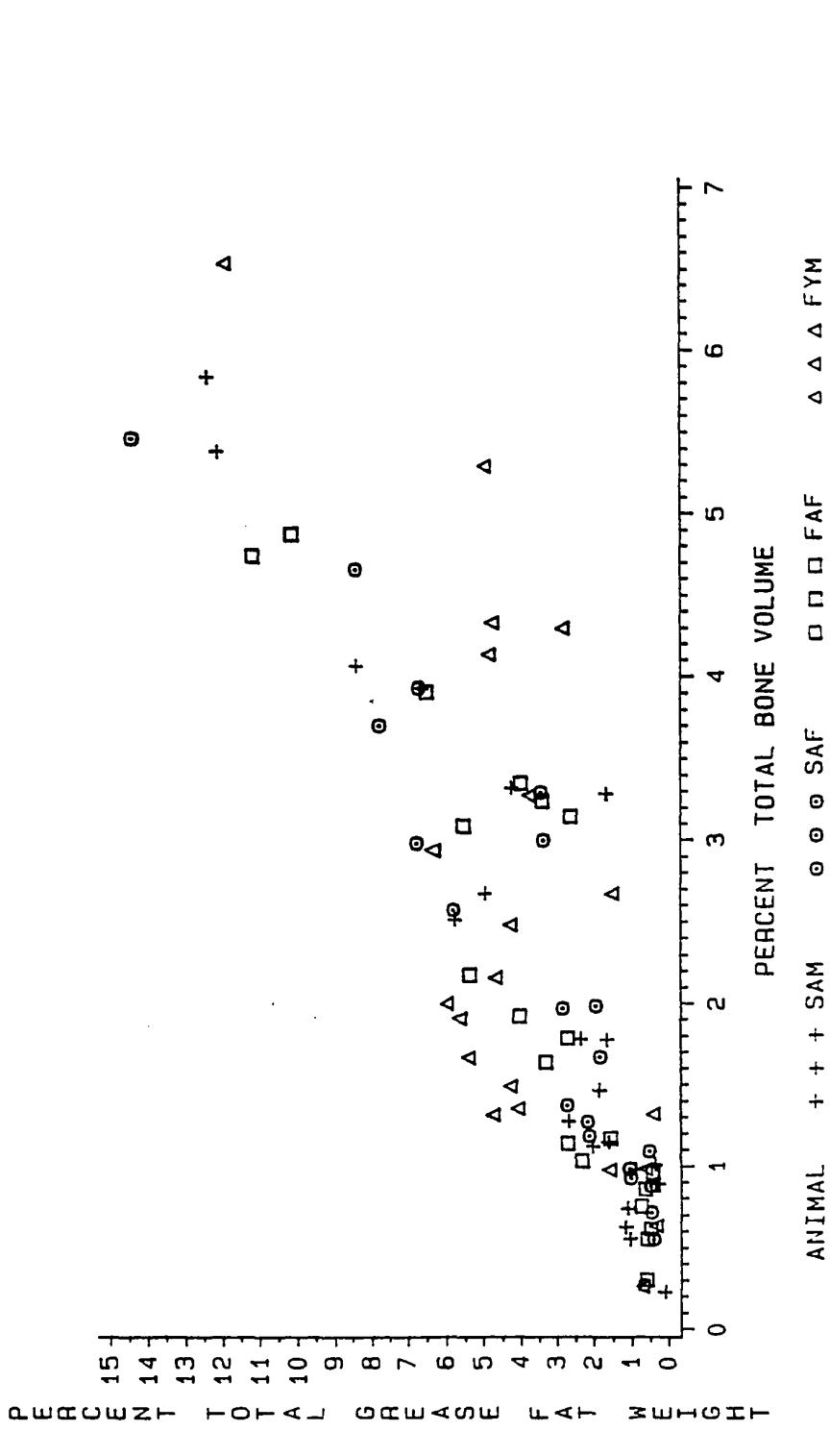

Figure 5.25. Regression of Grease Fat Weight Distribution on Bone Volume Distribution in Appendicular Units without Differentiation by Animal, Using Adjusted Axial-Appendicular Groups.

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Table 5.37. Bone Grease Fat Weight in Bison Side Carcasses

Part A. Yellow Grease Fat Weight (gm)

Unit	FYM	SAM	SAF	FAF
ATLAS	1.4	0.4	2.0	3.0
AXIS	0.6	0.7	3.0	1.4
C3C7	0.9	0.4	3.9	10.9
THOR	3.8	15.1	37.2	34.6
LUMB	16.7	22.8	24.4	24.1
SAC1	4.7	34.3	67.0	42.9
PELV	18.5	71.8	76.5	45.5
CAUD	2.2	0.6	6.8	4.7
RIBS	5.6	36.3	76.6	90.3
STER	0.2	4.9	0.8	9.9
Total	54.6	187.3	298.2	267.3

Part B. White Grease Fat Weight (gm)

Unit	FYM	SAM	SAF	FAF
SCAP	4.1	8.8	20.3	21.2
PHUM	15.4	73.6	83.0	86.5
DHUM	8.8	25.2	34.1	30.9
HUM	(24.2)	(98.8)	(117.1)	(117.4)
PRUL	11.7	9.9	33.5	20.4
DRUL	19.8	29.4	57.5	41.7
RUL	(31.5)	(39.3)	(91.0)	(62.1)
CARP	14.8	5.4	10.7	3.4

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Table 5.37. (continued)

Part B. White Grease Fat Weight (continued)

Unit	FYM	SAM	SAF	FAF
PMTC	1.9	1.7	5.0	5.0
DMTC	16.9	9.6	21.2	18.0
MTC	(18.8)	(11.3)	(26.2)	(23.0)
APHA	14.6	9.8	28.4	31.3
PFEM	14.8	49.9	66.3	50.3
DFEM	37.1	72.0	142.0	78.6
FEM	(51.9)	(121.9)	(208.3)	(128.9)
PATE	1.1	6.2	4.3	4.5
PTIB	15.1	39.3	76.8	26.5
DTIB	13.3	14.0	19.5	21.1
TIB	(28.4)	(53.3)	(96.3)	(47.6)
OTAR	5.0	6.9	4.9	3.7
AST	12.7	6.6	10.3	5.9
CALC	13.3	12.1	21.7	12.1
TARS	(31.0)	(25.6)	(36.9)	(21.7)
PMTT	1.3	2.2	5.4	3.4
DMTT	17.6	16.0	27.2	21.0
MTT	(18.9)	(18.2)	(32.6)	(24.4)
PPHA	18.7	11.0	18.4	25.8
Total	258.0	409.6	690.5	511.3

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Table 5.38. Comparative Distribution of White Grease Fat Between the Limbs

Description	FYM	SAM	SAF	FAF
Total White Grease Fat Weight (gm)	258.0	409.6	690.5	511.3
Forelimb White Grease Fat Weight (gm)	108.0	173.4	293.7	258.4
Hindlimb White Grease Fat Weight (gm)	150.0	236.2	396.8	252.9
Percent in Forelimb	41.9	42.3	42.5	50.5
Percent in Hindlimb	58.1	57.7	57.5	49.5
Ratio of Forelimb to Hindlimb Fat Weight	0.72	0.73	0.74	1.02

Note: all data are for side, rather than complete non-standard carcasses.

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dissimilarity of these values to those from FAF are immediately evident. If the differences between the values for these animals are not significant, this would indicate that there is neither age nor sex differences in the distribution of white bone grease between the fore- and hindlimb. If the difference between the values for these three animals and the female, FAF, are significant, it may suggest two possibilities: first, that changes in animal condition may be reflected in the changing production of white bone grease, and second, that this change is most evident in the reduction of bone grease fat produced in the hindlimb elements.

Support for this conclusion lies in several factors. Evidence of marrow fat content, described in the previous section, for these four animals showed the female, FAF, to be in poorer condition than the other three animals. Additionally, the lower total production of white bone grease for FAF than SAF, despite her comparable size in both liveweight and bone volume, also suggests that FAF is in poorer condition.

The greater decline in the production of the hindlimb elements in FAF is suggested in Table 5.38 by (1) the decrease in the proportion it represents of total white grease fat weight; (2) the differences in the ratio of fat weight between the fore and hindlimbs in this and the other three animals (Table 5.38); and (3) the closer comparability of the actual fat weights for the forelimb than for the hindlimb of the two females, FAF and SAF. The greater reduction in hindlimb fat production does not necessarily indicate the absence of a reduction in the forelimb--only that it is more pronounced in the former. Reich (1981) was cited above, however, showing that the medullary marrrow fat content of the hindlimb generally decreases earlier than in the forelimb under nutritional stress, although he indicated there was a great deal of individual variation. These factors

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should be kept in mind when examining the data for production and distribution in the individual bones or bone halves, in order not to assign possible causes for variability that may be due to other factors.

Variability in White Grease Fat Production. Table 5.39 lists the extractable white grease fat weight and percent of total white grease fat weight for whole bones and bone halves in the appendicular skeleton. Figure 5.26 illustrates these data for each bison. Division of the long bones into proximal and distal elements is considered a legitimate approach here (whereas it was not viewed as such for bone marrow fat), because prior removal of the marrow, results in division of the bones into at least two segments. Selection may be made for whole bone as well, if marrow and grease recovery are delayed. Both whole and partial bone are considered in the discussions below.

Range of Variability in White Grease Fat Weights--A graph (Figure 5.27) of the fat weight data in Table 5.39, shows the wide range of variability in white grease fat production in the bones of these animals. With the exception of the scapula, the bones of the upper limbs, including the humerus, radius-ulna, femur, and tibia, all show wide ranges of white grease fat production. The more distal bones, and the scapula and patella, all show a much smaller range of variability between animals. The fact that the bones which produce the most bone grease fat (the combined fat weights of the major long bones range from 52.7 percent of the total white grease fat for FYM to 76.5 percent for SAM) are the most variable in their production between animals, accentuates the importance of identifying those factors which influence that production.

Sex Differences in White Grease Fat Production--The data in Table 5.39 and Figure 5.27 also illustrate that in most bones (excluding the carpals,

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Table 5.39. Comparative White Grease Fat Weight and Distribution in the Bison Side

Unit	White Grease Fat Weight (gm)				Percent of Total White Grease Fat Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	4.1	8.8	20.3	21.2	1.6	2.1	2.9	4.1
PHUM	15.4	73.6	83.0	86.5	6.0	18.0	12.0	16.9
DHUM	8.8	25.2	34.1	30.9	3.4	6.2	4.9	6.0
HUM	(24.2)	(98.8)	(117.1)	(117.4)	(9.4)	(24.1)	(17.0)	(23.0)
PRUL	11.7	9.9	33.5	20.4	4.5	2.4	4.9	4.0
DRUL	19.8	29.4	57.5	41.7	7.7	7.2	8.3	8.2
RUL	(31.5)	(39.3)	(91.0)	(62.1)	(12.2)	(9.6)	(13.2)	(12.1)
CARP	14.8	5.4	10.7	3.4	5.7	1.3	1.5	0.7
PMTC	1.9	1.7	5.0	5.0	0.7	0.4	0.7	1.0
DMTC	16.9	9.6	21.2	18.0	6.6	2.3	3.1	3.5
MTC	(18.8)	(11.3)	(26.2)	(23.0)	(7.3)	(2.8)	(3.8)	(4.5)
APHA	14.6	9.8	28.4	31.3	5.7	2.4	4.1	6.1
PFEM	14.8	49.9	66.3	50.3	5.7	12.2	9.6	9.8
DFEM	37.1	72.0	142.0	78.6	14.4	17.6	20.6	15.4
FEM	(51.9)	(121.9)	(208.3)	(128.9)	(20.1)	(29.8)	(30.2)	(25.2)
PATE	1.1	6.2	4.3	4.5	0.4	1.5	0.6	0.9
PTIB	15.1	39.3	76.8	26.5	5.9	9.6	11.1	5.2
DTIB	13.3	14.0	19.5	21.1	5.2	3.4	2.8	4.1
TIB	(28.4)	(53.3)	(96.3)	(47.6)	(11.0)	(13.0)	(13.9)	(9.3)
TARS	31.0	25.6	36.9	21.7	12.0	6.3	5.3	4.2
PMTT	1.3	2.2	5.4	3.4	0.5	0.5	0.8	0.7
DMTT	17.6	16.0	27.2	21.0	6.8	3.9	3.9	4.1
MTT	(18.9)	(18.2)	(32.6)	(24.4)	(7.3)	(4.4)	(4.7)	(4.8)
PPHA	18.7	11.0	18.4	25.8	7.2	2.7	2.7	5.0

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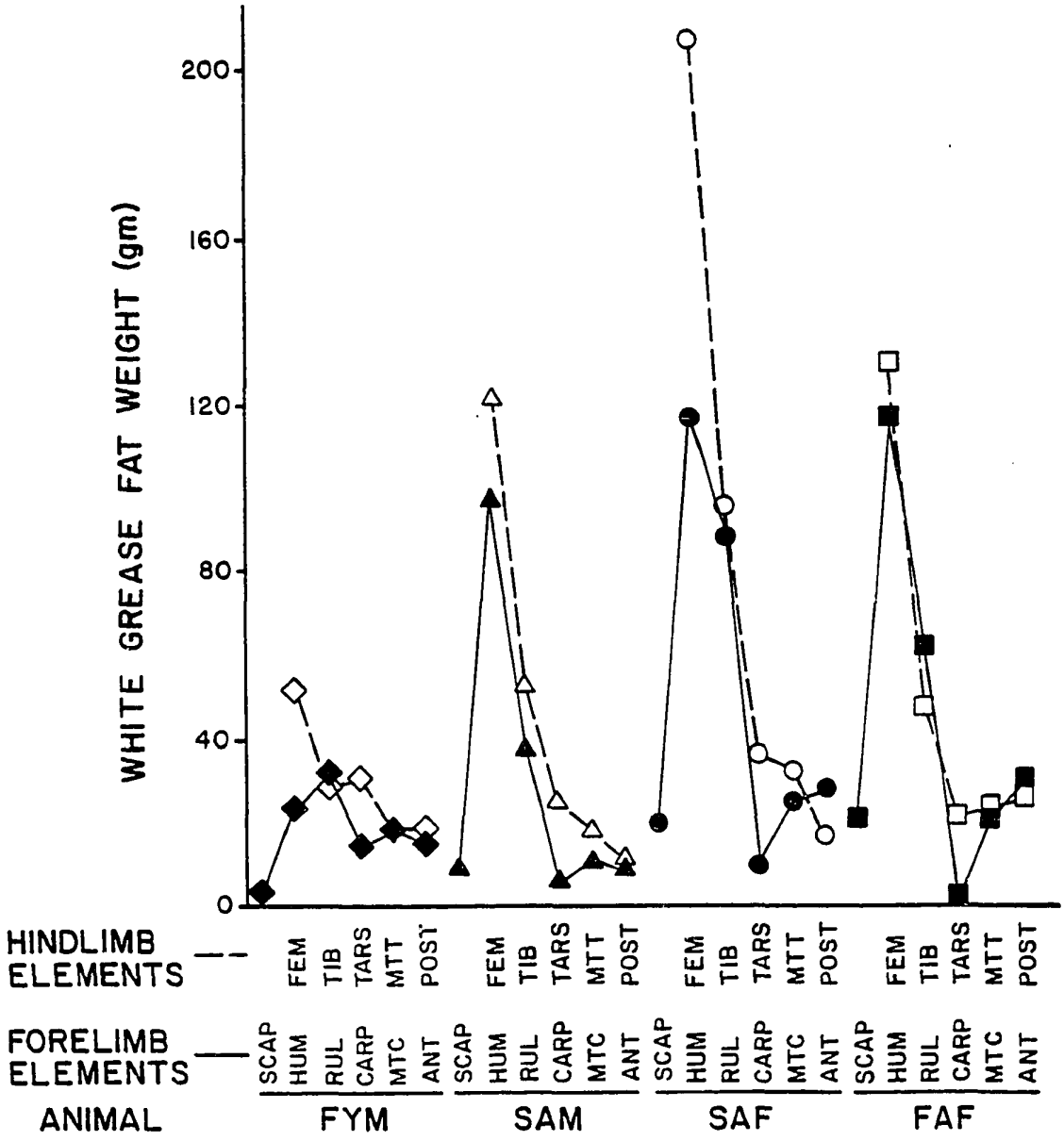

Figure 5.26. Comparative Production of White Grease Fat in the Bison Side Carcass.

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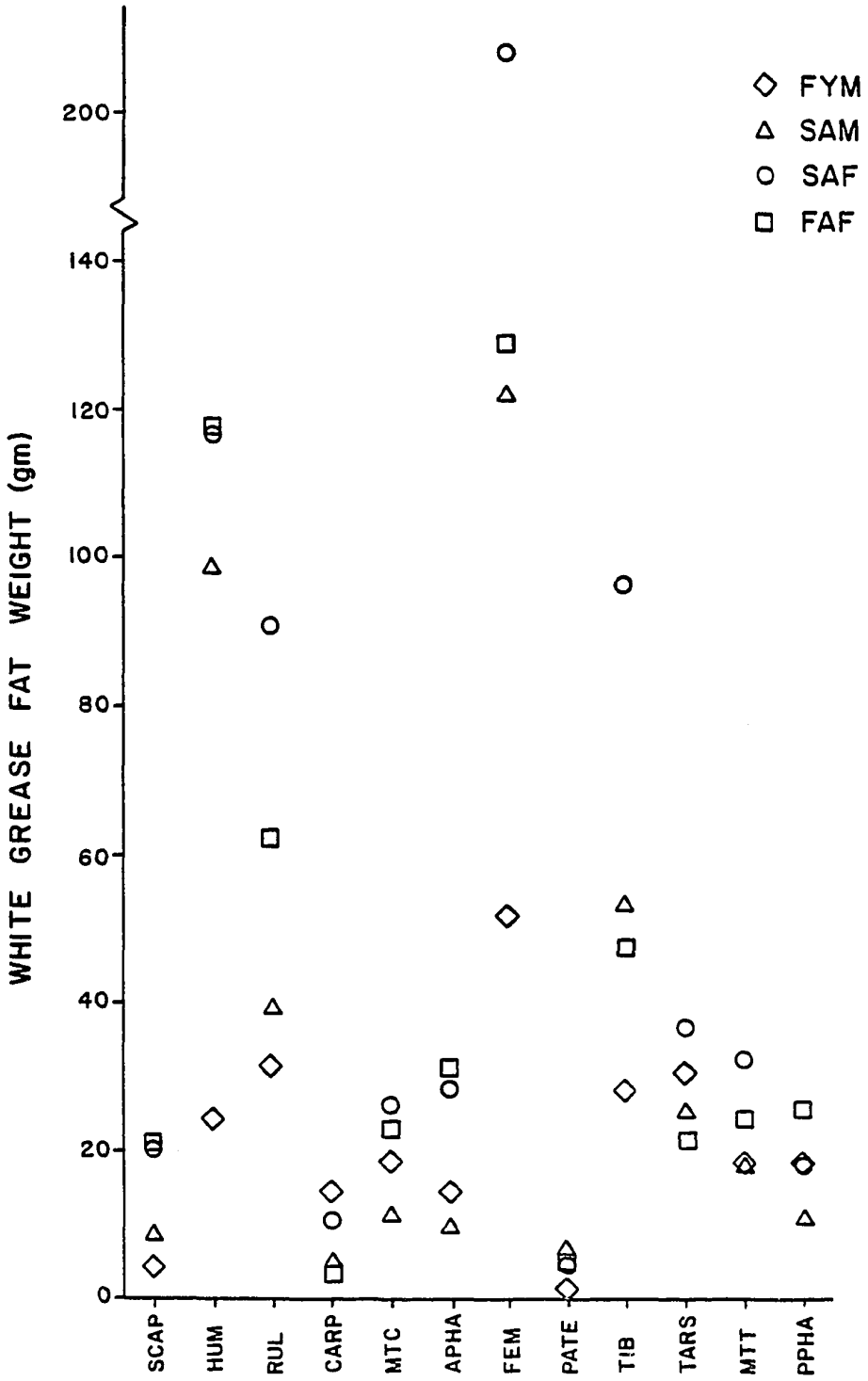

Figure 5.27. Range of Variability in White Grease Fat Yield in the Bison Side Carcass.

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patella, tibia, tarsals, and posterior phalanges), each of the females produced more white bone grease fat than either of the two males. Of the bones noted above which do not follow this pattern, all are relatively minor white grease fat producers, with the exception of the tibia. If the data from FAF are excluded--given the earlier assessment that she was in relatively poor condition--the tibia and tarsals follow the same pattern as noted above, with the other female, SAF, producing a greater amount of white bone grease fat than either of the males. Ignoring differences in quality as influenced by the fatty acid composition, this suggests that if a choice is to be made, and bone grease fat is the desired product, then females rather than males should be the target animals. Unless there are major differences in the fatty acid composition of male and female bone grease, it seems doutful that this factor would alter the ranking of males and females for bone grease recovery. It is doubtful that such differences would improve the ranking of males, regardless. In carcass fat depots that show sex-related differences in fatty acid composition (Leat 1976:186), it is the females that have the greater proportion of unsaturated fats. Therefore, if bone grease is like these fat depots, it should be the females that are preferred on the basis of fat quality as well as quantity.

Age Differences in White Grease Fat Production--The data (Table 5.39) also illustrate an interesting relationship between the fat production levels of the immature male, FYM, and the adult male, SAM. In Figure 5.27 one can see that the male, SAM, produced more bone grease fat in the proximal elements (the scapula, humerus, radius-ulna, femur, patella, and tibia), while the immature male, FYM, produced more bone grease in the carpals, tarsals, and more distal bones of the fore and hindlimb. The sites in which the fat weight for FYM exceeded that of SAM are small grease fat

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producers and show only minor differences in these weights (ranging from 0.7 to 9.4 gm)--differences which might not be significant if tested with a larger sample of animals, and which probably would not be considered important by hunters processing these bones. Age differences in white grease fat production between the more mature male, SAM, and the immature male, FYM, appear to show a division in the predominance of the proximal and distal limb bones, with the break occuring between the radius-carpal and tibia-tarsal joints.

For the major long bones of the limbs (the humerus, radius-ulna, femur, and tibia), the adult male, SAM, produced substantially more white bone grease fat than FYM, especially in the humerus and femur. The smaller (though still pronounced) degree of variability between the radius-ulna and tibia of these two animals suggests that age is an important factor in the production of bone grease in the limbs, and that it takes longer, during growth, to reach adult levels in the femur and humerus. This relationship echoes the reported hierarchy of growth that Hammond (c.f., Hafez 1969a) found, which begins with the distal elements and proceeds proximally.

Condition Differences in White Grease Fat Production--In the analysis of bone marrow fat, it was shown that the female, FAF, was in poorer condition than the female, SAF. Bone grease fat weights should reflect this as well. A comparison of the bone grease fat data of individual bones of the adult bison provides some insights into how animal condition differences are reflected in bone grease fat production. As noted above, the female bison carcasses produced more bone grease than the males (Figure 5.26), but this difference is much more pronounced between the males and the female, SAF. The older, and poorer conditioned female, FAF, has much less white bone grease fat in the femur, tibia, and radius-ulna than the female, SAF.

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The differences in the white grease fat production for the humerus are nearly negligible for the females. If the relationship of the conditions of SAF and FAF have been properly interpreted, then the femur, tibia, and radius-ulna appear to strongly reflect animal condition with lowered production of bone grease.

Whole Versus Partial Bone, White Grease Fat Production--White bone grease production of halves of limb bones is not comparable to production for whole bones (Table 5.39). The long bones, divided perpendicular to the longitudinal axis, often show wide differences in the production of white grease fat between the proximal and distal ends. In many cases, this difference is not so large that it would discourage processing of both ends. In the case of the metapodials, however, bone grease production of the proximal ends is so small in all four animals, that it seems unlikely that these elements would be processed unless the quality of this fat is high enough to warrant the effort for such small amounts, or if the need for white grease fat product is very high.

Division of the major white grease bones into proximal and distal halves is suggested by Binford (1978) to be a legitimate practice for construction of carcass utility models, because the Nunamiut often treat the ends differently in the bone grease recovery process. Within a single carcass, the importance of bone ranking decisions as they relate to white grease fat recovery is relatively clearly illustrated by the proportional data found in Table 5.39, described above.

The importance of differences in fat production between animals, as it affects particular bones, is perhaps more clearly illustrated when one considers this group of four bison as a single sample (i.e., as the equivalent of a very small bison kill). Table 5.40 presents the white

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Table 5.40. Cumulative Production of White Bone Grease Fat in the Half Carcass

Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
SAF	DFEM	142.0	142.0	7.6	SAF	DHUM	34.1	1,025.6	54.9
FAF	PHUM	86.5	228.5	12.2	SAF	PRUL	33.5	1,059.1	56.7
SAF	PHUM	83.0	311.5	16.7	FAF	APHA	31.3	1,090.4	58.3
FAF	DFEM	78.6	390.1	20.9	FYM	TARS	31.0	1,121.4	60.0
SAF	PTIB	76.8	466.9	25.0	FAF	DHUM	30.9	1,152.3	61.6
SAM	PHUM	73.6	540.5	28.9	SAM	DRUL	29.4	1,181.7	63.2
SAM	DFEM	72.0	612.5	32.8	SAF	APHA	28.4	1,210.1	64.7
SAF	PFEM	66.3	678.8	36.3	SAF	DMIT	27.2	1,237.3	66.2
SAF	DRUL	57.5	736.3	39.4	FAF	PTIB	26.5	1,263.8	67.6
FAF	PFEM	50.3	786.6	42.1	FAF	PPHA	25.8	1,289.6	69.0
SAM	PFEM	49.9	836.5	44.7	SAM	TARS	25.6	1,315.2	70.4
FAF	DRUL	41.7	878.2	47.0	SAM	DHUM	25.2	1,340.4	71.7
SAM	PTIB	39.3	917.5	49.1	FAF	TARS	21.7	1,362.1	72.9
FYM	DFEM	37.1	954.6	51.1	FAF	SCAP	21.2	1,383.3	74.0
SAF	TARS	36.9	991.5	53.0	SAF	DMIC	21.2	1,404.5	75.1

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Table 5.40. (continued)

Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
FAF	DTIB	21.1	1,425.6	76.3	FYM	PFEM	14.8	1,692.3	90.5
FAF	DMTT	21.0	1,446.6	77.4	FYM	APHA	14.6	1,706.9	91.3
FAF	PRUL	20.4	1,467.0	78.5	SAM	DTIB	14.0	1,720.9	92.1
SAF	SCAP	20.3	1,487.3	79.6	FYM	DTIB	13.3	1,734.2	92.8
FYM	DRUL	19.8	1,507.1	80.6	FYM	PRUL	11.7	1,745.9	93.4
SAF	DTIB	19.5	1,526.6	81.7	SAM	PPHA	11.0	1,756.9	94.0
FYM	PPHA	18.7	1,545.3	82.7	SAF	CARP	10.7	1,767.6	94.6
SAF	PPHA	18.4	1,563.7	83.6	SAM	PRUL	9.9	1,777.5	95.1
FAF	DMTC	18.0	1,581.7	84.6	SAM	APHA	9.8	1,787.3	95.6
FYM	DMTT	17.6	1,599.3	85.6	SAM	DMTC	9.6	1,796.9	96.1
FYM	DMTC	16.9	1,616.2	86.5	FYM	DHUM	8.8	1,805.7	96.6
SAM	DMTT	16.0	1,632.2	87.3	SAM	SCAP	8.8	1,814.5	97.1
FYM	PHUM	15.4	1,647.6	88.1	SAM	PATE	6.2	1,820.7	97.4
FYM	PTIB	15.1	1,662.7	88.9	SAM	CARP	5.4	1,826.1	97.7
FYM	CARP	14.8	1,677.5	89.7	SAF	PMTT	5.4	1,831.5	98.0

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Table 5.40. (continued)

Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
SAF	PMTC	5.0	1,836.5	98.2	FAF	CARP	3.4	1,861.2	99.6
FAF	PMTC	5.0	1,841.5	98.5	SAM	PMTT	2.2	1,863.4	99.7
FAF	PATE	4.5	1,846.0	98.7	FYM	PMTC	1.9	1,865.3	99.8
SAF	PATE	4.3	1,850.3	99.0	SAM	PMTC	1.7	1,867.0	99.9
FYM	SCAP	4.1	1,854.4	99.2	FYM	PMTT	1.3	1,868.3	99.9
FAF	PMTT	3.4	1,857.8	99.4	FYM	PATE	1.1	1,869.4	100.0

grease fat data ranked from most to least productive units, tabulates the production of each bone or bone part as a percent of total kill white grease fat weight, and presents the cumulative percent that the addition of each bone of successively smaller fat producing units adds to the percent of total production. The data in this table clearly demonstrate that it takes only a few bones to recover the majority of the available white bone grease fat. Ranking bone units in this manner also illustrates the low priority that most of the bones from the immature male, FYM, have in selection for processing, as well as the importance of particular units in the overall scheme of bone grease fat processing. This ranking could be expected to change somewhat with the addition of more animals to the sample, or with a change in the age and sex structure of the herd or sample. Nevertheless, it clearly illustrates the disparity in value of proximal and distal ends of many long bones, as compared with the values for whole bones, and leads one to expect differential use of the ends of bones when a large kill is made and selectivity is encouraged.

Summary of White Bone Grease Fat Production Differences--The relationships found in white grease fat production values of these four bison, all of which need to be further tested with a larger sample, may be summarized as follows: (1) bones that produce the largest quantities of white bone grease fat, show the greatest variability in fat production levels between animals; (2) bones may show large differences in the quantity of white grease fat between proximal and distal ends--particularly in the metapodials--and these differences may be important when a large kill provides the option for selective bone grease processing; (3) females generally produce more white bone grease fat than males in the large grease producing bones; (4) young, immature animals produce less bone grease fat

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than mature animals in the major long bones (i.e., the femur, tibia, humerus, and radius-ulna); (5) poor condition in the female, FAF, results in white bone grease fat production comparable to, but somewhat larger than that of the adult male, SAM; and (6) comparing the fat weights for SAF and FAF, poor condition in FAF (the extent of which cannot be specifically quantified) appears to have resulted in declining grease production, most dramatically in the femur and tibia, substantially in the radius-ulna, but not that could be determined in the humerus.

Variability in White Grease Fat Distribution. While differences in fat production exist between animals, these differences also may extend to how grease fat is distributed between the grease producing bones. Examination of the white grease fat percentage data in Table 5.39 shows that the bone elements are not consistent from animal to animal in the proportions of white grease fat they produce, unlike the marrow data examined earlier. This may be indicative of one, or a combination of two factors. White grease fat may be highly variable in its production between individuals in general, as Berg and Butterfield (1976:143) report for carcass fat in cattle. Additionally, these animals may be in different stages of bone grease fat mobilization. The latter may be assumed based upon low marrow fat content of FAF compared with the other three bison. Without a larger sample of animals in each age and sex class, or without additional data from cattle or wildlife studies, it is difficult to interpret these data. If one assumes that the female, SAF, is in relatively good condition, and that SAM and FYM are intermediate in condition between FAF and SAF, then several observations may be made.

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Age Differences in White Grease Fat Distribution--Examining the differences between the two males first, in order to evaluate possible age differences due to the attainment of adult maturity, one sees a very different picture of white grease fat distribution (Table 5.39). In the immature male, FYM, the more distal limb elements form a much larger percentage of the total white grease fat weight than in the adult male, SAM, or in the adult females. This is especially noticeable in the comparatively inflated value of the tarsals. The depressed values of the more proximal bones of the limbs are most noticeable in the femur and humerus, and less pronounced in the tibia and radius-ulna. Recalling the comparisons of actual fat weights from Table 5.39, this pattern of inflated values for the distal elements and depressed values for the proximal elements, is clearly due to the smaller production of bone grease fat in the proximal elements, rather than consistently greater production in the distal elements. Furthermore, the earlier completion of mature bone development in more distal elements, may explain the depressed values of the femur and humerus, and the less depressed values of the tibia and radius-ulna. If red marrow has not been replaced in the proximal elements, this pattern might be expected. It should be noted, however, that if nutritional stress is a factor, it is also the proximal elements that lose fat at a greater rate than the distal elements. Although both conditions may be in effect here, I would suggest that the age difference is probably more pertinent here than nutritional stress, because of the pattern of marrow fat content discussed above, and because of the fall season death of FYM.

Condition Differences in White Grease Fat Distribution--Examining the relationships of values reported for the two adult females (Table 5.39), and considering the effects of poorer animal condition upon white grease fat

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distribution, one notes the smaller proportional production of the femur, tibia, and tarsals in the older female, FAF, and the resultant inflated value for the humerus. In FAF, the humerus, phalanges, and scapula apparently lose fat at a slower rate than the loss in total fat, because their percent values are higher than those for the female, SAF, who was in good condition. The radius-ulna, and metapodials show comparable proportion in both animals, because the total grease fat production for the female, FAF, is lower and the smaller amount of fat in these bones drops in proportion to the total drop in fat production.

Sex Differences in White Grease Fat Distribution--Comparing the male, SAM, with the female, SAF, (a comparison of two animals in good or moderately good condition), one notes that the scapula, femur, tibia, tarsals and carpals, metapodials, and phalanges are more or less comparable in their proportion of the production of the total white grease fat. This echoes the pattern seen in the analysis of possible sex differences in bone volume distributions (Table 5.21). The major differences between the distributions of these two animals lie in the humerus and the radius-ulna; the former produces a larger proportion of total fat weight in the male than in the female, and the latter a smaller proportion. In the analysis of bone volume distribution, both account for larger proportions of total bone volume in males than in females. This suggests the difference in volume distribution in the radius-ulna between animals was not large enough to compensate for the greater overall fat production in females than in males.

Examining Table 5.39, it is evident that the extremely high white grease fat weight for the femur in SAF suppresses the importance of the fat weight of the humerus and the other units, and the much smaller weight of the femur in the male, SAM, results in higher proportions for the other

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units in that animal. A larger sample would help to clarify where the break from normal distribution is occurs, if it exists. It is possible that the humerus fat weight for SAF is abnormally low, given the production and distribution data for the other adult bison. Referring once again to Figure 5.25 of the regression of the percent grease fat weight and percent bone volume, the former seems to be the case. Excluding the FYM data, the distal humeri for all three adults produce a smaller proportion of the total white grease fat weight than the general pattern of the relationship between bone volume and fat weight would suggest, and the distal femur of SAF alone produces more than expected. Given that all animals have low humeri grease fat production and only SAF has high distal femur production, the differences in distribution appear to be related to this value of the SAF femur. It does not appear from this figure that the lack of full maturity in SAM is important.

Rank Orders of White Grease Fat Production--The importance of the differences in the distribution of white grease fat attributed to animal age, sex, and condition is evaluated here. Differences in rank, evaluated in conjunction with the actual production data, indicate where the selection of bones for white grease fat recovery might differ for animals of different classes, when individual carcasses are processed. Rank order alone, however, does not necessarily indicate a difference in selection order. Rather, rank differences must be considered in conjunction with the production data to determine where differences in rank are meaningful, and would be potentially noticeable by hunters processing the bones. Figure 5.28 compares the rank orders of the bones or bone halves and lists their fat weights. Proximal and distal ends of the long bones are evaluated separately because they often produce greatly different amounts of bone

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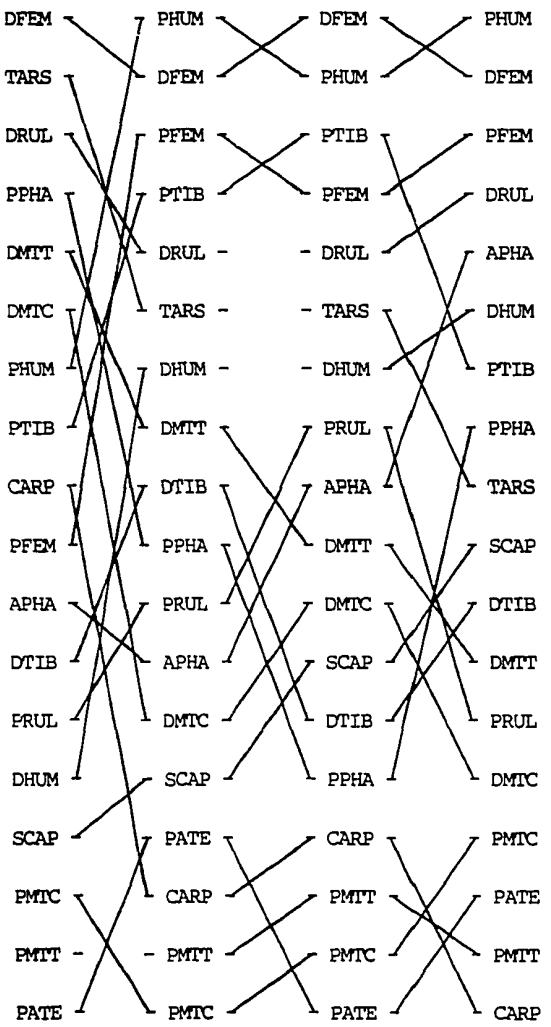
Figure 5.28. Rank Order of Bone and Partial Bone Units

for Side White Grease Fat Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DFEM	PHUM	DFEM	PHUM	37.1	73.6	142.0	86.5
TARS	DFEM	PHUM	DFEM	31.0	72.0	83.0	78.6
DRUL	PFEM	PTIB	PFEM	19.8	49.9	76.8	50.3
PPHA	PTIB	PFEM	DRUL	18.7	39.3	66.3	41.7
DMTT	DRUL	DRUL	APHA	17.6	29.4	57.5	31.3
DMTC	TARS	TARS	DHUM	16.9	25.6	36.9	30.9
PHUM	DHUM	DHUM	PTIB	15.4	25.2	34.1	26.5
PTIB	DMTT	PRUL	PPHA	15.1	16.0	33.5	25.8
CARP	DTIB	APHA	TARS	14.8	14.0	28.4	21.7
PFEM	PPHA	DMTT	SCAP	14.8	11.0	27.2	21.2
APHA	PRUL	DMTC	DTIB	14.6	9.9	21.2	21.1
DTIB	APHA	SCAP	DMTT	13.3	9.8	20.3	21.0
PRUL	DMTC	DTIB	PRUL	11.7	9.6	19.5	20.4
DHUM	SCAP	PPHA	DMTC	8.8	8.8	18.4	18.0
SCAP	PATE	CARP	PMTC	4.1	6.2	10.7	5.0
PMTC	CARP	PMTT	PATE	1.9	5.4	5.4	4.5
PMTT	PMTT	PMTC	PMTT	1.3	2.2	5.0	3.4
PATE	PMTC	PATE	CARP	1.1	1.7	4.3	3.4

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grease fat, and because the recovery process, which involves breaking the bone into small pieces before boiling (Leechman 1951), might not be handled similarly for both ends when such differences occur.

Age differences in the rank orders (as represented by comparison of the FYM and SAM orders) are numerous in Figure 5.28, but the similarity in the weights of the units from FYM indicates that many of these differences are probably unimportant. In the rank order for FYM (Figure 5.28), from the distal radius-ulna (DRUL) through the distal humerus (DHUM), the difference in fat weight is only 11 gm. Despite the apparently large differences in rank orders for FYM and SAM, therefore, it is doubtful that selection order would be altered from that of the older male, SAM. The exception to this might be the selection priority of the proximal humerus (PHUM) in the yearling. In SAM, this is the highest ranked unit, but in FYM this unit is at the top of the middle third of the order. The difference in fat weights of this unit and the distal femur in FYM is 21.7 gm, which represents a substantial drop in rank and production, a difference that probably would be recognized. The location of the proximal humerus near the upper third of the order, above units that produce similarly large amounts of fat, probably insures its inclusion in the group of bones processed. One would not expect to see major differences in the bones processed from a yearling, as opposed to a four year old male bison, when treated as individual carcasses, unless the production level of the FYM bones is considered too small to warrant processing.

Comparison of the rank orders and white grease fat weights (Figure 5.28) from the bone units of SAM and SAF indicate where differences due to animal sex might encourage differences in unit selection. The differences in unit rank between the proximal humerus (PHUM) and distal femur (DFEM),

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and between the proximal femur (PFEM) and proximal tibia (PTIB) are probably unimportant given the similar fat weights between the adjacent units of each pair showing rank changes. The differences in fat production in the other units that show evidence of rank change, probably are not of a large enough magnitude to influence the order of bone selection in processing individual carcasses. When individual carcasses are processed, therefore, it is not expected that selection decisions, concerning the order of processing, would differ if a male, rather than a female carcass were available.

Comparison of the two females, SAF and FAF, indicates where animal condition differences may influence unit selection for white grease fat recovery, when hunters process individual carcasses. Although the distal femur (DFEM) shows markedly lower fat weight in FAF, the difference in weight from the proximal humerus (PHUM) is not large. With bison in similar condition to FAF and SAF, the difference in unit rank between animals is relatively unimportant, but in more severely stressed bison this might change. Markedly lower fat weight and a drop in rank is also evident in the proximal tibia (PTIB). All other drops and increases in the rank of units from FAF compared to SAF represent differences in fat weights that are less that 10 gm, and thus, probably have little influence on selection order.

Currently, there is no literature indicating how submaintenance nutrition influences fat weight changes in bone grease production. One might suspect, however, that with continued mobilization, a similar proximal to distal gradient of the rate of fat loss as seen in bone marrow (Reich 1981) might occur. The effect of such a pattern would be to eventually increase the rank of more distal units while decreasing the rank of more proximal units. It also suggests that the more productive proximal units might eventually be excluded from the grease fat recovery process, but this would have to be

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confirmed with a larger sample of animals. It is possible that the large size of the proximal grease fat producing bones offsets their faster rate of fat mobilization compared to the smaller, more distal elements if the evaluation focuses on fat yield.

The concurrent evaluation of rank order and fat weight production from bone units producing white grease fat suggests that probably very few differences would be evident in the archaeological record when the carcasses of individual animals are processed. Similar selection orders should occur in males, females, and young animals, although the proximal humerus (PHUM) of young bison might be used with less frequency. The data for the two females showed only minor differences due to fat mobilization in FAF. The distal femur (DFEM) and proximal tibia (PTIB) both were lower in rank in the poorly conditioned female, FAF. These differences suggest, however, that continued fat mobilization might alter the way in which poorly conditioned animals are processed for white grease fat recovery.

Summary of White Grease Fat Production and Distribution Analyses. Evaluating the white grease fat production and distribution data from the perspective of someone who processes bone to recover grease fat, it is evident that the production figures provide more useful data for making selection decisions. Variability in white bone grease fat production between animals of different age and sex suggests that when fat quantity alone is used to determine selection, females should be preferred to males, and adult animals should be preferred to immature animals. Furthermore, if a large kill provides numerous animals from which to select grease fat bones, then processing decisions should probably reflect the differences in fat production between proximal and distal ends of long bones. Generally speaking, however, the distal femur and radius, and the proximal femur,

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humerus, and tibia, are the most productive units for the recovery of white bone grease fat. The fat from these bones is not as soft as that from the less productive, more distal bones, however, so preference for the more productive elements may be mediated somewhat to reflect the qualitative differences in the fat.

Production and Distribution of Yellow Bone Grease Fat

Yellow grease fat is the fat extracted from the rendered bone grease of the axial skeleton. Binford (1978) first noted the distinction between white and yellow bone grease, based upon the caribou and sheep carcass processing decisions made by the Nunamiut. Table 5.41 presents the fat weights of yellow bone grease bones and bone groups (excluding the skull, mandible, and hyoid) in the bison sample, as well as the percentage each represents of the total yellow grease fat weight.

Production of Yellow Bone Grease Fat in Individual Bones. Table 5.41 above, provides grease fat weights for individual bone groups of the axial skeleton, that Binford (1978) refers to as yellow grease bones. These data show that the low grease fat production of the immature male, FYM, is not concentrated in particular bones, but is lower in all of the skeletal elements except the cervical vertebrae. Animal age is thus a clear factor in between-animal differences in the weight of yellow grease fat of individual bone groups. The same is true for a comparison of the fat weights from the male, SAM, and the females (with the exception of the sternum from SAF, which has a value which looks odd in this data set), and indicates the presence of sex differences in the grease fat production of these bones as well.

Comparison of the yellow grease fat weights for SAF and FAF (Table 5.41), shows that the largest difference between these animals lies in the

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Table 5.41. Comparative Yellow Grease Fat Weight and Distribution in the Bison Side

	Yellow Grease Fat Weight (gm)				Percent of Total Yellow Grease Fat Weight			
Unit	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
ATLAS	1.4	0.4	2.0	3.0	2.6	0.2	0.7	1.1
AXIS	0.6	0.7	3.0	1.4	1.1	0.4	1.0	0.5
C3C7	0.9	0.4	3.9	10.9	1.6	0.2	1.3	4.1
CERV	(2.9)	(1.5)	(8.9)	(15.3)	(5.3)	(0.8)	(3.0)	(5.7)
THOR	3.8	15.1	37.2	34.6	7.0	8.1	12.5	12.9
LUMB	16.7	22.8	24.4	24.1	30.6	12.2	8.2	9.0
SAC1	4.7	34.3	67.0	42.9	8.6	18.3	22.5	16.0
PELV	18.5	71.8	76.5	45.5	33.9	38.3	25.7	17.0
CAUD	2.2	0.6	6.8	4.7	4.0	0.3	2.3	1.8
RIBS	5.6	36.3	76.6	90.3	10.3	19.4	26.7	33.8
STER	0.2	4.9	0.8	9.9	0.4	2.6	0.3	3.7

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weights of the sacrum and pelvis. Other differences are either minor, or indicate that the fat weight for the female, FAF, is larger than that of SAF. If, as suggested, animal condition is poorer in FAF, and if one assumes that hypothetical fat weights for FAF when in good condition would be comparable to, or higher than those of SAF given the age difference of the females, then these data suggest that a decline in animal condition is registered in yellow grease fat weights most dramatically in the sacrum and pelvis. This may not represent the largest proportional drop in fat weight, but in terms of hunter selection of bone for yellow grease fat recovery, this may be an important change.

The importance of differences in the amount of fat produced by each bison (Table 5.42), together with the fact that yellow grease fat is not homogeneously distributed in the bones of the axial skeleton, are clearly illustrated in Table 5.43. This table lists, by increasinng weight, each yellow grease fat producing unit (from all four individuals), together with the cumulative percent that the addition of that unit to those previously listed represents of the total yellow grease fat. In effect, the table indicates the order in which bone units should be selected to maximize yellow grease fat recovery. Although one would not expect strict carcass unit selection on the basis of yellow grease fat production alone, these data do suggest how bones might be used if yellow grease fat is a desired carcass product.

Several important points are illustrated by the cumulative percent data. First, one need process only a small number of the total units available to recover half or three quarters of the yellow grease fat total. Second, nearly 85 percent of the available yellow grease fat is accounted

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Table 5.42. Comparative Carcass Yield of Yellow Grease Fat

	FYM	SAM	SAF	FAF
FYM	---	29.2	18.3	20.3
SAM		---	62.8	70.1
SAF			---	111.6
FAF				---
Fat Weight (gm)	54.6	187.3	298.2	267.3

Note: cell values equal vertical animal fat weight as a percent of horizontal animal fat weight.

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Table 5.43. Cumulative Production of Yellow Bone Grease Fat in the Half Carcass

Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
FAF	RIBS	90.3	90.3	11.2	FYM	LUMB	16.7	719.5	89.1
SAF	RIBS	76.6	166.9	20.7	SAM	THOR	15.1	734.6	91.0
SAF	PELV	76.5	243.4	30.1	FAF	C3C7	10.9	745.5	92.3
SAM	PELV	71.8	315.2	39.0	FAF	STER	9.9	755.4	93.6
SAF	SAC1	67.0	382.2	47.3	SAF	CAUD	6.8	762.2	94.4
FAF	PELV	45.5	427.7	53.0	FYM	RIBS	5.6	767.8	95.1
FAF	SAC1	42.9	470.6	58.3	SAM	STER	4.9	772.7	95.7
SAF	THOR	37.2	507.8	62.9	FYM	SAC1	4.7	777.4	96.3
SAM	RIBS	36.3	544.1	67.4	FAF	CAUD	4.7	782.1	96.9
FAF	THOR	34.6	578.7	71.7	SAF	C3C7	3.9	786.0	97.3
SAM	SAC1	34.3	613.0	75.9	FYM	THOR	3.8	789.8	97.8
SAF	LUMB	24.4	637.4	78.9	SAF	AXIS	3.0	792.8	98.2
FAF	LUMB	24.1	661.5	81.9	FAF	ATLAS	3.0	795.8	98.6
SAM	LUMB	22.8	684.3	84.8	FYM	CAUD	2.2	798.0	98.8
FYM	PELV	18.5	702.8	87.0	SAF	ATLAS	2.0	800.0	99.1

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Table 5.43. (continued)

Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent	Animal	Carcass Unit	Grease Fat Weight (gm)	Cumulative Fat Weight (gm)	Cumulative Percent
FYM	ATLAS	1.4	801.4	99.3	SAM	CAUD	0.6	805.8	99.8
FAF	AXIS	1.4	802.8	99.4	FYM	AXIS	0.6	806.4	99.9
FYM	C3C7	0.9	803.7	99.5	SAM	C3C7	0.4	806.8	99.9
SAF	STER	0.8	804.5	99.6	SAM	ATLAS	0.4	807.2	100.0
SAM	AXIS	0.7	805.2	99.7	FYM	STER	0.2	807.4	100.0

for before the first unit from the yearling male, FYM, appears in the list. Third, the units from the male, SAM, generally do not appear in the list until the corresponding unit(s) in the female(s) have already been listed. In other cases, age, sex, or condition does not uniformly affect the order of unit appearance in the cumulative weight table. If animal class characteristics affect the distribution of yellow grease fat weight, this might account for the lack of regular patterning in the appearance of animal units in the list--at least in the case of units that produce moderate to large amounts of grease fat. In the case of small producing units, small variations in weight can lead to variations in the order of appearance that are insignificant, and therefore, are not considered here.

Yellow Bone Grease Fat Distribution. Table 5.41 above, also lists the percent of the total yellow grease fat that is found in each bone group. These data show a great deal of variability which makes it difficult to make conclusions concerning age, sex, or condition differences in fat distribution. Possible age- or sex-related differences may be evident in the percentages for the thoracic and lumbar vertebrae. The thoracic vertebrae show smaller percentages of total yellow grease fat weight in the two younger males than in the other females, and the lumbar vertebrae show higher percentages. Age appears to be important in the proportion that the sacrum and ribs represent of the total yellow grease fat weight. These units represent smaller proportions of total yellow grease fat weight in the yearling, FYM. Sex appears to be potentially important in the distribution for the pelvis and ribs, with males having a greater percent of their total yellow grease fat in the pelvis, and females a greater percent in the ribs.

The degree of variability in values between animals leads me to be particularly cautious about these assessments. Clearly, a much larger

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sample of animals of known age, sex, and condition are needed to fully understand the yellow grease fat weight distribution data. Perhaps the assessment of Tavassoli and Yoffey (1983) that red marrow fat is as mobile as body fat depots, and Berg and Butterfield's (1976) assessment that quantities of fat in body fat depots are highly variable between individual cattle, might account for the high degree of variability seen in the weight and distribution of yellow grease fat in these bison. The importance of the differences may be evaluated by examining the rank orders of bones between animals.

Rank Orders for Yellow Grease Fat Production--Figure 5.29 includes yellow bone grease fat weights and a comparison of the rank orders of bones for fat production between animals. Examination of these data suggests that the differences evident in the ranks of the neck (ATLAS, AXIS, and C3C7) and sternebrae (STER) units are probably meaningless in terms of hunter selection of bones for grease fat recovery, because these bones produce so little fat in any of the animals. It also appears that so little yellow fat is produced by any of the bones of the immature male, FYM, that it leads one to question whether the return would be adequate to compensate for the effort needed to recover it. It is doubtful that following winter and early spring season energy demands, male bison of this age (yearling to two years old) would have sufficient amounts of yellow bone grease to justify the processing of the bones of this animal, except possibly the pelvis and lumbar units.

The grease fat weights of the ribs (RIBS) and pelvis (PELV) of the male, SAM, compared to those of FYM, suggest that age does influence the distribution of yellow grease fat in these units. The rank of the pelvis, however, remains stable between animals, and the rank of the ribs is only

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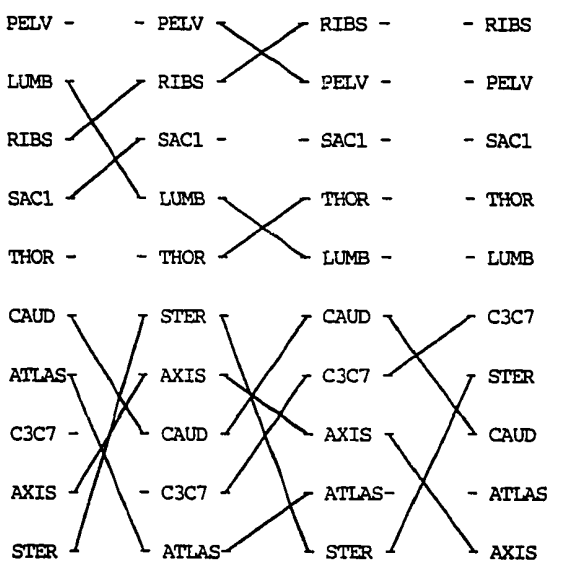
Figure 5.29. Rank Order of Carcass Units for Side Yellow Grease Fat Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
PELV	PELV	RIBS	RIBS	18.5	71.8	76.6	90.3
LUMB	RIBS	PELV	PELV	16.7	36.3	76.5	45.5
RIBS	SAC1	SAC1	SAC1	5.6	34.3	67.0	42.9
SAC1	LUMB	THOR	THOR	4.7	22.8	37.2	34.6
THOR	THOR	LUMB	LUMB	3.8	15.1	24.4	24.1
CAUD	STER	CAUD	C3C7	2.2	4.9	6.8	10.9
ATLAS	AXIS	C3C7	STER	1.4	0.7	3.9	9.9
C3C7	CAUD	AXIS	CAUD	0.9	0.6	3.0	4.7
AXIS	C3C7	ATLAS	ATLAS	0.6	0.4	2.0	3.0
STER	ATLAS	STER	AXIS	0.2	0.4	0.8	1.4

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slightly lower in the younger male, FYM. The comparability of the fat weights of the pelvis and ribs units in SAF, however, suggests that the rank difference between this female and the male, SAM, is probably unimportant. In four year old males, one would be best rewarded by selecting the pelvis (PELV) for processing, but it would be surprising if the ribs (RIBS) also were not used.

Age also appears to effect the ranking of the thoracic (THOR) and lumbar vertebrae (LUMB) units. With increased animal age, the rank of the lumbar unit drops (Figure 5.29) as other units, particularly the ribs and thoracic vertebrae units begin producing larger proportions of the total yellow grease fat weight (Table 5.41). This change is evident when one compares the ranks of the ribs, thoracic, and lumbar units between all four bison in Figure 5.29.

It is possible that animal sex, rather than age, is responsible for the changes in unit rank, evident in Figure 5.29, between the male, SAM, and the female, SAF. The data in Table 5.36 above, suggest that SAM has a mature distribution of yellow to total grease fat weight, when the fat weights are grouped by bone maturation class (e.g., Jones et al. 1978). A sample including fully mature males is needed to clarify this issue.

The fat weight data from SAF and FAF indicate that the drop in condition in FAF probably has resulted in some loss of yellow fat weight. Although it may not be limited to this unit, the greatest difference evident in Figure 5.29 between the females is in the fat weights of the pelves (PELV). Due to the magnitude of the difference in production between the pelvis and the thoracic vertebrae, however, the condition difference has no effect on the rank order of units. Unless the decline in animal condition is more severe and is differentially manifested in yellow grease fat weight,

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the order of unit selection in individual carcasses probably would not differ.

It appears that very few, if any, differences would be expected to occur in how bone units are selected from individual carcasses for the recovery of yellow grease fat, depending upon animal age, sex, and condition. The major difference evident here, is that the importance of the thoracic (THOR), ribs (RIBS), and sacrum (SAC1) units increase with age, and that of the lumbar (LUMB) unit decreases. It seems likely, however, that in adults, if axial units are collected for yellow grease fat recovery, the lumbar unit would be processed despite its lower rank, because the amount of fat produced is relatively high. It is not clear, however, that the thoracic, ribs, or sacrum units would be processed in young males, due to the small levels of fat production.

Conclusions

Age, sex, and condition differences were examined for the bone and bone product data of four bison from Theodore Roosevelt National Park. A comparison of bone measurements to marrow fat and bone grease fat weights showed that marrow fat weight is predicted better than bone grease fat weight and does not require division of the data into age and sex classes.

These analyses showed that marrow fat found in the medullary cavities of bone is relatively less mobile compared to bone grease fat (especially, fat from units of the axial skeleton), and the relationship between medullary cavity volume and marrow or marrow fat weight is not substantially improved by the grouping of bones from animals of particular age or sex classes. Nevertheless, inspection of individual fat content values and fat weights did show the effects of poor nutrition in the older female, FAF,

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when compared to the data from the other three bison. The largest declines in the marrow fat weight of FAF (using SAF as an estimate of the standard) with declining animal condition, came in the marrow of the proximal and medial limb elements. This is important, given that these are the bones which produce the major portion of the available bone marrow. This pattern of proximal to distal mobilization of marrow fat correlates with that found by Reich (1981) for impala.

For the purposes of understanding prehistoric patterns of bone marrow processing, the positive correlation between bone marrow cavity volume and marrow fat weight, regardless of animal sex, indicates that marrow exploitation should focus on adult male bison to maximize the return from processing efforts. Adult males have larger bones, marrow cavity volumes, marrow weight and probably during most of the year, more marrow fat weight than females--a pattern which contrasts with that for bone grease fat.

In this chapter, bone grease fat was considered in both its physiological and archaeological classifications. Understanding the differences in these classifications and understanding the function of physiological marrow and marrow fat clarifies where one might expect to see variability in medullary cavity marrow and bone grease fat production and distribution. In the analysis of bone grease fat, major differences were found in the productivity of grease fat in males and females, and between immature and mature animals. Unlike medullary marrow, bone grease fat is less abundant in the larger boned male bison, SAM. The analyses also showed that the per unit bone volume grease fat production was smaller for the males than the females, and the distribution of grease fat weight in the appendicular skeleton is markedly higher in the yearling male.

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In each analysis of bone, marrow, and white and yellow grease fat, data from the four bison were compared to identify specific areas where age, sex, or condition differences appeared to be manifested through differences in product distributions in the animal carcass. In the distribution of bone marrow fat, animal age had very little effect on the ranking of marrow producing bone (Figure 5.24). Differences in rank occurred only in bones which produce very little marrow. Differences in the distribution of bone size and marrow weights were registered between the sexes, but like animal age, these were not large enough to affect the rank order of marrow producing bones. All differences noted between FAF and the similarly ranked bones of SAM and SAF could be attributed to minor variability in small marrow weights. Based on these data, one would expect to see a uniform treatment of bones from the carcasses of males and females, young and old, when a single carcass is available and selection for bone marrow recovery occur.

The distribution of bone grease, distinguishing between white and yellow grease fat, was also examined for evidence of the influence of animal age, sex, and condition. The importance of these differences were then examined first, by comparing the rank orders of bones for the production of white and yellow grease fat, to determine whether the differences were of a large enough magnitude to affect rank, and second, by determining whether the weight differences between units that showed rank changes and those that are adjacently ranked were large enough that they might be perceived as being different by hunters selecting bones for processing.

These data suggest that in the recovery of white grease fat, only minor differences would occur in the selection of bones from individual animals depending upon animal age and sex. Specifically, in young animals

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comparable to FYM, the proximal humerus is poorly developed compared to adults. The greatest variability in the selection of white grease fat producing bones probably would be evident between adults in good and poor condition. In this sample of bison, the female, FAF, showed the greatest drop in bone unit rank for the production of white grease fat in the proximal tibia. Fat loss in the distal femur was also evident, but had only a minor effect on rank order at this stage in the fat mobilization process.

The analysis of the yellow grease fat weight data and rank orders indicates that very few important differences in the selection of bone occur due to animal age, sex, or condition differences. The major difference, evident in these bison, is that the lumbar unit is highly ranked in young animals, and as the animals develop and the rate of fat deposition in other units increase, this unit drops in rank. The ribs, thoracic, and sacrum units conversely, increase in their rank for yellow grease fat production with age. In adult animals in good condition, no important sex-related differences in unit rank are evident. In this sample, the female, FAF, was not in a condition poor enough to result in any major changes in the rank order of unit selection for yellow grease fat recovery. It is not clear, from these data, or the literature, how continued condition decline might alter this relationship. If yellow grease fat is processed, therefore, a similar order of selection from individual animals might be expected, regardless of sex or condition, but with some differences due to age.

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CHAPTER 6. VARIABILITY IN CARCASS COMPOSITION, PART TWO: MEAT, ORGANS, AND INTRAMUSCULAR FAT

Previous studies (e.g., Binford 1978, Metcalfe and Jones 1988) of animal carcass composition developed for application to archaeological data, discussed meat weight distributions in animal carcasses, using the combined weight of all non-dry bone products to calculate the relative importance of each carcass unit. Admittedly, meat is often the most abundant tissue in these carcass units, but ocassionally, as in the distal leg units of the bison, there is no associated meat. By referring to these calculations as meat utility indices (MUI) and using these values in the later construction of general utility indices, a casual reader might assume that meat is the only resource evaluated in Binford's MUI. In fact, the MUI includes everything except dry bone--meat, intramuscular and intermuscular fat, marrow and bone grease, and non-edible tissues such as cartilage, ligaments, and tendon. Metcalfe and Jones (1988) recognized this semantic problem and used Binford's meat utility index, with some modification to the method of model construction, to produce what they refer to as the Food Utility Index (FUI), clearly calling attention to the fact that the index includes more than meat weight data.

In the present study, however, the objective has been to understand how variability in carcass resource production and distribution between animals might affect utility index construction or suitability of application. In doing so, the differences and similarities for each carcass product are considered separately, and in the case of carcass meat, this means that it

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is separated from bone products such as marrow and bone grease, and from other fat and fasciae associated with the meat. Previous researchers (e.g., Ledger 1963) have argued that wild ungulates carry very little body fat, suggesting that failure to separate carcass fat from muscle should not lessen the value of the derived indices. Without knowing how much of a unit's weight is derived from fat, however, it is impossible to understand how the relative importance of different carcass units might change during periods when low forage availability for animals coincides with low food availability for humans, and animal carcass fat becomes a premium resource. In this study therefore, I have separated the meat from all but intramuscular fat during the dissection process. I have also determined the percent fat in the meat of each carcass unit by extracting the fat using anhydrous ether as the solvent. Other fat products (subcutaneous, intermuscular, and cavity fat) usually lumped with the meat weight of carcass units by other researchers, are considered separately in the next chapter.

In this chapter, the production and distribution of meat and intramuscular fat in each bison carcass are discussed following an assessment of the relationship between meat weight and dry bone weight. Meat production and distribution are considered in two groups: muscle and a limited group of organs. Muscle weights are discussed both as grouped muscles from associated bone units, in which muscles are often divided at joints between units, and as individual muscles, cross-cutting carcass units. As in the previous chapter, differences in animal age, sex, and condition are examined for their effects upon these data.

Carcass composition of livestock is frequently studied by animal scientists, but less frequently by researchers studying wild ungulates.

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Where appropriate, non-bison studies are compared with the results of this bison carcass analysis. The small size of the bison sample precludes making more than suggestive remarks concerning the contribution of muscle and intramuscular fat to the bison carcass. The exception to this is in the discussion of the relationship between the combined meat and intramuscular fat weight, and dry bone weight where the unit of study is the bone or bone group. While animal age and sex class may be considered by adding or deleting groups of bones belonging to particular animals, conclusions drawn from such manipulations suffer from the same sample size problems as the production and distribution analyses. These data provide interesting insights into the possible relationships between animal class, bone group, and muscle and intramuscular fat weights, but larger sample sizes from additional studies are necessary before these results can be shown to be representative for bison.

Relationship Between Meat and Dry Bone Weight

The relationship between meat and dry bone weight in units of the bison carcass (Figure 6.1) is examined in this section. Meat here, includes the weight of muscle and intramuscular fat, but excludes organ meats (e.g., tongue, brain). Figure 6.1 includes two regression lines. The line with the smallest slope is for the analysis that includes all data points. The low coefficient of determination (R^2 = 0.1153, Table 6.1), indicates that the data points do not fall closely around this line. Inspection of the Figure 6.1 suggests that the relationship between meat and dry bone weight is different for the head (SKWOT, the head without the tongue and brain) and the remainder of the body, and that it is the four head units that are pulling the regression line so low. The head (SKWOT, skull-mandible-hyoid)

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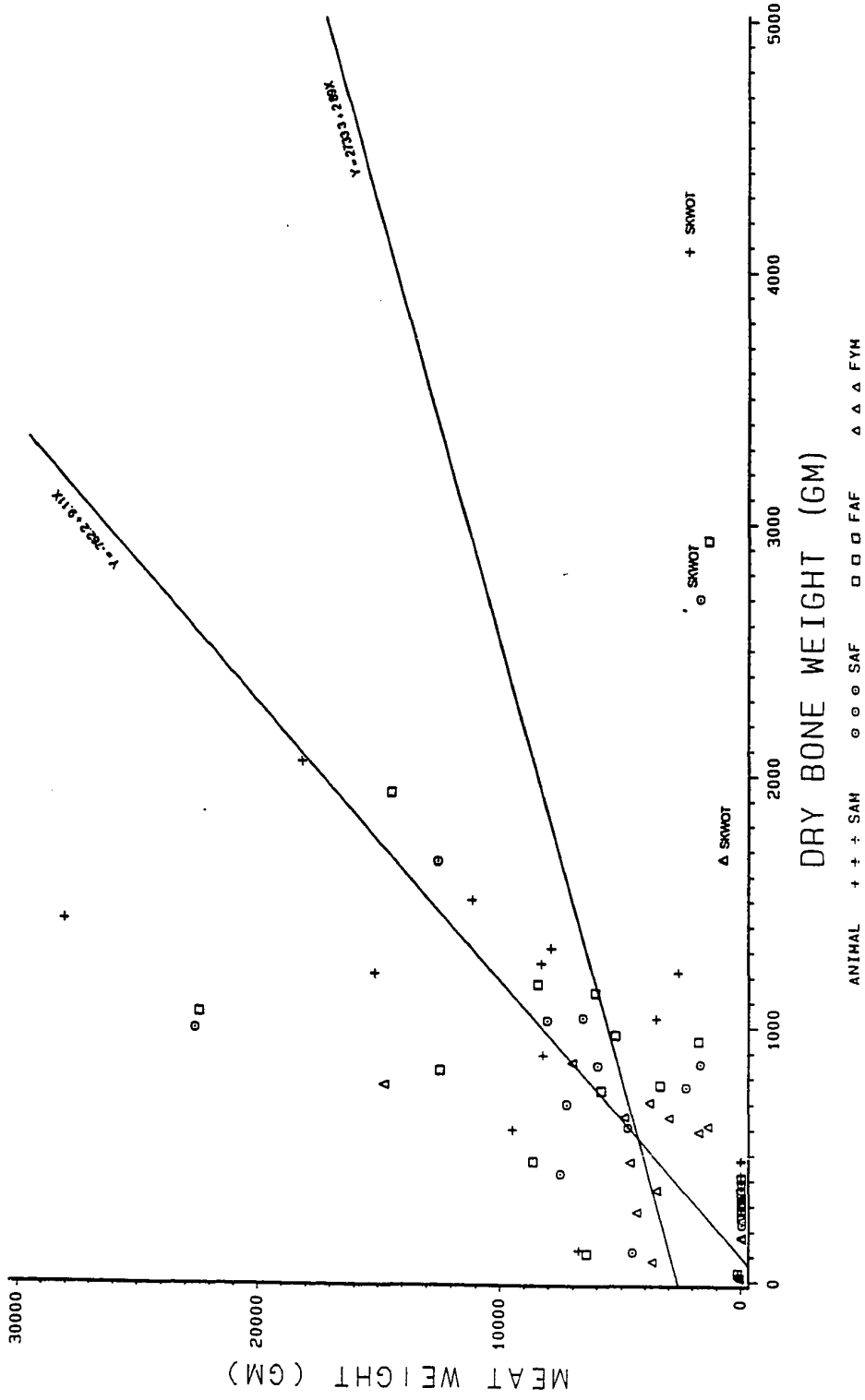

Figure 6.1. Regressions of Meat Weight on Dry Bone Weight without Differentiation by Animal, with and without Head (SKWOT) Units. Corresponds to first regressions reported in Parts A and B of Table 6.1.

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Table 6.1. Regression Analyses of Meat Weight on Dry Bone Weight

Part A. Regressions Using All Carcass Units

Reference Number	Animal	Probability > F	R^2	Parameter Estimates	
				Y-Intercept	Slope
1	All	0.0035[a]	0.1153	2733.3	2.89
2	FYM	0.2632	---	---	---
3	SAM	0.2402	---	---	---
4	SAF	0.2062	---	---	---
5	FAF	0.2320	---	---	---
6	Females	0.0694	---	---	---
7	Males	0.0274[a]	0.1351	2547.0	3.02
8	Adults	0.0213[a]	0.0978	3329.3	2.66

Part B. Regressions without Head Units

Reference Number	Animal	Probability > F	R^2	Parameter Estimates	
				Y-Intercept	Slope
1	All	0.0001[a]	0.4748	-762.2	9.11
2	FYM	0.0083[a]	0.3808	-723.7	8.97
3	SAM	0.0014[a]	0.5035	-1392.7	9.78
4	SAF	0.0046[a]	0.4249	-763.0	9.13
5	FAF	0.0061[a]	0.4044	-97.5	8.23
6	Females	0.0001[a]	0.4147	-407.6	8.62
7	Males	0.0001[a]	0.5306	-1062.1	9.52
8	Adults	0.0001[a]	0.4614	-758.5	9.11

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Table 6.1. (continued)

Part C. Elements from Regression Analyses without Head Units with Studentized Residuals Greater than ±2.0

Reference Number	Animal	Unit	Studentized Residual
1	SAM	FEMP	3.64
	SAF	FEMP	3.23
	FAF	FEMP	3.07
2	FYM	FEMP	3.11
3	SAM	FEMP	2.90
4	SAF	FEMP	3.27
5	FAF	FEMP	2.90
6	SAF	FEMP	3.16
	FAF	FEMP	3.02
7	SAM	FEMP	3.72
8	SAM	FEMP	3.31
	SAF	FEMP	2.94
	FAF	FEMP	2.79

[a] Significant at $p < 0.05$.

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has very little meat given the weight of the associated bone. If this unit is excluded from the analysis, the slope of the regression line rises, and the R^2 value improves to 0.4748. This represents a substantial improvement over the coefficient of determination found when the head unit is included.

In previous analyses of bone and bone products, the division of the data into groups from individual animals, or classes of animals (e.g., by sex), improved the fit of the regression line to the data points (e.g., see Chapter 5). This is not true of the meat and dry bone weight regression analyses. Table 6.1 lists these regression analysis results where the units from individual animals and groups of animals (males, females, adults) were examined. In Part A, all data points are included; in Part B, the head unit of each animal is excluded.

Very few of the analyses showed significant relationships between the independent and dependent variables when the head units were included with the data (Table 6.1, Part A). Where they were significant, the results were much improved (based upon R^2 values) when the analysis was rerun excluding the head units (i.e., the skull-mandible-hyoid unit, designated SKWOT in Figure 6.1).

It does not appear, however, that breaking the data into groups by animal, sex, or age substantially improves the fit of the regression line. As previously noted, the R^2 value for all animals (excluding heads) was 0.4748. The only analyses with higher coefficients of determination were those run on the data from the male, SAM (R^2 = 0.5035) and on the combined data of both males (R^2 = 0.5306). The improvements are small enough that separation of bone by animal sex for purposes of estimating meat weight may not be worth the effort of analysis.

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Part C of Table 6.1 lists those units from the regression analyses (excluding heads) that have studentized residual values greater than ±2.0. There were no cases in these analyses where data points were less than -2.0. Rather, all of the values exceeding ±2.0 were positive, indicating that the unit produced more meat than one might expect given the relationship of dry bone to meat weight. In all cases, it is the femur-patella (FEMP) unit that has more meat than one would expect. Given these studentized residuals, it is evident that use of the regression equations would not produce very good estimates of the amount of meat associated with the bison femur. Such estimates of meat weight would be substantially lower than the actual weights.

In Figure 6.2, the individual data points of the previously described scatterplot are identified by carcass unit. Examination of this figure suggests that the poor R^2 values result because the relationship between dry bone and meat weight differs for different groups of units. The head (SKWOT) for example, shows very little increase in meat weight despite substantial differences in dry bone weight. Other units show greater differences in meat weight associated with small differences in dry bone weight (e.g., the cervical (CERV) and femur-patella (FEMP) units). Other units show relationships with meat weight that more closely follow changes in bone weight (e.g., the ribs (RIBS), thoracic vertebrae (THOR), sacrum-pelvis (SPEL), scapula (SCAP), and humerus (HUM)). With a larger sample, it seems probable that regressions run by carcass unit would all be linear, but would have regression lines with widely different slopes. Although such regression analyses were not run due to the limited number of animals in the sample, one would expect that in predicting meat weight on the basis of dry bone weight, they would provide much better estimates than regressions using either grouped animal data, or individual animal data. The relationships

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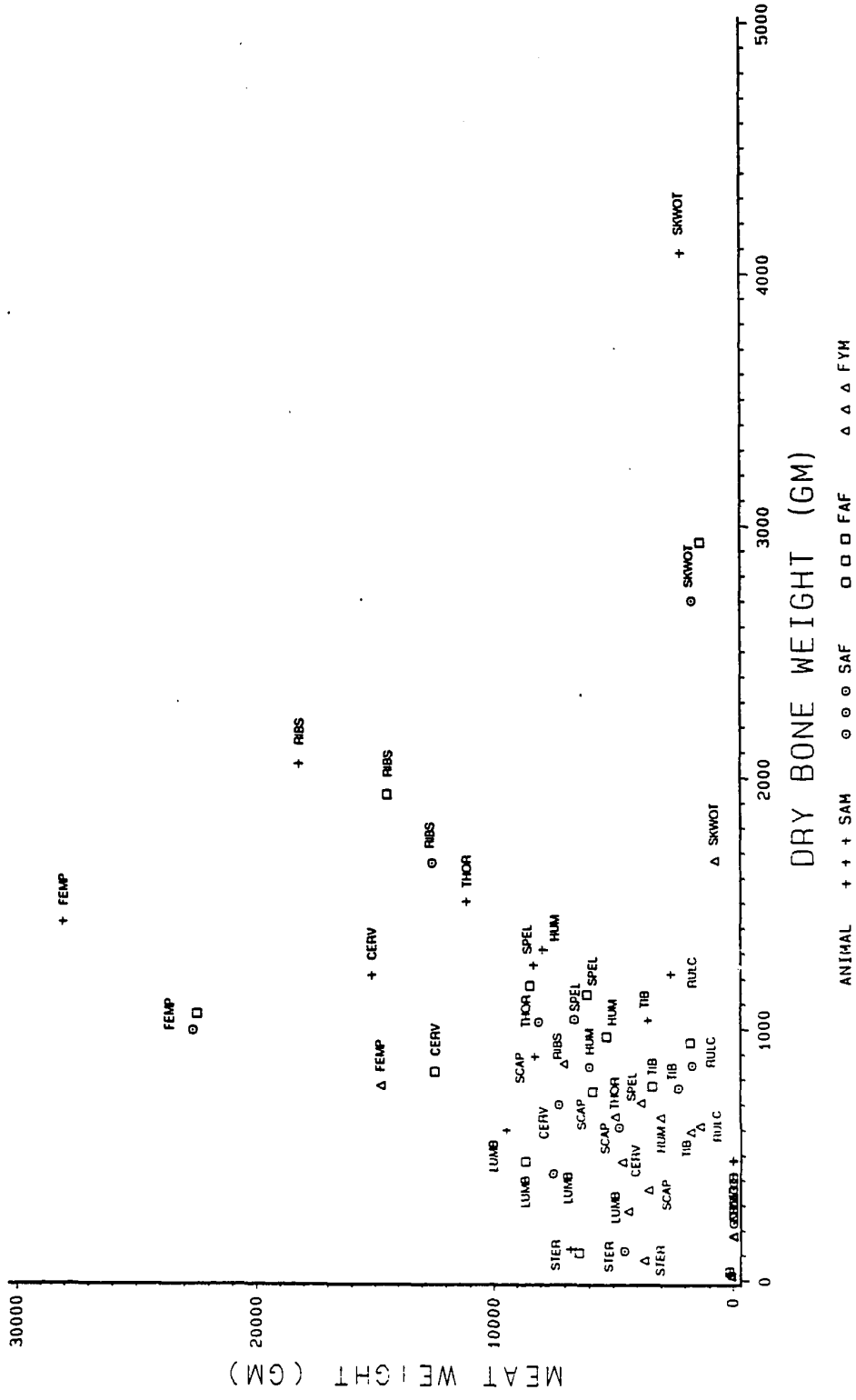

Figure 6.2. Regression of Meat Weight on Dry Bone Weight with Carcass Units Identified.

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between the units of different animals also suggest that meat weight is largely controlled by animal size, and that animal age and sex are important only because they affect body size.

In these analyses, the relationship between dry bone and meat weight was found to be significant, but the regression line has a relatively poor fit to the data. Excluding the heads, which have a much lower ratio of meat to dry bone weight, improves the fit of the regression line to the grouped data. Grouping data by animal, age or sex does not substantially improve the coefficient of determination, and is not recommended. Inspection of the scatterplot with carcass units identified (Figure 6.2), however, shows that grouping the data by carcass unit would probably greatly improve the results of the regressions, and lead to greater accuracy in predicting meat weight from dry bone weight.

Meat Production and Distribution

Meat production and distribution in the bison carcass is discussed in this section. Meat production and distribution refers to the analysis of the combined muscle and intramuscular fat resource. Although intramuscular fat is a component of meat weight, its production and distribution are considered separately below. Organ meat and its fat component are considered separately below as well. The production analysis is presented first, followed by the analysis of the distribution of meat weight in the bison carcass.

Variability in Meat Production

The data in Table 6.2 indicate that meat weights for bone and bone groups of the carcass (1) increase from young, immature to mature

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Table 6.2. Weight of Meat (with Intramuscular Fat) in the Half Carcass

Anatomical Unit	Meat Weight (kg)			
	FYM	SAM	SAF	FAF
SKWOT	0.8	2.2	1.7	1.4
CERV	4.7	15.1	7.3	12.5
THOR	4.9	11.1	8.1	8.4
LUMB	4.4	9.5	7.5	8.6
SPEL	3.8	8.3	6.6	6.1
CAUD	0.1	0.1	0.1	0.1
RIBS	7.0	18.2	12.5	14.4
STER	3.7	6.8	4.6	6.4
SCAP	3.5	8.2	4.8	5.8
HUM	3.0	7.9	6.0	5.2
RULC	1.4	2.6	1.7	1.8
MTC	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0
FEMP	14.7	28.0	22.6	22.4
TIB	1.8	3.5	2.3	3.4
TARS	0.001	0.004	0.004	0.001
MTT	0.01	0.01	0.01	0.02
PPHA	0.0	0.0	0.0	0.0
Total	53.7	121.5	85.9	96.7

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individuals (e.g., compare the weights of FYM and SAM), and (2) are larger in the four year old male than in the females (compare SAM to either SAF or FAF). Exceptions to these patterns exist, but occur in carcass units that have very small amounts of meat (i.e., the caudal vertebrae, tarsals, and metatarsal). Meat weights in these three units are comparable between adult animals, and often between all four bison. The meat weight of the tail remains somewhat smaller in the immature male, FYM.

The range of weight differences between the two adult females varies between carcass units (Table 6.2). This variability might be attributable to differences in animal size and/or condition, or fall within the normal range of values for adult females. Carcass units that show the greatest variability in meat production between these two animals include the cervical vertebrae (CERV, 5.2 kg difference), ribs (RIBS, 1.9 kg difference), and sternebrae (STER, 1.8 kg difference) units. The older female, FAF, is larger in each of these units. From the analysis of dry bone weight and bone volume above, we know that the older female was a slightly larger animal than the younger female, but it is not clear whether the difference was large enough to account for the meat weight differences noted here.

The side weights of the non-standard carcass (including the head, feet, and tail) for both female bison are listed in Table 6.3. Also included are the percentages that the meat weight of each carcass unit (i.e., the half carcass) represents of total carcass weight. The differences between animals, by unit, are listed in the third column. By dividing carcass unit meat weight by total carcass weight, the effects of differences in animal size are negated. Where differences between animals are large, therefore, age or condition differences might be responsible.

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Table 6.3. Unit Meat Weight in the Half Carcass as a Percent of Side Non-Standard Carcass Weight

Anatomical Unit	Percent of Non-standard Carcass Weight		
	SAF	FAF	FAF - SAF
SKWOT	1.2	1.0	-0.2
CERV	5.2	8.2	3.0
THOR	5.8	5.4	-0.4
LUMB	5.4	5.6	0.2
SPEL	4.6	4.0	-0.6
CAUD	0.08	0.06	-0.02
RIBS	8.8	9.4	0.6
STER	3.2	4.2	1.0
SCAP	3.4	3.8	0.4
HUM	4.2	3.4	-0.8
RULC	1.2	1.2	0.0
MTC	0.0	0.0	0.0
APHA	0.0	0.0	0.0
FEMP	16.0	14.6	-1.4
TIB	1.6	2.2	0.6
TARS	T	T	---
MTT	0.01	0.01	0.0
PPHA	0.0	0.0	0.0

Note: Side non-standard carcass weights: SAF: 140.9 kg; FAF: 152.8 kg.
T < 0.01.

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It was noted above that the cervical vertebrae (CERV), sternebrae (STER), and ribs (RIBS) units, each weighed more in the older female. The values in the third column of Table 6.3 indicate that each of these units is relatively larger in the older female, but the difference is greatest in the cervical vertebrae unit. The femur-patella (FEMP) and humerus (HUM) units, however, are smaller in FAF than in SAF. It is not known whether these represent significant differences, but both units contain muscles that Berg and Butterfield (1976:94) refer to as having a high growth impetus. They (1976:99) further note that muscles with a high growth impetus show larger percentages of weight loss than muscles with a low growth impetus when carcass weight losses occur. This is discussed in greater detail below, but their assessments of growth and weight loss, together with these data on unit meat weight as a percent of carcass weight, suggest that condition, and possibly age differences, are evident between the two females. Differences in animal size alone, cannot explain the differences in meat weight noted.

The differences in meat weights cannot be attributed to a greater proportion of intramuscular fat in the older animal either, despite her advanced age and the expectation that fat accumulates as animals age. Intramuscular fat weights are discussed in greater detail below. It is sufficient here to indicate that fat weight differences do not explain these differences in meat weight. Rather, based on the data presented here, the difference appears to represent real differences in muscle tissue weights between the two animals.

The implication of these analyses of meat production in bison are that hunter selection might focus first on adult males, followed by adult females, and then on immature animals, if the amount of available meat is the sole factor influencing the selection. Data from Halloran (1961:214,

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215) and the liveweight studies presented in Chapter 2 indicate that male bison usually surpass females in liveweight and presumably in the production of meat, measured by muscle plus intramuscular fat weight, between 2-1/2 and 3-1/2 years, but may do so earlier. Differences in animal age or condition might also affect the production of meat between adult females. The older, poorer conditioned female had greater meat weight in the neck (CERV), sternum (STER), ribs (RIBS), and tibia (TIB), but smaller meat weight in the femur (FEMP), humerus (HUM), and sacrum-pelvis (SPEL). The high weights of the tibia and the low weights of the femur and sacrum-pelvis agree with Berg and Butterfield's (1976:99) assessment that weight loss is greatest in late developing muscles and least in early developing muscles, but the other units appear to contradict the weight loss-growth impetus rule. The significance of these differences is not known.

Variability in Meat Distribution

In the previous section, it was shown that increases in body size are accompanied by increases in meat weight, as one would expect. In this section, the increases in body size associated with age and sex differences are examined to determine whether they are correlated with differences in meat weight distribution in the bison carcass, or if the young male is just a smaller version of the older male, and the females are smaller versions of the younger, but larger male, SAM. Several lines of evidence are evaluated, including grouped and individual muscle data.

The distribution analyses focus on three sets of data. In the first analysis, meat weight distribution differences between major components (i.e., the limbs and axial skeleton) of the bison carcass are examined. Next, the unit of analysis is the smaller carcass unit; the weights of all

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muscle from a bone or bone group are combined to calculate the unit percentage of total meat weight. In the third analysis, individual muscle weights determined for the male, SAM, and the female, SAF, are used. Individual muscle weights are not available for the male, FYM, or the female, FAF, to compare with the spring-killed animals.

Meat Distribution Between Major Carcass Divisions

Age and sex influences on the distribution of meat between major divisions of the carcass (i.e., between the fore- and hindlimbs and the axial skeleton) are examined in this section. These data are summarized in Table 6.4, and they provide information on four points. First, they illustrate that regardless of age or sex, the axial skeleton provides the majority of the meat in the bison carcass, followed by the hindlimb, and then the forelimb. The difference between the two limbs is substantial, with the hindlimb producing at least twice the weight of the forelimb in all but the youngest male, FYM. In this young bison, the forelimb is almost half the weight of the hindlimb (0.48). This may not be significantly different from the proportions seen in the adult bison.

Second, these data illustrate the effects of sex upon meat weight distribution in major segments of the body. The ratio of the hindlimb meat weight just reported, highlights possible sex differences between the adult animals. In both females, the meat weight of the forelimb is half that of the hindlimb. In the male, SAM, however, this ratio is larger. The forelimb, though still smaller than the hindlimb, is a greater proportion of carcass weight in SAM. This is a pattern consistent with Berg and Butterfield's (1976:8) description of sex differences in cattle. It is a pattern found in wild species as well. Ledger (1963:27) states that mature

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Table 6.4. Meat Weight Distribution and Ratios Between Major Divisions of the Carcass

Part A. Percent of Total Meat Weight in Major Carcass Divisions

Carcass Division	Percent of Total Meat Weight			
	FYM	SAM	SAF	FAF
Axial Skeleton	54.6	58.6	56.4	60.0
Forelimb	14.7	15.4	14.6	13.3
Hindlimb	30.8	26.0	29.0	26.7
Combined Limbs	45.5	41.4	43.6	40.0

Part B. Ratios of Meat Weight Distribution

Ratio	FYM	SAM	SAF	FAF
Forelimb to Hindlimb	0.48	0.59	0.50	0.50
Limbs to Axial Skeleton	0.83	0.71	0.77	0.67

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male ruminants in East Africa always have a smaller percentage of carcass weight in the hindquarter compared to females and compared to immature animals of either sex.

The third point illustrated by the data in Table 6.4 concerns the combined effects of age and sex on muscle weight distribution between major carcass segments. The forelimb to hindlimb meat weight ratio in FYM is 0.48, which is more like adult females than males. Distribution of total meat weight between major carcass segments shows a similar pattern of age and sex differences. Berg and Butterfield (1976:119) indicate that until male sex hormones are present in the body, muscle development and distribution in immature males is more like that of adult females than males. The male sex hormones increase the impetus for growth in muscles important to males in intraspecific competition.

The fourth point concerning weight distribution in the major carcass segments, pertains to another effect of age differences. The pattern of distal to proximal tissue development seen in previous analyses of bone are repeated to some extent in the meat weight data presented here (Table 6.4). Age differences in muscle weight distribution are evident, with limbs in young animals producing a larger percent of the total meat weight than in adults. This shows up best in the ratio of meat weight in the limbs compared to the axial skeleton. In the adults, this ratio ranges from 0.67 to 0.77, but in the immature male, FYM, the ratio is 0.83 (Table 6.4). This suggests that FYM is closer to adult size in more of the appendicular than axial units. This pattern is not true for all units (Table 6.5), and the differences are not particularly large, but it appears that the tendency is for appendicular units of immature bison to be closer in size than the axial units, to those of the male, SAM. A larger sample is needed to verify

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Table 6.5. Meat Weight Ratios Between Carcass Units of the Yearling and Four Year Old Male Bison

Anatomical Unit	Meat Weight Ratio FYM : SAM
SKWOT	0.36
CERV	0.31
THOR	0.44
LUMB	0.46
SPEL	0.46
CAUD	1.00
RIBS	0.38
STER	0.54
SCAP	0.43
HUM	0.38
RULC	0.54
FEMP	0.53
TIB	0.51
TARS	0.25
MTT	1.00

Note: Data from Table 6.2 were used to calculate ratios.

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that this difference is significant. Fortin et al. (1980:1294), however, report that in cattle, the proportion of muscle relative to total muscle, decreases in the limbs and increases in the trunk.

In sum, it appears that both age and sex differences are evident in muscle weight distributions between major segments of the bison carcass. Immature bison appear to produce a relatively larger proportion of total muscle weight in the limbs than adults, and show a forelimb to hindlimb weight distribution pattern more comparable to females than males. Males appear to have a larger ratio of forelimb to hindlimb muscle weight than females. In all cases, regardless of age or sex, meat production is highest in the axial skeleton, followed by the hindlimb, and then the forelimb.

Distribution of Meat by Carcass Unit

The meat weight distribution data for the four TRNP bison, when muscles are grouped by carcass unit, are presented in Table 6.6. In many cases, use of the bone unit divisions results in the splitting of individiual muscles where they extend across two or more units. The data in Table 6.6 show where differences in animal maturity and possibly sex affect meat weight distribution. Differences between the muscle weight distributions of the females may be indicative of age or condition differences, or be representative of the range of variability in female bison meat weight distribution.

Age Differences in Meat Weight Distribution. The values for FYM and SAM in Table 6.6 suggest the occurrence of meat weight distribution differences between immature and mature male bison. The male, SAM, is not yet fully mature, but in the previous section it was shown that the ratio of limb to axial skeleton meat weight for this animal was comparable to that of

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Table 6.6. Distribution of Meat by Carcass Unit

Anatomical Unit	Percent of Total Meat Weight[a] (kg)			
	FYM	SAM	SAF	FAF
SKWOT	1.4	1.8	2.0	1.4
CERV	8.7	12.4	8.5	12.9
THOR	9.1	9.2	9.4	8.7
LUMB	8.2	7.8	8.8	8.9
SPEL	7.1	6.8	7.7	6.3
CAUD	0.1	0.1	0.1	0.1
RIBS	13.1	14.9	14.6	14.9
STER	6.9	5.6	5.3	6.7
SCAP	6.5	6.8	5.5	6.0
HUM	5.6	6.5	7.0	5.4
RULC	2.6	2.1	2.0	1.8
MTC	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0
FEMP	27.5	23.0	26.3	23.2
TIB	3.3	2.9	2.7	3.5
TARS	0.0	0.0	0.0	0.0
MTT	0.0	0.0	0.0	0.0
PPHA	0.0	0.0	0.0	0.0

[a] Meat weight includes intramuscular fat.

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the fully mature females. The distribution of meat weight for older males might differ from that seen in this young adult male, but one might expect that such changes, if they do occur, would reflect the greater development of muscles associated with male dominance behavior, and possibly represent relatively smaller changes than those already seen between the two male carcasses in this study. In the following paragraphs, therefore, the comparison between the two males might be considered potentially representative of the changes occurring between these two age groups. Additional changes might be evident in a comparison of either of these males and a fully mature male bison. It is expected, however, that the differences would be smaller in the comparison of the older male, SAM, to fully mature males, than a comparison of the yearling would be.

The carcass units that show the largest differences in the percent of total meat weight (Table 6.6) between the immature male, FYM, and the adult male, SAM, include the cervical vertebrae (CERV), ribs (RIBS), sternum (STER), humerus (HUM), and femur (FEMP). The remainder all show less than a 0.5 difference between their percentage values. The units in which the older male is substantially larger include the cervical vertebrae, ribs and humerus. The sternum and femur-patella units are a much larger proportion of total meat weight in the young, immature male, FYM. The larger proportion of the meat weight in the the neck, ribs, and proximal forelimb of the adult male, might be attributed to the development of muscles used in fighting and aggressive displays. Comparisons of the values for SAM and the two females, however, suggest that they might also be attributable to the attainment of adult proportions, given that the values for this male do not differ substantially from those of the females. The reason for the larger proportion of total meat weight in the sternum in the young male is unclear.

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The larger proportion in the femur-patella unit, however, might reflect its early development compared with muscles of the axial skeleton.

Effect of Animal Condition Differences on Meat Weight Distribution. The occurrence of sex-related differences in meat weight distribution in the bison carcass is difficult to assess, due to the large degree of difference found in the values of the two females. It is possible that these differences merely reflect a wide range of variability in how meat weight is distributed in females, but it seems more likely that they are indicative of age or condition differences between the animals. Before assessing whether sex differences exist between the females and the male, SAM, it is necessary to determine whether normal variability, or age or condition influenced variability is responsible for the differences seen in the distribution of meat weight in the females.

Although declining animal condition affects muscle as well as fat weight (e.g., Warrington et al. 1988, Torbit et al. 1985), Berg and Butterfield (1976:14) note that eventually, the relative effect is greater on fat than on muscle. Fowler (1976:287) reports that changes in proportionality associated with undernutrition are limited, being most pronounced in the head, the fat depots, and the organs. The head and organs become proportionately larger, and the fat depots a proportionately smaller percentage of carcass weight. The abnormality of the dentition of FAF makes it impossible to assess the importance of the differences in the proportional size of the heads of these two females.

Berg and Butterfield (1976) extensively discuss the affects of starvation on muscle weight and suggest that changes in proportionality are not limited to the head, fat, and organs, but affect the proportions of most muscle groups depending upon whether they have a high or low impetus for

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growth, and are thus late or early maturing. In their assessment, muscles that are well developed at a young age (reported to have a low impetus for growth) are slower to show the effects of starvation than muscles that develop late (and have a high growth impetus), because early developing muscles are most essential to survival. The exceptions to this are muscles of the neck in males which are late developing (high growth impetus), but which are protected from depletion, Berg and Butterfield (1976:129) suspect, because they are closely linked to survival in intraspecific competition. Muscles that have a low impetus for growth and are thus already well developed, and are also protected from decline during starvation, include muscles in the distal limbs (radius-ulna and tibia) and some muscles in the proximal thoracic limb (scapula and humerus). During periods of nutritional stress, therefore, if starvation is pronounced, these parts of the body might become proportionately larger, because they lose weight at a slower rate than other parts of the body. The scapula (SCAP) and tibia (TIB) have a higher proportion of total meat weight in FAF than in SAF, but the radius-ulna (RULC) and humerus (HUM) do not. The existence of condition differences between these females based upon meat weight distribution is not clear, therefore.

In a discussion of the effects of aging, Curtis (1969:165) notes that muscle mass decreases with advanced age, but the degree of this change is quite variable. It is unclear whether or not age-related meat weight loss has occurred in FAF, and if it has, what the extent and nature of that loss has been.

Given (1) the earlier assessment that the older female, FAF, appears to have mobilized some marrow fat and appears to be in declining condition; (2) her advanced age and the possibility that muscle mass may be decreasing; and

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(3) the lack of clear evidence of how age or condition might be responsible for the differences seen between the two adult female unit meat weight distributions, the comparisons between sexes must be limited to the younger, healthier female, SAF, and the male, SAM.

Sex Differences in Meat Weight Distribution. Differences in meat weight distributions in the carcasses of the male, SAM, and the female, SAF, appear to be evident in the cervical vertebrae (CERV), lumbar vertebrae (LUMB), sacrum-pelvis (SPEL), scapula (SCAP), and femur-patella (FEMP, Table 6.6). These differences are most pronounced in the cervical vertebrae unit and the femur-patella. Blumenschine and Caro (1986:279), in their study of African ungulates, found similar results in the neck and pelvic regions of gazelle, noting that males are more fleshy in the neck, and females and subadults are more fleshy in the pelvic-lumbar region. They did not find the differences in the proximal limb found for bison, above.

Berg and Butterfield (1976:115-116) note that the muscles of the neck and thorax in cattle are significantly larger in bulls than in steers and heifers, and this difference is balanced out by smaller variations in other muscle groups. They indicate that cows have larger muscles in the proximal hindquarter and abdominal wall and lighter muscles in the neck and thorax. The muscles of the abdominal wall posterior to the fourteenth rib were collected in the TRNP bison as part of the lumbar vertebrae unit, possibly accounting for the sex difference seen in Table 6.6.

Given Berg and Butterfield's (1976) and Blumenschine and Caro's (1986) assessments of cattle and African gazelles, the differences noted above for meat weight distribution in the bison carcasses of SAM and SAF appear to reflect sex differences common in other ungulates as well. The exception to this may be the difference noted for the proportions of total meat weight in

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the bison scapulae, with the male bison being proportionately larger in this area than the female. In Chapter 5, no differences in the distributions of dry bone weight or bone volume were found between the sexes of these bison. Muscles attaching the thorax to the thoracic limb (which according to Berg and Butterfield (1976) function to support the head and thus, to be proportionately larger in males) were not included with the scapula units, and could not be responsible for this difference. I expect that the greater forelimb size in males is tied to the greater need for support in the forequarters, and thus indirectly related to intrasexual competitive behavior in males. If so, the larger relative size of the scapula is understandable. In cattle Mukhoty and Berg (1973:325) also found males to be proportionately larger in the neck and shoulder than females. The larger size of the male bison shoulder appears to be evident here, as well.

In sum, comparing the young adult male, SAM, and the younger of the two adult females, SAF, it appears that male bison are more fleshy in the neck, and probably in the scapula, and that females are more fleshy in the pelvic and proximal hindlimb area including the abdominal wall.

Weight Distributions of Individual Muscles

In order to provide more detailed information on bison muscle weights, two of the animals in this study were dissected and individual muscle weights were determined. The availability of these weights makes it possible to more directly compare differences in the muscle weight distributions of the male and female bison, using the same divisions of the carcass that Berg and Butterfield (1976) describe for their studies of cattle carcass composition. The data for this analysis are presented in Table 6.7. It does not list the actual muscle weights, but presents the

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Table 6.7. Comparison of Muscle and Muscle Group Weights in Male and Female Bison

Muscle Group	Muscle	Muscle Weight as a Percent of Tctal Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
I. Proximal Pelvic Limb	Group Total	30.7	28.8	31.9
	adductor femoris		1.9	2.0
	biceps femoris		6.5	7.6
	gemelli		0.1	0.1
	accessory gluteal		0.3	0.5
	deep gluteal		0.4	0.3
	middle gluteal		3.2	3.4
	gracilis		1.2	1.3
	external and internal obturator		0.6	0.5
	quadratus femoris		0.1	0.1
	rectus femoris		1.8	2.0
	sartorius		0.3	0.3
	semimembranosus		4.3	5.3
	semitendinosus		2.6	2.6

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
I. Proximal Pelvic Limb (cont.)	tensor fasciae latae		1.3	1.5
	vastus intermedius, articularis genu		0.3	0.5
	vastus lateralis		2.1	2.6
	vastus medialis		1.1	0.7
	pectinus		0.7	0.6
II. Distal Pelvic Limb	Group Total	4.2	4.4	4.3
	lateral digital extensor		0.2	0.2
	long & middle digital extensor, peroneus tertius		0.5	0.5
	deep digital flexor		0.9	0.8
	superficial digital flexor		0.4	0.4

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
	peroneus longus		0.1	0.1
	popliteus		0.3	0.3
	cranial tibial		0.1	0.1
	gastrocnemius et soleus		1.9	1.9
III. Spinal Column	Group Total	12.7	14.9+	15.3+
	psoas minor, psoas major, quadratus lumborum, iliacus, & intertransversarii lumborum		3.1	3.3
	iliocostalis		1.0	0.7
	longissimus (all[c])		6.8	6.5
	multifidi (all[d])		1.7	1.7
	spinalis et semispinalis thoracis and cervicis		2.3	3.0

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
III. Spinal Column (cont.)	coccygeus		T	T
	other tail muscles		T	T
IV. Abdominal Wall	Group Total	6.9	7.2	7.5
	cutaneus trunci		1.3	1.3
	external abdominal oblique		2.7	2.5
	internal abdominal oblique		1.5	1.6
	retractor costae[d]		0.0	0.0
	rectus abdominis		0.8	1.0
	serratus dorsalis caudalis		T	T
	transverse abdominis		0.9	1.1

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
V. Proximal Thoracic Limb	Group Total	13.0	13.1	11.8
	anconeus		0.1	0.1
	biceps brachii		0.7	0.6
	brachialis		0.5	0.5
	coracobrachialis		0.1	0.1
	infraspinatus		2.6	2.1
	subscapularis		1.2	1.0
	supraspinatus		1.6	1.8
	tensor fasciae antibrachii		0.1	0.1
	deltoideus, teres major, teres minor, triceps brachii		6.2	5.5
VI. Distal Thoracic Limb	Group Total	2.3	2.4+	2.0+
	abductor pollicis *longus*		T	T

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
VI. Distal Thoracic Limb (cont.)	common & medial digital extensors		0.2	0.1
	lateral digital extensor		0.1	0.1
	extensor carpi radialis		0.6	0.5
	ulnaris lateralis		0.3	0.3
	deep digital flexor		0.7	0.5
	flexor carpi radialis		0.1	0.1
	superficial digital flexor		0.3	0.3
	flexor carpi ulnaris		0.1	0.1
VII. Neck to Thoracic Limb	Group Total	8.7	8.2	7.3
	brachiocephalicus		1.0	1.2

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
VII. Neck to Thoracic Limb (cont.)	omotransversarius		0.4	0.3
	rhomboideus		1.7	1.1
	serratus ventralis cervicis		4.1	3.6
	trapezius		1.0	1.1
VIII. Thorax to Thoracic Limb	Group Total	8.8	8.0	9.4
	latissimus dorsi		1.9	2.6
	ascending (deep) pectoral		2.8	3.8
	descending (superficial) pectoral		1.3	1.1
	serratus ventralis thoracis		2.0	1.9

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
IX. Thorax and Neck	Group Total	11.4	12.9	10.0
	external and internal intercostals, intertransversarii thoracis, and levator costarum		4.5	4.0
	longus colli, intertransversarii cervicis, obliquus capitis caudalis, rectus capitis, and longus capitis		3.9	2.9
	longissimus capitis et atlantis and cervicis		see Group III[c]	see Group III[c]
	multifidi cervicis		see Group III[d]	see Group III[d]
	dorsal and medial scalenus		0.6	0.6
	semispinalis capitis		1.6	1.2
	serratus dorsalis cranialis		0.1	0.1

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Table 6.7. (continued)

Muscle Group	Muscle	Muscle Weight as a Percent of Total Muscle Weight[a]		
		Berg & Butterfield[b] Male	TRNP Male SAM	TRNP Female SAF
IX. Thorax and Neck (cont.)	splenius		1.8	0.9
	omohyoideus		0.1	T
	rectus thoracis		0.1	0.1
	transverse thoracis		0.2	0.2

Note: T indicates less than 0.0 percent; + indicates muscle group includes trace amounts not included in total.

[a] The total muscle weight values used to determine the percent of total muscle weight for each individual muscle were determined using the muscles listed by Butterfield and May (1966) and thus, do not include all muscles in the carcass, but exclude the following: muscles from the head and tail, the diaphragm, pronator teres, sternocephalicus, sternothyrohyoideus, and subclavius. The muscle weight total used to calculate the percent of total muscle weight for each muscle for SAM was 116,859.6 gm (116.9 kg), and for SAF, was 82,635.7 gm (82.6 kg).

[b] Source: Berg and Butterfield (1976:190). The total side muscle weight for this bull is 70.9 kg, compared to 116.9 kg for the TRNP bison, SAM.

[c] This proportion includes the weight of the capitis et atlantis and cervicis muscles that belong in the Thorax and Neck muscle group, but were not separated in the bison, SAM and SAF. Consequently, these muscle percentages and the total for the muscle group should be slightly high.

[d] This proportion includes the weight of the multifidus cervicis that should go with the Thorax and Neck muscle group, but were not separated in the bison, SAM and SAF. Consequently, these weight muscle percentages and for the muscle group should be slightly high.

proportion each muscle weight represents of the total. Appendix B lists individual muscle weights for the male, SAM, and the female, SAF.

Before the data in Table 6.7 are discussed, three factors influencing the makeup of the contents must be reported. First, it should be noted that Berg and Butterfield (1976) use Butterfield and May's (1966) work on the anatomy of cattle to define muscle groups and then to determine the growth impetus of muscles and groups of muscles in animals of different age and sex. Butterfield and May (1966) were using terminology for muscle identification different than that currently accepted. As a result, there is some degree of dissimilarity in the analyses. In some cases the current muscle could not be identified in their analysis, and on the basis of comparative weights did not appear to be subsummed under another muscle identification. In other cases, no mention was made of muscles which were collected and weighed as a part of this study of bison anatomy, but are usually excluded from the standard cattle carcass. These muscles (listed at the base of Table 6.7) have been omitted from the totals used to determine the percentages for muscle weight distribution in order to make the bison data comparable to that of the cattle, and thus, to growth impetus data.

The second note that should be made regarding Table 6.7 is that, in several cases, muscles from the bison dissections were combined in groups. This occured when clear separations could not be made between muscles across all the carcass units in which they were found, or when inexperience early in the dissection process lead to confusion concerning muscle identifications. In some cases, this grouping of muscles may obscure the presence or absence of sex differences in muscle weight distribution in the carcass. It is viewed as a conservative approach, however, that reduces the

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likelihood of attributing sex differences erroneously when individual weights are uncertain, but combined weights are well defined.

The third comment concerns the total muscle weight used to determine the muscle percentages and the fact that it differs from the total unit meat weight listed in Table 6.2. The meat weights listed for SAM and SAF in that table are based upon average weights of the left and right sides of the carcasses. The weights used to determine the distribution of individual muscle weight, on the other hand, represent weights or averages of weights of individual muscles. These averages may differ, and over numerous muscles the differences accumulate, producing slightly different meat weight totals. In this dissertation, the accumulated total based upon individual muscle weights, is used to determine only individual muscle weight distributions, because of the likelihood of compounding small measuring errors. For use in comparisons with cattle data, however, it is important that the total weight represents the total of these muscle weights.

The data in Table 6.7 are organized by muscle groups defined by Berg and Butterfield (1976) for the purpose of comparing compositional anatomy of different species of animals. These divisions do not correspond directly to those used above in the study of bison carcass composition. In addition to indicating the proportion of total muscle weight for each individual muscle, Table 6.7 includes the totals for each carcass division. The actual muscle weights used to compile these data are presented in Appendix B, Table 1. With the proportional data in Table 6.7, the muscles largely responsible for sex differences in carcass divisions as a whole can be identified.

Proximal Pelvic Limb. This group contributes 28.8 and 31.9 percent of total muscle weight in the male and female bison (SAM and SAF, Table 6.7). This represents a difference of 3.1 percentage points between animals, with

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the female showing the larger proportion of total carcass meat weight. Most of this difference is found in the weights of three muscles, the biceps femoris, the semimembranosus, and the vastus lateralis. These three muscles are primarily associated with the femur. The female is proportionately larger in this unit than is the male, as would be suspected given Berg and Butterfield's (1976) report that the pelvic limb in cattle is proportionately larger in cows than in bulls.

Distal Pelvic Limb. This group includes the muscles that are found primarily associated with the tibia, but which may extend to the tarsals and metatarsal. The group percentage of total muscle weight, as well as the individual muscle percentages show no evidence of sex differences in these bison. As an early growth location important to animal survival (Berg and Butterfield 1976:94,104-105), sex differences should not be evident, and are not.

Spinal Muscles. This group includes muscles that lie along the spinal column, but excludes some that are associated with the spinal column in the neck. It crosscuts divisions used above in the analysis of carcass unit meat weight distributions. Several muscles in this group were so small in weight that they register only as a trace of total muscle weight. The percentages for this muscle group, therefore, are slightly more than 14.9 and 15.3 percent of total muscle weight for the male and female, respectively (Table 6.7). This is a relatively small difference and does not appear to represent an area of sexual differentiation. The differences between individual muscle weight distributions are also relatively small, and do not appear to indicate sex differences at that level either.

Abdominal Wall. This group includes muscles associated above with the lumbar vertebrae, ribs, and sternebrae units. Berg and Butterfield

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(1976:109) note that the females were larger than males in their study, but that their sample was too small to have statistical significance. The group percentages for these two bison show only slight differences. The female in this case shows 7.5 percent of the total muscle weight in this group and the male 7.2 percent (Table 6.7). This does not appear to be a very large difference, but its significance cannot be evaluated.

Proximal Thoracic Limb. This group includes muscles that above, were primarily associated with the humerus and scapula. The percentages this group represents of total muscle weight in the male, SAM, and female, SAF, are 13.1 and 11.8 percent (Table 6.7). This represents a difference of 1.3 percentage points, with the male proportionately larger in this group. This difference is most pronounced in the infraspinatus and in the undifferentiated muscle group that includes the deltoideus, teres major and minor, and the triceps brachii. These differences are relatively small and might or might not be significant when tested on a larger sample of animals. Berg and Butterfield (1976:110-111) did not identify sex differences in the growth or distribution of weight in this group relative to carcass weight. It is possible the bison difference reflects a species difference or that it is non-representative of bison due to small sample size.

Distal Thoracic Limb. The muscles of this group are associated primarily with the radius-ulna unit. The male bison has a slightly larger percentage of total muscle weight in this group than the females (2.4 versus 2.0 percent), and very small differences in the proportions that individual muscles represent of the total. It seems doubtful that these differences would be significant if tested on a larger sample because they are early developing muscles, and in cattle do not show sexual differentiation (Berg and Butterfield 1976:111).

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Neck to Thoracic Limb. In the carcass unit meat weight distribution analysis above, the muscles in this neck to thoracic limb group were associated with the neck and thoracic vertebrae units. In this analysis, the male is larger here with 8.2 percent of total muscle weight in this group, while the female carries 7.3 percent of muscle weight in this location (Table 6.7). The major differences in the percentages of total muscle weight are in the rhomboideus and the serratus ventralis cervicis. These differences are relatively small, but may be significant. In cattle, Berg and Butterfield (1976:113) report that females are smaller than males, with 5.2 percent of total muscle weight in this group compared to 5.5 percent in bulls. Bison are clearly larger in this area, a difference they (1976:191) attribute in their analysis of bison, to the elongated spinous processes and greater development of the rhomboideus muscle.

Thorax to Thoracic Limb. This group includes muscles associated with the ribs and sternebrae carcass units. The female muscle group percentage (9.4 percent) is higher than that of the male (8.0 percent), and the individual muscle percentage differences are most pronounced in the latissimus dorsi and the deep pectoral (Table 6.7). The female is proportionately larger in these muscles. The latissimus dorsi flexes the shoulder and the deep pectoral adducts the thoracic limb. It is not clear why these should be larger in females. Perhaps the difference would not be significant when tested on a large sample. Berg and Butterfield (1976:112) found no sex differences in this group in their study of cattle.

Thorax and Neck. This group includes a variety of muscles associated with the neck, ribs, and thoracic vertebrae units. The male has proportionately more meat associated with this muscle group (12.9 percent) than the female (10.0 percent, Table 6.7). The individual muscle

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proportions are most dissimilar in two groups of combined muscles, and in the semispinalis capitis and splenius, all of which are larger in the male. Berg and Butterfield (1976:115) cite Brannang, who reported that the splenius is the muscle most affected by masculinity in cattle. The importance of fighting in the male sex is often cited as the reason behind the larger development of the muscles of this group (Berg and Butterfield 1976:99). This sex difference appears to be evident in bison, as well.

Conclusion. These data appear to echo the sex-related differences in meat weight distribution found in the analysis of carcass units. They also point out, however, that sex differences in grouped data often reflect the influence of a small number of individual muscles, rather than the combined effect of very small differences in numerous muscles. Clearly, additional data are needed to verify the significance of the patterns that appear to be manifested in these bison data. These data on individual muscle weight distributions in the carcass and the percentages that the grouped muscle weights represent of total muscle weight suggest that male bison carry proportionately more weight in the proximal thoracic limb, neck to thoracic limb, and thorax and neck muscle groups, while the females are proportionately heavier in the proximal pelvic limb and the thorax to thoracic limb. The greater proportion of the female abdominal wall is not as marked as the difference seen in the pelvic limb, and the difference between these two bison may not be representative of bison in general. These sex differences are similar to what Berg and Butterfield (1976) found in cattle, except that in bison there is a suggestion of differences for the thorax to thoracic limb and the proximal thoracic limb groups as well.

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Rank Order Evaluation of Distribution Difference Importance

Age and sex differences in meat weight are not always large enough that the order of carcass unit selection would change if meat weight alone were used to determine that order in the individual carcasses of these bison. Figure 6.3 presents the rank order of the carcass units (based upon the meat weight data). Examination of the rank orders of carcass units for FYM and SAM indicate that not all of the age differences noted for meat weight distributions are of a large enough magnitude to change the order of unit rank for meat production. In Figure 6.3, the difference in the cervical vertebrae (CERV) does show the expected relationship with the unit ranked higher in the older male, but inspection of the actual meat weights of the adjacent carcass units in the order for FYM suggests that the thoracic (THOR) and cervical (CERV) units are close in size and in a larger sample, might be inversely ranked. The difference in the size of the cervical unit in these two males, therefore, might not be significant in hunter selection of carcass units. A similar relationship is seen for the rank of the humerus.

The age differences in the femur-patella (FEMP) and ribs (RIBS) units are unimportant in terms of their effect on the relative ranking of carcass units for the production of meat in SAM and FYM. Although age differences were shown to exist in their relative contribution to total meat weight, they do not affect unit rank relative to other units.

The only clear effect of age-related differences in distribution that also appears to substantially affect carcass unit rank, is in the sternebrae (STER) unit. In the yearling, this unit produces proportionately more of the total meat weight than in SAM, and this difference is large enough to affect the ranking of units for meat production. This indicates that in

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Figure 6.3. Rank Order of Carcass Units for Meat Production

Unit Rank Order				Unit Meat Weight[a] (kg)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
FEMP	FEMP	FEMP	FEMP	14.7	28.0	22.6	22.4
RIBS	RIBS	RIBS	RIBS	7.0	18.2	12.5	14.4
THOR	CERV	THOR	CERV	4.9	15.1	8.1	12.5
CERV	THOR	LUMB	LUMB	4.7	11.1	7.5	8.6
LUMB	LUMB	CERV	THOR	4.4	9.5	7.3	8.4
SPEL	SPEL	SPEL	STER	3.8	8.3	6.6	6.4
STER	SCAP	HUM	SPEL	3.7	8.2	6.0	6.1
SCAP	HUM	SCAP	SCAP	3.5	7.9	4.8	5.8
HUM	STER	STER	HUM	3.0	6.8	4.6	5.2
TIB	TIB	TIB	TIB	1.8	3.5	2.3	3.4
RULC	RULC	RULC	RULC	1.4	2.6	1.7	1.8
SKWOT	SKWOT	SKWOT	SKWOT	0.8	2.2	1.7	1.4
CAUD	CAUD	CAUD	CAUD	0.1	0.1	0.1	0.1
MTT	MTT	MTT	MTT	0.01	0.01	0.01	0.02
TARS	TARS	TARS	TARS	0.001	0.004	0.004	0.001
MTC	MTC	MTC	MTC	0.0	0.0	0.0	0.0
AHPA	AHPA	AHPA	AHPA	0.0	0.0	0.0	0.0
PPHA	PPHA	PPHA	PPHA	0.0	0.0	0.0	0.0

[a] Meat weight includes intramuscular fat.

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conditions where selection for meat were made by carcass unit, the sternebrae unit would be used potentially earlier in the yearling than in similar circumstances where the carcass was that of a four year old male. Given that in both animals, this unit is in the middle third of the order, this difference might not have archaeological significance.

Evaluation of the reported sex differences in carcass units for meat production (compare SAM and SAF in Figure 6.3) indicate that the magnitude of difference is large enough to substantially affect the rank of carcass units only in the cervical vertebrae (CERV) unit. Similar rank is evident in the other units that showed sex differences in distribution. The femur-patella (FEMP) and sacrum-pelvis (SPEL) units are equally ranked in both SAM and SAF. For the scapula (SCAP) and lumbar vertebrae (LUMB) units, the differences in rank are in the expected direction, but the magnitude of difference with adjacently ranked units is not large.

From the analysis of meat weights and rank order, it appears that many of the identified age and sex differences are relatively unimportant in terms of their effect on the order in which carcass units might be selected for the recovery of meat when individual carcasses are processed. The exceptions to this are the sternebrae and cervical vertebrae units. The former is ranked higher in the yearling male, reflecting age differences, and the cervical vertebrae unit is ranked higher in the male, SAM, reflecting sex differences.

Intramuscular Fat Production and Distribution

Intramuscular fat is one of the eight major deposits of fat (often referred to as fat depots) that Leat and Cox (1980:138) describe for meat-producing animals. It is found between muscle fibers rather than between

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muscles, and it is the fat responsible for producing the marbling frequently sought in retail cuts of meat. Although intramuscular fat may be considered in conjunction with other carcass fats in some respects, it is frequently overlooked in discussions of fat distribution in the carcasses of meat-producing animals. The information on intramuscular fat presented here is generalized in part, from published studies of animal carcass fat.

In their discussion of cattle carcass composition, Berg and Butterfield (1976:143) note that fat is the carcass tissue that is most variable between animals of different species, breed, age, and sex, in terms of both the amount present and how it is distributed throughout the body. Like other body tissues, fat or adipose tissue has a pattern of growth and development. In newborn farm animals, total fat reserves range from one to four percent of body weight, compared with 16 percent found in newborn human infants (Leat 1976:178). In the domestic calf this figure is reported to be 2.8 percent (Leat and Cox 1980:151). At birth, bone comprises a larger percent of carcass weight than fat, but the proportion of fat gradually increases (Berg and Butterfield 1976:23). After the onset of the fattening stage, the fat component of the domestic animal carcass may even exceed that of the muscle component. Leat and Cox (1980:158) note that cattle may store four times as much fat as protein. Such excessive fatness does not occur in wild ungulates that are subject to cyclical peaks and troughs in the availability and quality of their food supply.

Like other body tissues, fat has a consistent order of development--a pattern in which lipids are deposited in the various fat depots. According to Leat (1976:178), this pattern is the same for domestic and wild species and proceeds beginning with the abdominal fat depots and continuing with the intermuscular, subcutaneous, and intramuscular depots. The ultimate

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composition of these deposits varies with species, age, sex, and animal condition. As in other components of the animal carcass, those tissues first deposited are often those used at the lowest rates when low energy balance occurs. Adamczewski et al. (1986a:372) report that fat loss in caribou (Rangifer tarandus groenlandicus) was most rapid in the depots latest to mature. Berg and Butterfield (1976:164-165) note in their comparison of three fat depots (subcutaneous, intermuscular, and kidney fat) in cattle under body weight loss conditions, that the largest percent decline occurred in the later forming subcutaneous deposit, although this did not represent a greater fat weight loss than that from the intermuscular depot. The point, however, is that the kidney fat depot showed the least loss of fat weight under semi-starving conditions. As a late developer, therefore, intramuscular fat should be subject to larger percentage fat weight losses than body cavity depots when poor nutritional conditions are in effect.

The effect of animal sex on fat development and distribution in cattle, has been discussed in detail by Berg and Butterfield (1976), and to a lesser extent by Leat and Cox (1980). Generally speaking, females have more adipose tissue than males at a given body weight. As Leat and Cox (1980:163) explain, the prolonged impetus for muscle growth in the male, delays the arrival of the fattening stage, and the rate of fat growth is slower as well.

Based upon these assessments, therefore, one may expect that (1) fat content of male meat samples should be lower than in females due to sex differences; (2) the younger male should have lower muscle fat content than the older male due to age and maturity differences; and (3) the older female may have lower muscle fat content than the younger female, SAF, because of

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poorer nutritional condition. The poorer condition of the female, FAF, may or may not have been severe enough or sustained for a long enough period of time for the fat content of her muscles to be lower than that of the male, SAM, given the fact that he is not fully mature. The lowered marrow fat values of this female and numerous reports (e.g., Harris 1945, Riney 1955, Brooks et al. 1977) that marrow fat is generally conserved (i.e., used at a slower rate), however, suggest that the intramuscular fat content of the meat of the female, FAF, should be lower than if she were killed in better condition.

Variability in the Production of Intramuscular Fat

Intramuscular fat production is considered in several respects. First, how do the animals compare in total intramuscular fat production, and second, is the rank of total production repeated in the ranking of carcass units? To answer these questions, fat was extracted from samples of the meat from each carcass unit using anhydrous ether as the solvent. This analysis provides data on the percent fat present in the meat. These percent fat data offer some insights into the variability between these four animals that should be considered before examining the total animal and carcass unit fat production differences. This analysis is important, because it is not necessarily true that the variability between animals seen in the meat fat content values are repeated in the production totals. Intramuscular fat production totals are greatly influenced by differences in meat weights.

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Variability in the Percent Extractable Fat

In Table 6.8, the results of the ether extraction analysis on meat samples collected from the four TRNP bison are presented. At the bottom of this table, one may find comparative results from a study of the lipid content of bison tissues collected from the Big Delta herd in Alaska (Wilber and Gorski 1955), and from a study of the hump meat of a bison bull calf (Morris et al. 1981). Wilber and Gorski (1955:306) report that sternomastoid muscle samples (from the neck) from six bison yielded an average of 4.11 percent fatty acids, and pectoralis major muscle samples (the deep pectoral of the breast) from 11 animals yielded 3.65 percent fatty acids. These values compare favorably with those determined for meat from the cervical vertebrae (CERV) and sternebrae (STER) units (Table 6.8) of the TRNP bison. The current analysis included grouped rather than individual muscle fat determinations, but the resulting values are within the range reported by Wilber and Gorski (1955).

Morris et al. (1981:218) report that the fatty acid content of hump meat (meat from the thoracic vertebrae unit) in the bison bull calf they studied was 5.00 percent. This value is substantially higher than that reported for the yearling bull in this study, but is within the range of values found for this carcass unit in the adult animals (Table 6.8). No information is provided concerning the feeding regime for the bull calf in the Morris et al. study. On a natural forage diet, this value appears to be somewhat high, if the value for the yearling bison, FYM, is representative. Crawford (1968:1330) reports that the total amount of lipids from muscle samples of domestic compared to wild bovids was generally ten times higher and that wild species held in captivity had fat levels comparable to domestic species. The fat content difference in the two young bison is not

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Table 6.8. Fat Content of Meat Samples from Bison

----- Part A. Meat Fat Content of TRNP Bison Measured for Carcass Units -----

Anatomical Unit	Percent Fat				Number of Samples			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	4.43	2.88	----	4.87	2	2	-	2
CERV	1.82	3.75	5.47	4.00	8	8	8	3
THOR	2.28	4.45	9.87	6.90	5	5	5	2
LUMB	0.31	2.80	4.71	4.79	5	5	2	3
SPEL	1.01	2.63	3.89	3.41	8	5	2	8
CAUD	2.33	2.54	7.09	9.99	8	5	5	5
RIBS	3.19	5.36	8.94	5.38	5	8	2	2
STER	2.80	3.80	5.99	5.95	5	8	2	2
SCAP	1.16	2.25	3.70	4.11	5	8	5	5
HUM	0.25	1.28	3.97	2.04	5	8	2	3
RULC	0.06	1.04	1.06	0.35	5	8	7	7
FEMP	0.12	1.42	1.63	1.68	5	8	5	5
TIB	0.00	0.50	1.74	1.82	7	8	3	5
MTT	0.19	1.18	0.71	3.66	4	2	2	5

------- Part B. Fat Content of Other Bison Meat Samples -------

I. TRNP specimen SFM, total carcass meat samples percent fat = 0.82, n = 5

II. Wilber and Gorski (1955) bison specimens,

sternomastoid muscle percent fatty acids = 4.11, n = 6

pectoralis major muscle percent fatty acids = 3.65, n = 11

III. Morris et al. (1981) bison specimen,

hump meat percent fat = 5.00, n = 5

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on the order of the ten-fold difference seen in Crawford's (1968) study, but a difference in feeding regime could be responsible for the differences seen here.

The values for the percent fat content in the meat of the TRNP herd animals (Table 6.8) show that some variability exists between the values for specific carcass units of different animals. As expected, the values for the youngest animal, FYM, are lower than those of both the older male, SAM, (except for the meat from the head or SKWOT unit), and the females. Animal age, as it reflects animal maturity, therefore, clearly affects the fat content of meat from each carcass unit.

The effects of animal sex also appear to be evident in meat fat content (Table 6.8), but it cannot be shown with the available data that the suppressed fat values for the male, SAM, are not due instead to his having not yet achieved full maturity. The values derived for this animal could easily be showing the effects of age, sex, or a combination of the two. Without additional data from fully mature males, it is not possible to determine whether animal maturity, or animal sex is responsible for the lower values seen here. Nevertheless, they do indicate that this four year old male bison had lower meat fat content than either mature female. This, coupled with the even lower values for FYM, suggest that the fat content for males four years of age or under should be lower than those of mature females, except perhaps in the distal limb units (the radius-ulna, tibia, and metatarsal). No information is available concerning the meat fat content of immature females or fully mature males. As a general rule, however, females are fatter than males, so the differences seen here may indeed be a reflection of sex differences.

Animal condition differences may be reflected in the meat fat content

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values for the two females. According to Curtis (1969:166), there is a tendency for animals and man to accumulate fat as they get older, a characteristic that Byers and Schelling (1988a:439) attribute to a change in metabolism that results from the decreasing fraction, in the older animal, of metabolically very active tissue. Additionally, there is a tendency for wild animals to cyclically deplete and replenish energy supplies stored as body fat, with peak fatness occurring prior to the senesence of food plants and greatest weight loss occurring in late winter-early spring, before new plant growth is available (e.g., Gates and Hudson 1981). In females, this period of low food availability is often concurrent with the increased energy demands associated with pregnancy and lactation (Fuller 1976:313-314). Spring-killed animals of the same sex, therefore, may be expected to have lower fat levels than fall-killed animals, and older animals in good condition may be expected to have higher fat levels than younger animals.

Under normal conditions, the older, fall-killed female, FAF, should have higher meat fat content than the younger, spring-killed female, SAF. If FAF was in poorer condition and/or if SAF did not calve the previous spring and subsequently was in better than normal condition, then SAF might have higher fat content. SAF was carrying a fetus when killed, but it is not known if she had calved the previous year. In eight of the thirteen carcass units producing meat for which fat content was determined, the younger, spring-killed female, SAF, had higher meat fat content. Samples in which the fat content of the older, fall-killed female, FAF, were higher include those from the lumbar vertebrae (LUMB), caudal vertebrae (CAUD), scapula (SCAP), femur-patella (FEMP), tibia (TIB), and metatarsal (MTT) units (Table 6.8). The fact that the fat content values of the forelimb of FAF are smaller than in SAF, while the hindlimb values are higher (or

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perhaps, comparable) in the females, suggests that intramuscular fat mobility may be more rapid in the forelimb. Binford (1978) suggested that the neck and forequarters in caribou are depleted first. Notably, the neck (CERV), thoracic vertebrae (THOR), and ribs (RIBS) units have appreciably smaller fat content values in FAF than SAF, while the lumbar (LUMB), sacrum-pelvis (SPEL) and sternebrae (STER) units are comparable between females (Table 6.9). This pattern, with the exception of the sternebrae unit, compares favorably with Binford's assessment of changes in body part use with changes in animal condition. It should be noted, however, that this contrasts with the apparent order of depletion found in the marrow and grease fat in these females and as reported for impala marrow fat by Reich (1981).

If one sums the positive and negative results of the FAF percent fat minus the SAF percent fat (Table 6.9), the sum of negative results (-11.16), in which the values for SAF were higher than those for FAF, is larger than the sum of positive results (6.47), in which the value for FAF was larger than that for SAF. This indicates that the units that have higher values in FAF than in SAF are less different between animals than those where the SAF value is larger. If one starts with the assumption that the female, FAF, should have had higher fat values, due to age and season of death, then these data suggest that FAF is in declining condition, SAF is in better than normal condition, or both conditions are in effect. The jaw and dental deformity in FAF and the lower fat content of the marrow relative to the males at a time of year when it should be high, suggest that FAF is in subnormal condition. It does not clarify whether the female, SAF, was in normal or above normal condition, however.

It is of interest that despite the fact that the female, FAF, appears to have been in declining condition (based on relative marrow fat content)

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Table 6.9. Comparison of Fat Content of Meat Samples from Female Bison

Anatomical Unit	Difference in Percent Fat (FAF - SAF)	
	Positive	Negative
CERV		-1.47
THOR		-2.97
LUMB	0.08	
SPEL		-0.48
CAUD	2.90	
RIBS		-3.56
STER		-0.04
SCAP	0.41	
HUM		-1.93
RULC		-0.71
FEMP	0.05	
TIB	0.08	
MTT	2.95	
Sum	6.47	-11.16

Note: based upon data from Table 6.8.

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when she was killed, her meat fat content values (Table 6.8) are still substantially higher than those of the male, SAM. This might lead one to suspect that older females might be selected over young males in selecting for maximum intramuscular fat, but it does not take into account the differences in the associated meat weight. The production of intramuscular fat is evaluated now with the intention of addressing this question.

Variability in the Production of Intramuscular Fat

When the meat weight of a carcass unit (Table 6.2) is multiplied by the percent fat content (derived from Table 6.8), the result is the weight of the intramuscular fat in that unit. The calculated weight of intramuscular fat for each carcass unit is presented in Table 6.10. Meat fat weight is not available for the head unit of the female, SAF. Although Leat and Cox (1980:156) argue that solvent extractions of intramuscular fat include some structural lipids in addition to storage lipid, this analysis assumes that the proportion of phospholipid is relatively small. Use of petroleum ether as the solvent reduces the amount of nonlipid included in the extraction (Dobush et al. 1985).

Total Carcass Intramuscular Fat Production. At the base of Table 6.10, the total weight of the intramuscular fat calculated for each animal is summed. As expected, the young and small bison, FYM, had the smallest quantity of intramuscular fat. Despite the larger muscle mass of the male, SAM, the meat fat content values per unit weight in this bull were low enough that the total production of intramuscular fat was lower than that in either female. Comparison of the fat totals for the two females showed the younger, better conditioned female, SAF, produced 384.6 gm (13.6 ounces)

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Table 6.10. Intramuscular Fat Weight in the TRNP Bison Side Carcass

Anatomical Unit	Fat Weight (gm)			
	FYM	SAM	SAF	FAF
SKWOT	33.4	62.1	----	65.8
CERV	84.7	566.6	397.2	498.3
THOR	111.7	495.8	797.5	582.9
LUMB	13.6	265.2	355.2	413.8
SPEL	38.5	217.9	257.0	207.9
CAUD	1.7	3.3	8.8	13.8
RIBS	224.2	973.3	1,121.5	776.9
STER	103.6	257.3	274.3	382.9
SCAP	40.8	185.1	176.2	240.4
HUM	7.5	101.0	238.6	107.0
RULC	0.8	27.0	18.3	6.2
MTC	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0
FEMP	17.7	397.6	368.3	376.6
TIB	0.0	17.7	40.0	61.1
MTT	0.0	0.2	0.1	0.6
PPHA	0.0	0.0	0.0	0.0
Total Excluding SKWOT	644.8	3,508.0	4,053.0	3,668.4

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more intramuscular fat. It was expected, on the basis of age and possibly sex, that the male, SAM, should produce less meat fat than the female, SAF, but it was not known whether the greater muscle mass of this male would compensate for lower meat fat content per unit weight when compared with the poorer conditioned female, FAF. Given the closeness of the total carcass fat weight values of the two animals, SAM and SAF (3508.0 gm and 3668.4 gm), two conclusions may be drawn. First, if muscle mass were higher in SAM, fat weight might exceed that of the female, SAF. The male, SAM was not fully mature, so one might expect that greater muscle mass in older males might yield greater intramuscular fat weight in fully mature males than in females, despite lower per unit weight fat content. Jones et al. (1980a:846) note that at constant physiological maturity, bulls are larger than heifers in cattle, and have significantly greater fat weight. Second, it seems probable that, in analysis at the level of the carcass unit, the male, SAM, may produce more intramuscular fat than the female, FAF.

In addition to these four animals, the female, SAF, was carrying a fetus. A single meat sample was collected from the carcass (excluding the head) of this animal (SFM), and the fat extraction analysis indicates that it had a fat content of 0.82 percent. Fat in this case, includes intramuscular and intermuscular fat. When the intramuscular fat weight of each of the other four bison is divided by the meat weight (excluding the head), the resulting values are comparable to that derived for the fetal bison, except that they exclude intermuscular fat. The total carcass percent intramuscular fat in the meat (fat weight divided by meat plus fat weight) of the four animals is as follows: FYM, 1.2 percent; SAM, 2.9 percent; SAF, 4.8 percent; and FAF, 3.8 percent. The difference between the fetal bison and the yearling male, FYM, represents a 46.3 percent increase

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in intramuscular fat content. The fat content of the female, SAF, represents a 485.4 percent increase in fat production. Fetal bison clearly provide little fat, from either intra- or intermuscular depots, and if they were a focus of selection, another trait (e.g., meat tenderness) must have been the controlling factor.

Variability in Carcass Unit Intramuscular Fat Production. From the data in Table 6.10, it is apparent that the immaturity of FYM is reflected in the production of meat fat weight at the level of the individual carcass unit as well as at the level of the complete carcass. In the case of the other three animals, however, meat weight differences override percent fat content differences and lead to unexpected relationships in carcass unit fat weights given their age, sex, and condition.

First, comparison of the fat weights of the carcass units in the male, SAM, to those in the females (Table 6.10), shows that the larger muscle mass of the neck (CERV), femur-patella (FEMP), and radius-ulna (RULC) in SAM, results in larger total unit fat weights in that animal despite the smaller per unit weight fat values. In the case of the scapula (SCAP), the larger muscle mass is sufficient for the fat weight to be higher than that in the younger female, SAF, but not in the older female, FAF. Clearly, the larger muscle mass in the male plays a major role in offsetting the lower percent fat values associated with these units.

Comparison of the meat fat weights in the carcass units of the two females shows the slightly larger body size of the older female becomes important only in the fat weight of the cervical vertebrae (CERV) and sternebrae (STER) units. Here, the greater muscle mass in FAF overrides the smaller percent fat content to produce more fat in this animal. In the other carcass units, muscle weight and fat content follow the expected

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patterns, probably because the differences in muscle weight are not that large between these two animals. The extremely large muscle mass of the cervical unit in FAF is unexplained. Its effect on the comparative meat fat weights is clearly evident.

Variability in the Distribution of Intramuscular Fat

The distribution of intramuscular fat in the bison carcass appears to show some variability in how age and condition affect fat distribution. Table 6.11 presents the percent that fat weight from each unit represents of total intramuscular fat weight (excluding fat from the head unit). The distribution of intramuscular fat in each of the carcasses of these arimals is quite variable, as one might expect, given Berg and Butterfield's (1976) assessment that fat is the most variable carcass tissue in cattle. The greater variability makes it difficult, if not impossible with such a small sample, to identify units that might differ due to sex, age, or condition differences. In the following paragraphs, the more markedly different values of percent total intramuscular fat weight between animals are discussed.

It appears that in the young male, FYM, the ribs (RIBS) unit, and to a smaller extent, the sternebrae (STER) unit provide a substantially larger proportion of total intramuscular fat weight than these units do in the adult bison from this study (Table 6.11). The proportion of total intramuscular fat in the femur-patella (FEMP) unit is much lower in this young male than in the adults.

Comparison of the male, SAM, with the female, SAF, shows the largest difference in proportions of total intramuscular fat weight produced is in the cervical vertebrae (CERV) unit. The male, in this case, has a much

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Table 6.11. Distribution of Intramuscular Fat in the TRNP Bison Carcass

Anatomical Unit	Percent of Total Intramuscular Fat Weight (gm)			
	FYM .	SAM	SAF	FAF
CERV	13.1	16.2	9.8	13.6
THOR	17.3	14.1	19.7	15.9
LUMB	2.1	7.6	8.8	11.3
SPEL	6.0	6.2	6.3	5.7
CAUD	0.3	0.1	0.2	0.4
RIBS	34.8	27.7	27.7	21.2
STER	16.1	7.3	6.8	10.4
SCAP	6.3	5.3	4.3	6.6
HUM	1.2	2.9	5.9	2.9
RULC	0.1	0.8	0.5	0.2
MTC	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0
FEMP	2.7	11.3	9.1	10.3
TIB	0.0	0.5	1.0	1.7
MTT	0.0	0.0	0.0	0.0
PPHA	0.0	0.0	0.0	0.0

Note: percentages based upon total fat weight excluding fat from SKWOT.

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higher percent of total fat weight in this unit than the female, SAF. It is also larger than that reported for the older female, but the difference is not as great. It appears that the male neck provides proportionately more of the total intramuscular fat weight than the female neck. This is due to the greater muscle mass of this unit in the male, as the per unit weight fat content is substantially higher in the female (Table 6.8). The only other unit that stands out with particularly different fat weights between animals is the thoracic vertebrae (THOR) unit (Table 6.10). In this case, the female, SAF, registers a higher percent of total intramuscular fat weight in this unit than the male (Table 6.11). It is not clear, however, whether this is a significant difference.

Carcass Unit Rank Based on Production of Intramuscular Fat. The importance of the differences noted above may be assessed by examining the effects these differences have upon the ranking of anatomical units by individual. Figure 6.4 presents the ranking of carcass units, by animal, based upon the amount of intramuscular fat they produce. In the case of the two males, examining potential age and maturity differences, there appears to be numerous changes in rank, but few changes that result in changes of more than two positions of rank. The units that change most in rank include the sternum (STER), lumbar vertebrae (LUMB), scapula (SCAP), and femur-patella (FEMP) units. In the younger animal, the femur-patella (FEMP) and lumbar vertebrae (LUMB) units are much lower in rank (positions 7 and 8) than in the male, SAM (positions 4 and 5). These low rankings appear to be due to their low percent fat content values, rather than due to any proportional differences in the meat weights of the two animals. The sternum (STER) and scapula (SCAP), on the other hand, are ranked higher in the younger animal, moving from positions three and five in the immature

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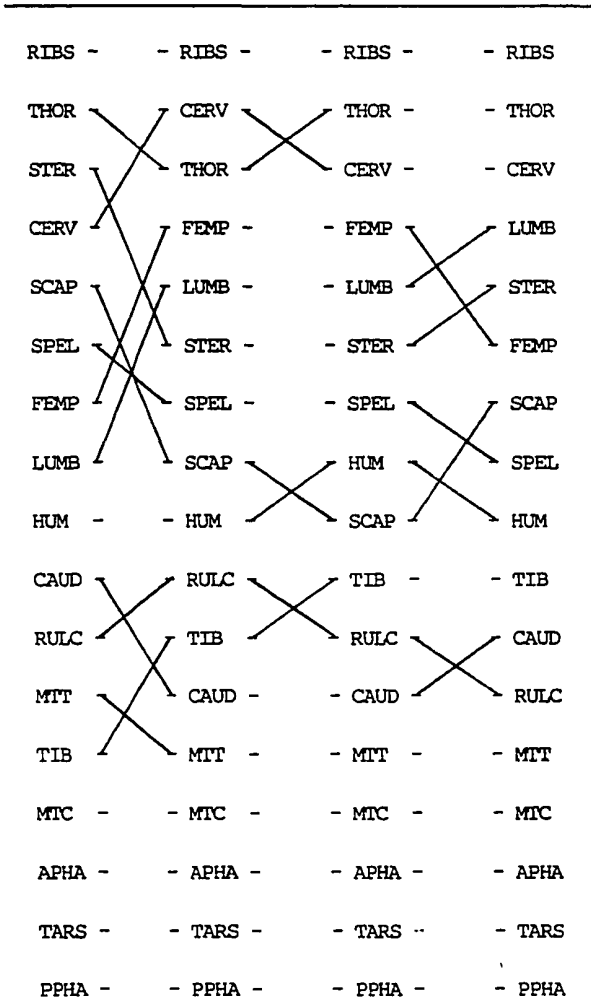
Figure 6.4. Rank Order of Carcass Units for Intramuscular Fat Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
RIBS	RIBS	RIBS	RIBS	224.2	973.3	1121.5	776.9
THOR	CERV	THOR	THOR	111.7	566.6	797.5	582.9
STER	THOR	CERV	CERV	103.6	495.8	397.2	498.3
CERV	FEMP	FEMP	LUMB	84.7	397.6	368.3	413.8
SCAP	LUMB	LUMB	STER	40.8	265.2	355.2	382.9
SPEL	STER	STER	FEMP	38.5	257.3	274.3	376.6
FEMP	SPEL	SPEL	SCAP	17.7	217.9	257.0	240.4
LUMB	SCAP	HUM	SPEL	13.6	185.1	238.6	207.9
HUM	HUM	SCAP	HUM	7.5	101.0	176.2	107.0
CAUD	RULC	TIB	TIB	1.7	27.0	40.0	61.1
RULC	TIB	RULC	CAUD	0.8	17.7	18.3	13.8
MTT	CAUD	CAUD	RULC	0.02	3.3	8.8	6.2
TIB	MTT	MTT	MTT	0.0	0.2	0.1	0.6
MTC	MTC	MTC	MTC	0.0	0.0	0.0	0.0
APHA	APHA	APHA	APHA	0.0	0.0	0.0	0.0
TARS	TARS	TARS	TARS	0.0	0.0	0.0	0.0
PPHA	PPHA	PPHA	PPHA	0.0	0.0	0.0	0.0

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male, FYM, to positions six and eight in the older male, SAM. The change in rank of these two units can largely be attributed to the increase in rank of the femur-patella (FEMP), lumbar vertebrae (LUMB), and cervical vertebrae (CERV) units in the older animal, which force a drop in the rank of the sternum (STER) and scapula (SCAP). The difference seen in the cervical (CERV) unit rank in these animals is attributable to both fat content and muscle mass differences, with the immature male smaller in each category. Based on fat weight, the neck (CERV) is ranked higher in the male, SAM (position 2 versus 4), as would be expected.

Differences in ranking between the male, SAM, and the female, SAF, are minimal, suggesting that there is very little affect from animal sex on the distribution of meat fat in the bison carcass. If there is a sex-related effect, it is that the cervical (CERV) units in males produce proportionately more of the intramuscular fat than in females. If SAF is in better than normal condition (i.e., if she did not calve the previous spring), the similarity in fat production rankings might be misleading. It does not appear so, however, given the patterns of rank changes noted for the two females.

Differences between the two females do not stand out as particularly marked either. The biggest rank changes occur in the femur-patella (FEMP) and scapula (SCAP) units (Figure 6.4). It is not clear if the differences are significant, or representative of condition-related changes in fat weights. Inspection of the unit fat weights, however, indicate that the femur-patella (FEMP) unit might be similarly ranked in both animals. The fact that so little difference is seen between either female and the male, SAM, in the order of carcass units ranked by intramuscular fat weight, suggests that intramuscular fat distribution in the carcasses of adult animals is similar.

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In sum, it appears that the greatest differences in intramuscular fat weight distribution in the bison carcass occur between the immature male and the adult, but not fully mature male, SAM. In the case of these two animals, the differences are large enough to markedly change the rank of some carcass units, particularly the femur-patella (FEMP), lumbar vertebrae (LUMB), sternebrae (STER), and scapula (SCAP) units. Few differences could be shown between the adult animals in the rankings of carcass units for the distribution of intramuscular fat. On the basis of these data, one might conclude that carcass unit selection by prehistoric hunters interested in procuring the maximum amount of intramuscular fat probably would not change their selection strategies, if the carcass were that of a male rather than a female, but might if it were an immature male. This analysis, however, overlooks the close relationship between intramuscular fat and the muscle it is found in.

Importance of Packaging in Intramuscular Fat Procurement

In previous discussions of carcass resources, the greater the amount of the product available, the higher a unit was ranked for potential selection. In the analysis of intramuscular fat, however, a different situation is evident. Unlike other sources of fat, intramuscular fat is not easily separated from the muscle with which it is associated. It is not a separate product, but comes as part of a meat package. Given this fact, two situations for fat use by hunters are possible. In the first, the amount of meat consumed with the fat is minimized; in the second, it is not. Under these two circumstances, the way in which bison meat is utilized to maximize intramuscular fat recovery is different.

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In the first case, if one does not wish to consume large amounts of meat in order to obtain a given amount of fat, then meat fat weights should be disregarded, except as they influence how selection of a unit affects the tally of fat procured. This strategy might be necessary because some units with large amounts of fat (e.g., SAM cervical vertebrae unit) also have a small fat to meat ratio. Under these circumstances, units with the lowest ratio of protein to fat should be used, because they reduce the amount of meat that must be consumed in order to gain access to the fat. The ratio of protein weight to fat weight (Table 6.12) could be used as a guide to carcass unit selection under these conditions. The necessity for adopting such a strategy is suggested by the works of Noli and Avery (1988) and Speth (1988, 1989). These authors discuss the upper limits of the proportion of protein in high-protein diets and the possible detrimental effects when maximum levels are exceeded. It is possible, therefore, that intramuscular fat might be sought as a source of food energy, while at the same time, attempts are made to limit the consumption of protein. This might occur when diets are focused on lean meat animals during periods when carbohydrates are generally unavailable. Carcass fat, under these conditions, would be a primary focus of procurement activities, and sources available that are not directly associated with meat protein (such as intermuscular fat, marrow, and bone grease) should be exploited first. If the problem persists, then meat units that maximize fat recovery while minimizing protein consumption should be preferred in selection decisions.

Using the second selection strategy, where the amount of meat consumed is less critical, the data in Table 6.10 that indicate the meat fat weight of each unit, would be the best source of information for making carcass unit selections. The comparative results of animal carcass unit rank using

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Table 6.12. Protein Weight in Half Carcass and Ratio of Protein to Intramuscular Fat

Anatomical Unit	Protein and Ash Weight[a] (gm)				Ratio of Protein : Fat			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	167.8	464.7	nd[b]	300.6	5.0	7.5	nd[b]	4.6
CERV	1,134.3	3,357.6	1,658.4	2,730.4	13.4	5.9	4.2	5.5
THOR	1,162.2	2,533.6	1,788.0	1,834.1	10.4	5.1	2.2	3.1
LUMB	1,079.7	2,206.1	1,797.0	1,854.9	79.4	8.3	5.1	4.5
SPEL	955.9	1,980.5	1,635.4	1,355.6	24.8	9.1	6.4	6.5
CAUD	18.1	30.1	28.7	28.8	10.6	9.1	3.3	2.1
RIBS	1,659.8	4,187.3	2,815.1	3,145.2	7.4	4.3	2.5	4.0
STER	888.7	1,552.2	1,041.6	1,351.5	8.6	6.0	3.8	3.5
SCAP	848.8	1,905.7	1,075.4	1,278.4	20.8	10.3	6.1	5.3
HUM	762.4	1,887.9	1,424.5	1,214.7	101.7	18.7	6.0	11.4
RULC	349.7	623.8	424.4	430.0	437.1	23.1	23.2	69.4
FEMP	3,725.6	6,799.1	5,702.5	5,292.8	210.5	17.1	15.5	14.1
TIB	422.1	866.3	575.0	775.7	---[c]	48.9	14.4	12.7
MTT	2.6	3.1	2.6	3.0	130.0	15.7	26.2	5.0
HEART	268.7	491.7	416.9	464.7	2.1	2.7	1.8	1.6
LIVER	998.4	1,445.3	1,244.5	1,770.0	11.7	10.2	17.1	3.1
KIDNEYS	53.1	100.8	75.9	101.9	2.5	3.5	2.1	3.4
TONGUE	153.5	249.5	224.4	287.2	1.1	0.6	0.7	0.9

[a] Weight equals side carcass unit meat weight multiplied by the dry weight extraction fraction; weights for organs are based upon complete organ weight.

[b] No data.

[c] No fat recovered in extraction.

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these two strategies are presented in Figure 6.5.

It is evident from these data that variability in ranking does occur, depending upon which selection strategy is employed. (It should be noted that a high protein to fat weight ratio results in low rank, because the objective in this strategy is to minimize protein intake.) In most cases, the change in rank position is minor, but in a few cases, carcass units rise or fall in rank quite dramatically. The greatest change in rank, depending upon whether percent fat content or fat weight is used to rank the units, occurs in the caudal vertebrae (CAUD) unit. It drops an average of 7.75 rank positions if the amount of fat is evaluated, rather than the ratio of protein to fat weight. In archaeological literature, the tails of bison are generally thought to be unimportant as a meat source. As a source of intramuscular fat and bone grease, however, it is possible that its importance has been underestimated.

The carcass unit that shows the second greatest degree of rank change in these two assessments is the femur-patella (FEMP) unit (Figure 6.5). It has a relatively high ratio of protein to fat weight (thus, low rank) and ranks from ninth to twelth, but due to the large muscle mass of this unit it ranks relatively high in meat fat production (ranging from fourth to seventh). It is not the most important meat fat producing unit, however.

In both strateiges for carcass unit selection, the units of the axial skeleton are generally higher rated than the elements of the appendicular skeleton. Given either method of ranking, the ribs and thoracic vertebrae are the best sources for intramuscular fat, and appear to be so, regardless of which animal is considered. If adequate amounts of fat are acquired focusing first on these units or other sources of fat, then a strategy maximizing fat return might then be applied. If fat is a prime resource,

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Figure 6.5. Comparative Unit Selection Based Upon Protein-Minimizing or Fat-Maximizing Strategies

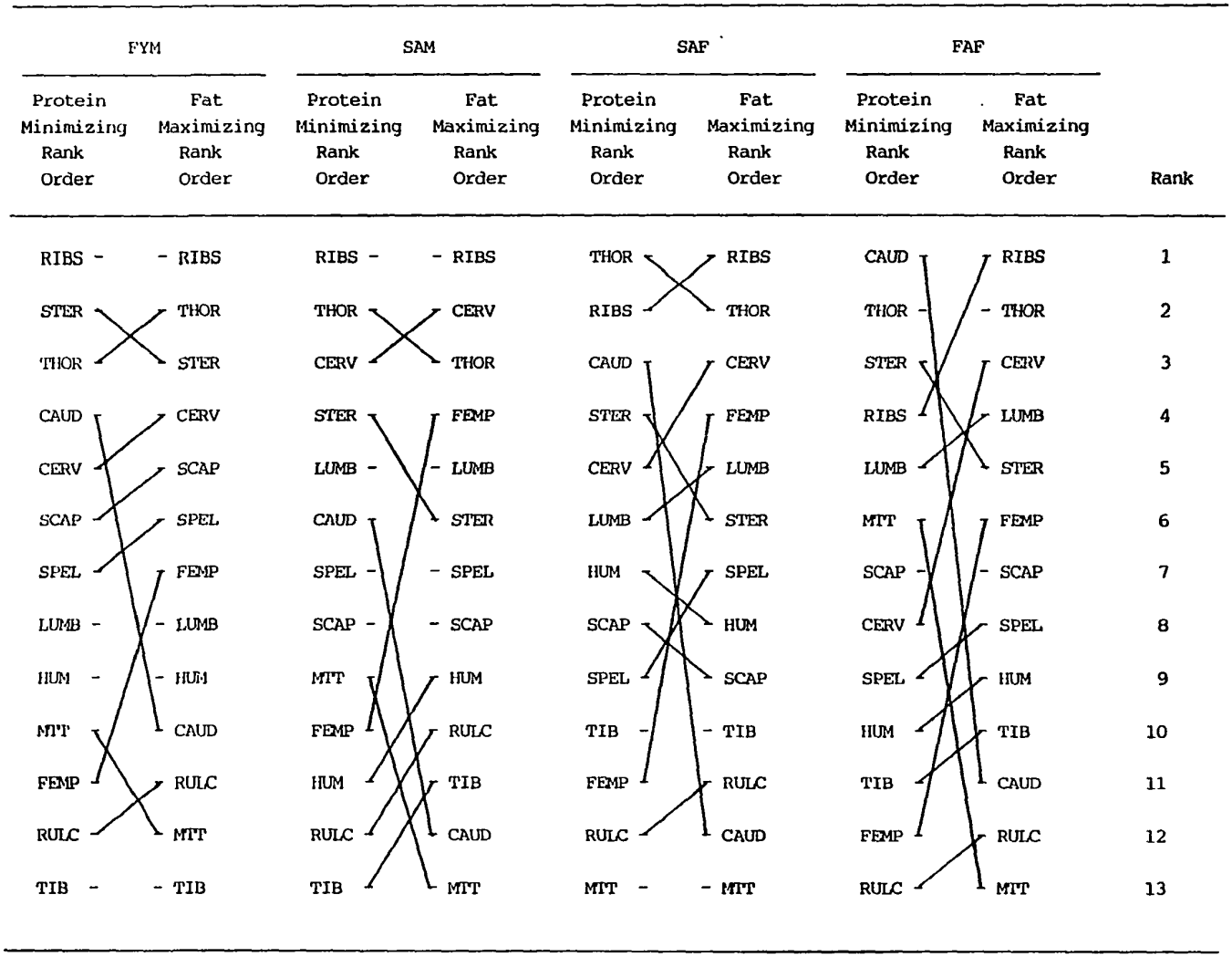

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Figure VII.5. (continued)

FYM		SAM		SAF		FAF		
gm Protein per gm Fat	gm Fat Weight	gm Protein per gm Fat	gm Fat Weight	gm Protein per gm Fat	gm Fat Weight	gm Protein per gm Fat	gm Fat Weight	Rank
7.4	224.2	4.3	973.3	2.2	1121.5	2.1	776.9	1
8.6	111.7	5.1	566.6	2.5	797.5	3.1	582.9	2
10.4	103.6	5.9	495.8	3.3	397.2	3.5	498.3	3
10.6	84.7	6.0	397.6	3.8	368.3	4.0	413.8	4
13.4	40.8	8.3	265.2	4.2	355.2	4.5	382.9	5
20.8	38.5	9.1	257.3	5.1	274.3	5.0	376.6	6
24.8	17.7	9.1	217.9	6.0	257.0	5.3	240.4	7
79.4	13.6	10.3	185.1	6.1	238.6	5.5	207.9	8
101.7	7.5	15.7	101.0	6.4	176.2	6.5	107.0	9
130.0	1.7	17.1	27.0	14.4	40.0	11.4	61.1	10
210.5	0.8	18.7	17.7	15.5	18.3	12.7	13.8	11
437.1	0.02	23.1	3.3	23.2	8.8	14.1	6.2	12
---	0.0	48.9	0.2	26.2	0.1	69.4	0.6	13

and is not recovered in adequate amounts in the units mentioned, a low meat strategy might best meet fat requirements without risking protein poisoning.

Organ Meat and Fat Production and Distribution

In addition to the carcass muscle used for meat by hunters, the internal organs, another source of protein and fat, often were eaten by prehistoric and historic hunting peoples. In this study, variability between animals in the meat weight, fat content, and fat weight of the heart, liver, kidney, and tongue are evaluated. Other internal organs (e.g., the brain, stomach, intestines) were also consumed as food and provided a source of protein and fat, but are not included in this study.

Variability in Organ Weight

The weights of the heart, liver, kidney, and tongue from each of the four TRNP bison are reported in Table 6.13 and each organ is ranked by size, between animals. Animal age and sex appear to be important factors in organ size and weight rank. The small size and low ranking of all organs from the immature male, FYM, indicate that animal maturity has a marked influence on organ size. The weights of the organs from the immature male, FYM, are from 48 to 73 percent of the weight of the same organ in the more mature male, SAM. Even where the organ weight of SAM is larger than that of the females, the organs of the immature male are still smaller than those of either female.

The differences in organ weights between the male, SAM, and the two females suggest that sexual dimorphism is evident in organ meat weights as well as muscle weight, and is seen at least as early as four years of age in some organs. The male, SAM, had larger kidneys and a larger tongue than

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Table 6.13. Organ Weights in TRNP Bison

Part A. Organ Weight (gm)

Organ	FYM	SAM	SAF	FAF
Heart	1,502.6	2,842.1	2,537.3	2,863.3
Liver	4,309.2	5,896.8	4,762.8	7,626.2
Kidneys	340.2	574.1	407.6	556.4
Tongue	850.5	1,771.9	1,396.2	1,679.7

Part B. Bison Ranked by Organ Weight

Organ	FYM	SAM	SAF	FAF
Heart	4	2	3	1
Liver	4	2	3	1
Kidneys	4	1	3	2
Tongue	4	1	3	2

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either female, despite his younger age. Although the heart of the male, SAM, is not as large as that of the older female, FAF, the difference is very small. The male heart weight is larger than that of other female, SAF. At four years of age, sexual dimorphism is not as pronounced in the heart as in the tongue or kidneys, but it appears that males older than SAM would probably have larger hearts than mature females, given the evidence from this male and the fact that he was not yet fully mature. This is in agreement with the results of a study of caribou by Adamczewski et al. (1987b:1154) who found that the heart maintains a strong proportionality to carcass weight, because it serves all body tissues.

The differences in liver size between the male, SAM, and the two females cannot be attributed as clearly to sex differences. The male, SAM, is larger than the youngest female, but is substantially smaller than the older female, FAF, as in the heart. Perhaps with full maturity, the male liver would be larger than that of the female. The difference between the females, however, is even larger than that between the male and females. The difference between the females cannot be explained by reference to differences in their carcass sizes. The possibility that the liver of FAF is abnormally large, perhaps due to poor condition, must be considered.

Stangassinger and Giesecke (1986:348) report that in studies of domestic sheep, livers increased in weight following increased feed intake. They note that liver size increases following either fasting or restricted feeding, and with voluntary increases in food intake that usually occur during lactation. Given that the female, FAF, was killed in October, the larger size of her liver is not attributable to increases associated with lactation. It is possible that a change in the level of her food intake did take place, but there is no way to verify that occurrence. The extent of

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sexual dimorphism in the liver, therefore, remains unclear. If the liver of the older female, FAF, is abnormally large then male livers might be expected to be larger than those of females under normal conditions. If the FAF liver is not abnormally large, then sexual dimorphism might still be in evidence in more fully mature males. Alternatively, liver weight might not be influenced by animal sex.

Organ Weight as a Percent of Non-Standard Carcass Weight

Table 6.14 presents the weight of each organ as a percent of non-standard carcass weight (skinned, eviscerated carcass weight including the head, feet, and tail). These data indicate that three of the four organs studied, the heart, kidneys, and tongue, are a relatively consistent proportion of animal weight, regardless of animal age or sex. The differences noted above in the weight of these three organs between animals of different age and sex, therefore, are attributable to differences in animal sizes. In turn, because animal age and sex influence animal size, the differences in organ weights in the heart, kidneys, and tongue may be attributed to those differences as well.

The liver data, on the other hand, show some variability between animals in the proportion it represents of the non-standard carcass weight. It is not clear, however, what factors are controlling the differences seen, given that the bison split into two groups with the youngest male, FYM, and oldest female, FAF, in one group, and the older male, SAM, and the female, SAF, in the other. One might suspect that the season in which the four animals were killed is a factor, with fall-killed animals having proportionately larger livers than spring-killed animals. A report by Dickinson (1976) on a five year old bison steer killed in early November,

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Table 6.14. Organ Weight as a Percent of Carcass Weight

Part A. Organ Weight as a Percent of Non-Standard Carcass Weight

Organ	FYM	SAM	SAF	FAF
Heart	0.8	0.7	0.9	0.9
Liver	2.4	1.5	1.7	2.5
Kidneys	0.2	0.1	0.1	0.2
Tongue	0.5	0.5	0.5	0.5

Part B. Bison Liver as a Percent of Standard Carcass Weight

Organ	FYM	SAM	SAF	FAF
Liver	2.7	1.7	1.9	2.8

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1975, however, indicates that if the season of kill is a factor in the TRNP animal figures, some other factor is varying along with season between these samples. In Dickinson's bison steer, the proportion the liver represents of the standard carcass (carcass excluding head, distal limbs, and tail) weight is 1.4 percent. In Part B of Table 6.14 the values for the liver as a percent of standard carcass weight are presented for the TRNP bison. These bison figures are all larger than the value derived for the Dickinson bison steer, but the spring-killed animals are closer in magnitude to that value than the fall-killed animals. If season alone were responsible, one would expect the bison steer value to be closer to that of the fall-killed animals given his November death. Perhaps a difference in feeding regime is responsible. Adamczewski et al. (1987b:1152) found major seasonal changes in caribou liver and kidney weights as proportions of carcass weight with high summer values and lower fall values. If this reflects changes in ratios of stable organ weights compared with changing carcass weights (due to differences in carcass fat content), then the TRNP bison data fit nicely with the seasonal explanation.

In conclusion, therefore, it remains unclear why the young male, FYM, and older female, FAF, have proportionately larger livers. The comparability suggests that animal age does not affect the size of the liver relative to carcass weight, although it is possible the similarity in proportional size is the result of multiple causes. If that were true, animal age might be a factor in liver size. Animal age differences are noted (Honda et al. 1987:680) for the relative weight of the liver, brain, lungs, and bone in the Japanese Serow, a type of goat, and these authors indicate that this is a pattern reported for other terrestrial and marine mammals as well.

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The comparability of the two spring-killed animals (one of either sex) indicates that animal sex is not responsible for the reported differences in the proportion of liver to carcass weight in these two groups of bison. Unlike the other organs studied, the liver is variable in size. The influence of sex, however, appears to be as unimportant here as in the relative size of the other organs. Some other factor(s) (perhaps age, season or condition differences) apparently are responsible for the enlarged sizes of the livers in the young male, FYM, and in the older female, FAF.

Variability in Organ Fat Content

Part A of Table 6.15 presents the percent fat for samples of the heart, liver, kidneys, and tongue, determined by ether extraction of the fat. For purposes of comparison, the mean values that Wilber and Gorski (1955) determined for a sample of bison from an Alaska herd are reproduced along with the number of individuals they studied to determine that mean (Table 6.15, Part B). They did not include the tongue in the group of tissues they studied.

It is evident that Wilber and Gorski's values are comparable for the heart and kidneys, but their value for the percent fat in the liver (10.33 percent) is substantially higher than that seen in samples from the TRNP bison (ranging from 1.53 to 7.43 percent). Wilber and Gorski (1955:306) note that their bison liver value is much higher than that seen in cattle (4 percent), but cite Kellogg who reported that wild animals of the same species have higher liver lipids than those kept in captivity. It is not apparent, however, why their bison liver lipid values should be so different from those reported here for the TRNP bison, nor why the older female, FAF, has a substantially higher liver fat content than the other three TRNP

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Table 6.15. Fat Content of Organ Samples from Bison

----- Part A. Organ Fat Content of TRNP Bison -----

Organ	Percent Fat				Number of Samples			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Heart	8.61	6.41	8.92	10.25	2	2	2	2
Liver	1.98	2.40	1.53	7.43	8	8	8	2
Kidneys	6.25	5.06	8.86	5.42	3	5	2	2
Tongue	16.88	25.03	22.27	18.66	5	2	2	5

------- Part B. Fat Content of Organ Samples in Wilber and Gorski Bison[a] -------

Organ	Percent Fat	Sample Size[b]
Heart	6.71	9
Liver	10.33	11
Kidney	5.98	11

[a] Source: Wilber and Gorski (1955).

[b] Sample size indicates number of animals tested, not number of samples evaluated.

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bison. Consideration of the effects of fasting on liver fat levels provide potential answers to the disparity in values for the TRNP bison, but not for the differences seen between the two herds.

The liver is one location in the body where the synthesis, or production of fat occurs. Leat (1976:188) reports that in a fasting animal there is a 99 percent depression in fatty acid synthesis and a release of free fatty acids. Schultz et al. (1988:510), reporting on ketosis and the fat cow syndrome in cattle, note that one symptom is a loss of appetite. They state that when a cow does not eat under these conditions, the liver is flooded with mobilized free fatty acids and a fatty liver results. Although they do not state that this is a condition resulting from all fasting experiences, it is implied by Leat's statement.

It was suggested earlier that the older female, FAF, was in poorer condition when killed than the female SAF, as evidenced by lower marrow fat content, lower bone grease fat production, and lower intramuscular fat production, despite the fact she was killed at a time when females should be in peak condition. A deformity in her jaw and dentition was noted and offered as partial explanantion for her poorer condition. Given this condition, one might suspect that the higher fat content of the liver of the animal FAF, compared with the other TRNP bison, might be related to the mobilization of fat to supply energy.

Alternatively, one might suspect that, as an older animal, fat may have been accumulating for many years in FAF, and fat levels might remain high in the internal organs. The fat content appears higher than in the other TRNP bison in both the liver and the heart, but not in kidneys or tongue. It is not clear whether age, animal condition, or both, are responsible for the fat content of the heart, liver, and kidneys in this animal.

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The fat content of these organs in these bison is quite variable, making it difficult to evaluate whether age and sex are reflected in their differences. Unlike other meat samples, the organ meat fat content values for the immature male, FYM, are not consistently lower than those for the older male, SAM. In the liver and tongue, the FYM percent fat content values are lower than those for SAM, but in the heart and kidney, the values are higher. Comparing the male, SAM, with the females, it does not appear that a sex difference is reflected in the fat content of these organs. A larger sample, or perhaps comparison with cattle or other wildlife data might add some insights here.

Ethnographic and historic accounts of bison hunters often record the preference given to the tongue as a portion of the carcass. From the perspective of a hunter interested in procuring fat, it is clear that the tongue and heart each have a particularly high fat content in these animals. In FYM, SAM, and SAF, the tongue has over twice as much fat as the carcass unit with the next highest meat fat content. In the older female, FAF, the difference is somewhat smaller with the fat content of the tongue (18.66 percent) 1.87 times higher than the fat content of the tail (9.99 percent fat). The percent fat in the tongue is quite high considering she may be in poor condition. Given that the tongue and heart both provide small amounts of meat, the high fat content would make them both ideal sources of fat when protein intake must be restricted. These two organs would out rank all carcass units in each respective animal, except in the female, SAF, where the thoracic vertebrae unit had a higher percent fat than the heart. It is not always necessary to minimize protein intake, however, and under those circumstances differences in total fat weight of the organs becomes important.

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Variability in Organ Meat Fat Weight

Although the differences in the percent fat content of the organ meat samples did not clearly show age or sex differences, when the weight of the organ is used to calculate organ meat fat weight (Table 6.16), age, but not sex differences do appear to be evident. It is clear, however, that the lower meat weights coupled with low percent fat content values of FYM are responsible for the lower total fat weights in that animal. With these animals as a model, a comparison of yearling and four year old male bison might show the older males provide larger amounts of fat due to their larger organ sizes.

The larger sizes of many of the organs of SAM compared to the females, however, do not always result in higher organ meat fat weights. Unlike FYM, who had consistently lower meat fat content values, the percent fat in the organs of the male, SAM, is variable. As note above, percent fat in this animal is sometimes larger and sometimes smaller than those reported in the females. As a result, meat fat weights in the male compared to the females are also variable. The tongue in SAM, is larger in size and higher in fat content than in the females, and this is reflected in a substantially higher total fat weight. The heart fat content values for the females are enough higher than that reported for the male, SAM, that the fat weights are also higher, despite the smaller heart weight in SAF and the comparable heart weight in FAF. Kidney fat weight was very low in all animals reflecting both low meat weights and low fat content. The male, SAM, has less fat than the females, but it does not appear to be a particularly large difference. The liver fat weights are variable. The female, FAF, has the largest liver fat weight, reflecting both the high percent fat and large meat weight. Although I cannot demonstrate it, I suspect that sex is not an important

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Table 6.16. Intramuscular Fat Weight of Selected Organs in the TRNP Bison

Part A. Organ Fat Weight (gm)

Organ	FYM	SAM	SAF	FAF
Heart	129.4	182.2	226.3	293.5
Liver	85.3	141.5	72.9	566.6
Kidneys	21.3	29.0	36.1	30.2
Tongue	143.6	443.5	310.9	313.4

Part B. Bison Ranked by Organ Fat Weight

Organ	FYM	SAM	SAF	FAF
Heart	4	3	2	1
Liver	3	2	4	1
Kidneys	4	3	1	2
Tongue	4	1	3	2

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factor in liver fat weight given the weights shown for SAM and SAF. A larger sample of animals is needed to better understand fat content and fat weight in these bison organs.

Summary of Organ and Organ Fat Analyses

Variability in bison organ meat weight is largely affected by animal size. Where animal age and sex influence variability in animal size, differences in organ meat weight may thus be correlated with these characteristics. Organ size, however, is generally proportional to animal carcass size, with no differences due to age or sex. The exception to this is the liver, which was enlarged in two animals, FAF and FYM, relative to carcass weight. The reason, however, remains unclear. The relationship between organ fat content, organ meat fat weight and characteristics of animal age and sex are less clear. The effects of age on animal organ size are dramatic enough that organ meat fat weights are lowest in the immature male, FYM. The fat content of the meat is variable, however, and unlike meat fat from the carcass, it is not consistently lower in the immature male, or in males in general. The organs studied in this analysis, therefore, are found to be more variable than other meat sources in the content and weight of intramuscular fat.

Conclusions

Variability in the production and distribution of bison meat and its associated intramuscular fat, and organ meat and fat was examined above. The first topic discussed was the relationship between meat weight (which includes both muscle and intramuscular fat, but which excludes the brain and tongue) and dry bone weight. When all carcass units were analyzed together,

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these two carcass characteristics were found to have a significant positive linear relationship, but with a moderately weak coefficient of determination (R^2 = 0.1153). Unlike the relationship between bone grease fat and bone characteristics, it did not improve the predictability of meat fat weight using dry bone weight, to divide the data into samples grouped by animal, age, or sex. Excluding the head unit, which has a comparably low ratio of muscle to bone weight, improved the R^2 value (0.4748). It appears that each unit of the bison carcass has a different relationship between bone and meat weight. The head unit is visibly different, having a very small slope, but examination of the relationships of the other units showed that they also appear to have positive linear relationships between meat and dry bone weight. The problem, however, is that the slope of the regression lines for each unit varies. One must conclude that with a larger sample, meat weight could best be predicted using bone weight, if regressions by carcass unit are used.

The second topic discussed in this chapter was varability in meat weight production and distribution in the bison carcass. This section included a variety of analyses. When the total carcass and carcass unit meat weights were evaluated, both age and sex differences were found to exist between the bison in this sample. The results of the analyses suggest that there is more meat in adult than immature animals, and more meat in adult males than females. Analysis of the relationship between meat weight and carcass weight, however, showed that meat weight is distributed differently in the carcasses of males and females, and between immature and mature bison. As in cattle and some other ungulate species, females carry a greater proportion of carcass weight in the hindlimb than males, while the males carry a larger proportion than females in the forelimb. Immature

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bison (represented by the yearling male, FYM) have more of their total meat weight in the limbs than do adult bison. In all four bison, regardless of age or sex, most of the meat weight in the carcass is found in the axial skeleton, followed by the hindlimb, and the forelimb.

More specific locations of age- and sex-influenced differences in meat weight distributions were identified by examining differences in percentages that carcass unit meat weights represented of total meat weight in each bison. Age differences were most evident in the weights of the humerus, cervical vertebrae, ribs, sternebrae, and femur-patella units, but the magnitude of these meat weight distribution differences often were not large enough to affect the ranking of carcass units for meat weight production. Neither the ribs nor the femur-patella unit showed any change in weight rank between the immature bison, FYM, and SAM. The sternebrae unit is proportionately larger in the young animal and the neck and humerus are both larger in the older male. The rank position changes in both cases, however, are relatively minor.

Sex differences in meat weight distributions in the bison carcasses were evident in the cervical vertebrae and scapula units (the units are proportionately larger in SAM than in SAF), and in the lumbar vertebrae, sacrum-pelvis, and femur-patella units (the units are proportionately larger in SAF than in SAM). These carcass unit differences were most marked in the larger size of the cervical unit in the male, and resulted in the most pronounced change in unit rank for production of meat between this male and female. The other rank changes noted in the units of SAM and SAF, were minor.

The large size of the neck in the older female, FAF, was matched in proportion of total meat weight and in rank of units for meat production to

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that seen in the male, SAM, which may call the observation of sex-linked differences in this unit into question. The sternebrae in the older female, FAF, was also much higher in rank than in either of the other two adult bison, and together with the change in the rank of the neck may indicate two possible differences associated with either old age, poorer condition, or both.

Meat weight distribution differences in the bison carcasses of the male, SAM, and the female, SAF, were also studied at the level of the individual muscle, and in muscle groups defined by Butterfield and Berg (1976). These data indicated that a limited number of specific muscles were generally responsible when sex-linked differences in muscle group weights were identified. Although the muscle groups differed somewhat from the carcass unit divisions outlined above, similar differences between the sexes were identified.

The third major topic discussed in this chapter was the production and distribution of intramuscular fat. The percent fat per unit weight in meat samples and the weight of intramuscular fat in each animal and in each carcass unit were discussed. The meat fat content was lowest in the immature male, FYM. It was also low in the male, SAM, compared to the females, though this might be due to age differences. Percent meat fat was mixed between the two females, and suggests earlier mobility of fat in the meat of the forelimb, neck, thoracic vertebrae, and ribs unit, than in the hindlimb or hindquarter axial units.

The relationship between intramuscular fat and its meat package was evident in the differences in meat fat weights. Low meat weights coupled with low percent fat values kept the fat weights in FYM the lowest of the four bison. Greater muscle mass in the male, SAM, sometimes worked to

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offset smaller percent fat content and lead to higher fat weights by carcass unit. The effect of large muscle mass is expected to be larger yet in male bison that are fully mature. In those males, it is anticipated that intramuscular fat weight might be greater than in adult females. In this study, with a four year old male used in the animal sex comparison, the cervical vertebrae, femur-patella, and radius-ulna units produced more fat in the male than in the females due to greater muscle mass.

The distribution of intramuscular fat in the bison carcass differed somewhat for the immature animal, FYM, than for the adults (more of total intramuscular fat was found in the ribs and sternebrae units, less in the femur-patella unit), and for the male, SAM, than the females (more of total intramuscular fat was found in the cervical vertebrae unit and less in the thoracic vertebrae unit). The effects these distribution differences have on the rank of carcass units for the production of intramuscular fat, however, are variable, but are most marked in the comparison of the immature male, FYM, and the adult male, SAM. The changes in carcass unit rank were most pronounced in the cervical vertebrae, lumbar vertebrae, and the femur-patella units, which increase in rank in the older, more mature male. The sternebrae and scapula units drop in rank in response to the rise of these three units.

Very few rank changes are seen in the order of carcass units in the production of intramuscular fat in males compared to females. Where rank order changes, it is by one position only. The differences seen in the distributions are reflected in the switching of the rank order of the cervical and thoracic vertebrae units in the male, SAM, and the female, SAF.

Greater differences were seen in the rank order of carcass units for intramuscular fat production in the two females, possibly indicating

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condition- or age-related differences in fat weight distributions. In the older female, proportionately more intramuscular fat was produced in the scapula unit and less in the femur-patella unit than in the younger, better conditioned female.

The fourth topic discussed in this chapter was the relationship between hunting strategies and the ranking of carcass units for selection. Unlike other carcass resources previously discussed, intramuscular fat is associated with a second resource, meat protein. Depending upon whether one is trying to (1) maximize fat return, regardless of the amount of associated protein, or (2) minimize the amount of associated protein during fat recovery, the criteria used to rank carcass units changes somewhat. Using the first strategy, where the amount of associated meat is less critical, the rank order based upon meat fat weight provides the best information for carcass unit selection. In the second strategy, where the ratio of protein to fat weight is critical because protein procurement must be minimized, the rank based upon the inverse order of that ratio, provides the best information for carcass unit selection. Depending upon which strategy is used, the rank order of carcass units changes. This rank change is minor except in the caudal vertebrae and femur-patella units. In the protein minimizing strategy, the caudal vertebrae unit is ranked high and the femur-patella unit is ranked low. In the strategy where the level of protein intake is less critical, the femur-patella is ranked high and the caudal vertebrae unit is ranked low. The ribs and thoracic vertebrae units are ranked high regardless of the strategy applied, if intramuscular fat is the primary resource sought. This differs somewhat from the rank order suggested when meat (muscle plus intramuscular fat) is the primary target, regardless of associated fat weight. Under those conditions, the femur-

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patella moves to the top of the rank ahead of the ribs and thoracic vertebrae units, from a middle or lower ranking position. Other changes in rank order are relatively minor.

The fifth, and final topic of this chapter, was a discussion of variability in the weights of organ meat and organ meat fat. The four organs studied included the heart, liver, kidneys, and tongue. As with other resources, the weights of the organs themselves were smallest in the immature male, FYM, indicating the effects of age upon body size and its associated carcass products. In the adult bison, the larger body size of the male, SAM, than the females, appears to account for larger organ weights or the suggestion of larger weights in older males, except in the liver.

Unlike the other organs whose size appears to be dictated by body size, the liver is much more variable in weight, and in the proportion it represents of carcass weight. Neither age nor sex could be successfully used, with this sample of bison, to explain the differences in liver size seen between these animals.

The fat content of the organs was variable, both between organs and between animals. Unlike carcass meat, where immature age dictated low fat content, the fat content of the organs is variable between the immature male, FYM, and the older male, SAM. Sex differences in fat content are not clear either, but are variable with some organs having higher fat content in the male, and others in the females.

The tongue and heart, in each animal, had the highest fat content values, usually followed by the kidneys and the liver. The liver showed a marked difference in fat content between the female, FAF, and the other three bison. The higher fat content in that animal may be indicative of the mobilization of fat to supply energy needs, as the liver is one of the

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primary sites for metabolizing fat. The high fat content in this organ, together with the generally high levels in the other organs, but especially in the tongue, may provide an explanation for the often reported, early consumption of these organs following a kill. Whether this preference is related to problems of spoilage, the desire for meat with high fat content, or some other factor is unclear. Speth (1983, 1987, 1988, 1989), however, has argued that fat can become a highly prized commodity when caloric intake is low and carbohydrates are unavailable.

At a hunting site, one might expect that organs would be used first from adult animals and then from immature animals, if maximum fat weight procurement was the goal. This conclusion is based upon the fact that small organ size in immature animals offsets the potentially comparable fat content. When the amount of protein must be minimized, the organs of any of the animals are probably good sources of fat, due to their relatively high fat content. Perhaps with a larger sample, age or sex differences might become evident in organ fat content, but with the present sample, no clear differences are evident, though the females tend to have high fat content values. Until greater certainty can be found in the comparative fat contents of organs in bison of different age and sex, one might suspect that selection at a bison kill site would be variable. However, with access to other sources of fat at the kill (marrow and subcutaneous fat particularly), one might expect that unless the animals were severely fat-depleted, there would be less likelihood of immediate problems with protein poisoning, and organ selection and consumption would probably focus on adults, and possibly females.

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CHAPTER 7. VARIABILITY IN CARCASS COMPOSITION, PART THREE: DISSECTIBLE AND TOTAL CARCASS FAT

Adipose tissue, or fat, like other carcass tissues, is not homogeneously distributed throughout the mammal carcass. It is found in concentrations, called depots, in particular parts of the body. The focus of this chapter is on differences in fat quantity and quality in the bison carcass, as demonstrated by the four TRNP bison, and as suggested by studies of other wildlife and domestic livestock. The discussion of fat quantity includes an examination of the variability in fat production (comparative weights), partitioning (division of carcass fat between the depots), and distribution (division of each depot fat between carcass units). The discussion of fat quality relies on a review of the lipid composition literature to formulate expectations for variability in bison, and how that would influence human selection and use of the bison carcass.

In this study of bison carcass composition, three fat depots were studied for variability in their relative production and distribution in the carcass, in addition to the previously described skeletal and intramuscular fat. These are the subcutaneous, intermuscular, and body cavity fat depots. In this study, subcutaneous fat is the adipose tissue found peripheral to the outer layer of muscles that lies beneath the skin. Some loss of subcutaneous fat during dehiding is probable, but care was taken in removing the hide in order to leave as much of the subcutaneous fat layer as possible. The second fat depot, intermuscular fat, is the dissectible carcass adipose tissue found between individual muscles, usually following

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the path of major blood vessels and nerves. Fat beneath the superficial cutaneous trunci muscle was included in this depot. The third fat depot includes the adipose tissue found within the body cavity including that located anterior to the diaphragm, immediately dorsal to the posterior end of the sternebrae, as well as that found around the kidney and lining the pelvic area of the carcass cavity. Other fat depots, not studied in this analysis, but available for use by prehistoric and historic hunters, include the mesenteric (intestinal) and omental (stomach) depots. The pericardial depot (fat found around the heart) was included in the analysis of the meat of that organ. Although skeletal and intramuscular fat were reported in Chapters 5 and 6, some discussion of these depots must be included in this chapter where the topic includes the relative importance of fat depots to total carcass weight or total carcass fat weight.

Quantitative Studies of Carcass Fat

A discussion of the quantity of fat in the bison carcass should include three aspects of its availabilty. First, how much fat does each animal produce? Second, how is fat partitioned into depots within the carcass? For example, how much of total fat weight is in the subcutaneous, rather than the other fat depots? Third, how is fat in each depot distributed in the carcass? For example, what proportion of subcutaneous fat is found with the thoracic vertebrae carcass unit? The distinction between partition and distributicn is important to later discussions and should be noted. In each of these three aspects of quantitative studies of carcass fat, the effects of age, sex, and animal condition are considered.

Before beginning this discussion, a point concerning the methods of fat weight measurement needs to be made. In many studies of differential

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partitioning and distribution of animal carcass fat, the weight of dissected adipose tissue has been assumed to correlate directly with fat weight. Jones et al. (1981), however, illustrate that there is not a one-to-one relationship between tissue weight and fat weight, and as expected, chemical fat weight is less than dissected tissue weight. In this study, chemical fat weight was determined by solvent extraction for depots discussed above (i.e., marrow fat, bone grease fat, intramuscular and organ fat). Although it would have been preferable to have chemical fat weights for the adipose tissue dissected as subcutaneous, intermuscular, and body cavity depots, time and budget constraints did not permit it. An alternative approach was used which more closely approximates fat weight than dissected tissue weight, but which must be considered less accurate than chemical fat weight. The method of fat recovery used in this study was to render the dissected adipose tissue by boiling the ground tissue in water and collecting the fat from the water surface. Much of the excess water collected with the fat was discarded after further separation by warming the fat to the melting point. Some excess water remains, but its weight is assumed to be less than that of the non-fat fraction in the original samples.

Fat Production

Table 7.1 presents the weights of fat recovered from seven depots in one half (or side) of each of the four bison carcasses, as well as the combined sums of these totals. In this and all future tables, total fat weight excludes the weight of omental and mesenteric fat, which were not included in this study.

Despite the larger carcass size of the male, SAM, total fat weight in the half carcass (11.0 kg) is less in this animal than in either female

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Table 7.1. Fat Depot Weights in the Half Carcass

Description	Fat Type[a]	FYM	SAM	SAF	FAF
A. Individual Depot Weights:					
subcutaneous fat weight (gm)[b]	R	306.4	966.9	2742.8	1766.6
intermuscular fat weight (gm)	R	2227.2	3405.9	4047.2	5187.7
body cavity fat weight (gm)	R	735.8	1141.4	1401.9	1276.8
intramuscular fat weight (gm)[c]	C	644.8	3508.0	4053.0	3668.4
marrow fat weight (gm)	C	385.5	618.1	514.1	451.8
bone grease fat weight (gm)	RC	312.6	596.9	988.7	778.6
combined organs fat weight (gm)	C	379.6	796.2	646.2	1203.7
B. Summary Weights and Proportions:					
total side fat weight (gm)[d]	-	4991.9	11033.4	14393.9	14333.6
carcass side weight (kg)	-	90.2	193.0	140.9	152.8
fat per unit carcass weight (gm/kg)	-	55.3	57.2	102.2	93.8
percent carcass fat content	-	5.5	5.7	10.2	9.4

[a] Fat Type: Rendered (R), Chemical Extraction (C), Chemical Extraction of Rendered fat (RC).

[b] Depot totals exclude the weight of subcutaneous fat from the SKWOT unit.

[c] Depot totals exclude the weight of intramuscular fat from the SKWOT unit.

[d] Total side fat weight excludes the omental and mesenteric depots.

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(14.4 and 14.3 kg fat in SAF and FAF, respectively). This results in a proportionately leaner carcass in the male (approximately six percent fat) than in the females (between 9 and 10 percent fat). The weight of fat in this male, however, represents a substantial increase over that seen in the yearling male, FYM (5.0 kg), but does not represent a large difference in the proportion of fat weight to carcass weight (5.5 versus 5.7 percent for FYM and SAM, respectively).

Given that SAM has not yet achieved full maturity, additional growth and fattening might eventually result in greater fat weights in fully adult males than in adult females (and conceivably more comparable values of carcass fat content). This is suggested by the work of several researchers. Wagner et al. (1988:606) indicate that, in cattle, total fat (as well as protein) is dependent upon the size of the animal. Jones et al. (1980a:846) concur, noting that at equal physiological maturity, bulls are larger than cows and have significantly greater fat weight in all depots. Jones (1982:382) finds the same relationship in sheep, although the difference is smaller. One may conclude that, other things being equal, at full maturity, given the larger body size of male bison over females, that total fat weight should be larger in bulls than in cows. At four years of age, male bison (as represented by SAM) appear to have not yet reached the point of maturity that yields greater fat weight in bulls over mature females.

Despite the potentially larger fat production of fully mature bull bison, historic and prehistoric hunters often focused their efforts on cow/calf groups, although seasonal differences in the difficulty of handling bison sometimes made bull groups a preferred target (Speth 1983). This is understandable given the larger herd sizes and the fact that cows reach full maturity at a younger age, and therefore, fatten earlier. Focusing efforts

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on small bull groups might yield some fat bulls with large quantities of fat, but a more dependable approach would be to focus on the more abundant, but smaller females.

If a cow/calf group is taken, fully mature females should be selected before immature animals of either sex, when maximum fat recovery is necessary. The yearling, FYM, produces only 35 percent of the fat weight of the females, SAF and FAF. Furthermore, if bison develop as cattle, one might expect that young adult females (two to three years old) have more fat than males of the same age, due to the earlier onset of the fattening stage in cows than in bulls. This would have to be verified in bison, although the liveweight growth curves presented in Chapter 2 suggest that maturity as meassured by liveweight is, in fact, achieved earlier in females than in males.

A selection strategy based on total animal fat production, however, ignores differences in fat quantity and quality between and within fat depots. It assumes that all fat is equally desirable, which might be true when hunters are suffering from sub-maintenance nutrition. It would not be the case during fall and early winter hunts when animals are in prime condition and other sources of human food energy (e.g., carbohydrates) are abundant. During such periods of time, one might expect that differences in fat partition, distribution, and quality would be important and would influence herd selection, as well as processing decisions after the kill.

Studies of Fat Partition

The way in which fat is partitioned in the carcass differs between species of mammals and with animal maturity. For example, Tyler (1987:215) reports that Svalbard reindeer (Rangifer tarandus) store 87 percent of their

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fat in the subcutaneous depot, whereas in cattle (and these four bison), the largest fat reserves are found in the intermuscular depot (Leat and Cox 1980:156). Animal maturity influences fat partitioning in that the development of a fat depot is related to the total fatness of the animal (e.g., see Leat 1977 and Wright and Russel 1984 for cattle, and Jones 1982 for sheep). In a review of partition and distribution studies in sheep, pigs, and cattle, Kempster (1981) concluded that when animal carcasses are studied at equal total side fat weight in order to compare animals of similar maturity, there are only minor sex differences in fat partitioning. Jones et al. (1980a) found no sex differences in fat partitioning measured at like maturity between the sexes in their studies of cattle.

The lack of sex differences in partitioning, when animals are compared at equal fatness, does not mean that males and females are identical in the growth and development of carcass fat. At equal muscle plus bone weight (which in sexually dimorphic species compares young males with older females), females are fatter than males (Mukhoty and Berg 1971:226). Leat and Cox (1980:162) indicate that the differences seen between males and females are due, in part, to differences in the timing of the onset of the fattening phase. Females generally begin fattening at an earlier age and lighter body weights than males. Mukhoty and Berg (1971:224), however, indicate that there is not a corresponding difference in the rate of fattening--that is, once the fattening stage begins, fat accumulates at similar rates in males and females.

Based upon these assessments in other animal species, it is suggested that any differences seen in the partitioning of fat in the four TRNP bison are probably due to either differences in the stage of maturity, or to differences in the nutritional conditions of the animals. The immaturity of

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the male, FYM, as well as the lack of full maturity in the male, SAM, may be expected to result in a different partitioning of depot fats relative to total fat weight in these young animals compared to the fully mature females.

After bison have reached full maturity, differences in fat partitioning must reflect condition differences, if they fall outside the normal range of variability. Given the older age of the female, FAF, one might expect her carcass to be fatter than that of SAF, because animals tend to accumulate fat with age due to the greater efficiency of supporting a larger percentage of body weight as fat than as muscle tissue. The older animal, FAF, however, was not as fat as the younger female, SAF (Table 7.1), suggesting that SAF is in better condition than FAF, especially given the younger animal's slightly smaller size. Given this difference, one might expect some difference in fat partitioning between these two animals, if the fat weights do not represent a normal range of variability.

Truscott et al. (1983:268) showed that when cancelling the effects of age and stage of development in steers, there were no differences in fat partitioning associated with differences in animal fatness. Animals of different sizes should have similarly partitioned fat, therefore. However, this does not indicate that partitioning is the same under conditions of sub-maintenance nutrition and weight loss. One might expect still that the poorer condition of the older female should result in differences in depot fat partitioning, specifically in a reduction of the subcutaneous depot fat weight.

The nature of the age and condition differences expected between these four bison are dictated by the order of fat depot development. As in other body tissues, the order of development (determined by differences in growth

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rates) is opposite the order in which fat is mobilized (again reflecting differences in rates) to supply energy needs during submaintenance nutrition. Examination of the order of development and mobilization should clarify the relationship between these bison in terms of their maturity and condition.

Development and Mobilization of Fat Depots

The accepted order of fat depot growth and development, and the order of mobilization during periods of submaintenance nutrition has changed in recent years with carcass composition studies that examined the internal fat deposits in more detail. The previously accepted order of relative development was intra-abdominal, intermuscular, subcutaneous, and intramuscular (Truscott et al. 1983:265). Where it was previously thought that all internal fat depots were earlier developing than the subcutaneous fat depot, it is now known that subcutaneous fat may develop earlier than some internal depots (Butler-Hogg and Wood 1982:260). According to Truscott et al. (1983:265) the mesenteric (intestinal) depot is relatively early developing, but the other intra-abdominal depots are late developing like the subcutaneous depot. In Friesan cattle, Butler-Hogg and Wood (1982) report that the order of fat depot development is as follows: intermuscular, mesenteric (intestinal), perirenal-retroperitoneal (kidney and pelvic channel fat), subcutaneous, and omental (stomach fat). They also report that in a more extreme dairy breed, Jersey cattle, the subcutaneous depot develops earlier than the perirenal-retroperitoneal depot. Bison might be expected to be more like Friesan than Jersey cattle in order of fat development, given that they are not developed for milk production. When Hereford cattle (a beef production breed) are compared with dairy breeds,

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and all body cavity depots are lumped together, there is no difference between the breeds in the relative growth of the depots (Jones et al. 1980a:846) and the subcutaneous depot is later developing than the body cavity depot. For the purposes of this report, therefore, I assume the order of development recorded above for Friesan cattle applies to bison as well. The other depots not included above, appear to be both early and late developing. According to Leat and Cox (1980:156), intramuscular fat is a late developing fat depot, and skeletal fat, including both medullary cavity bone marrow and cancellous tissue bone grease, is early developing.

The mobilization of fat to provide energy during submaintenance nutrition occurs in all fat depots, but the rate of loss differs between depots, being greatest in late developing depots and least in early developing depots, and thus, generally follows the inverse of the order of development. Adamczewski et al. (1987a:372) report this pattern in their study of caribou, noting that fat was lost most rapidly in late maturing depots, although there was no discrete sequence of mobilization. In a study of mature cows, Wright and Russel (1984:30) suggest that under nutritional restriction, the rate of fat mobilization of the intermuscular depot may change, starting out at a slower rate than total fat, but mobilizing at a faster rate once other, later developing depots have been heavily utilized as submaintenance nutrition continues. This implies that fat weight loss may occur in multiple depots simultaneously, and that fat mobilization is characterized by differential rates of loss, rather than the sequential mobilization and complete utilization of one depot fat, prior to the initial use of another.

The effect of this pattern is that early developing fats are generally preserved until late in the period of submaintenance nutrition, and late

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developing fats are utilized relatively early, although not exclusively. During submaintenance nutrition, therefore, one may expect that drops in fat weight should be seen first in the late developing depots (i.e., the intramuscular, omental, subcutaneous, and perirenal-retroperitoneal deposits), and later in the early developing depots (i.e., the mesenteric, intermuscular, and skeletal deposits).

Partition of Fat in Bison

In Table 7.2 the partitioning of fat between the seven depots analyzed in this study of bison carcass composition is presented. Given the assessment that sex differences should not be present, and if bison partition fat in a similar manner as livestock animals and wild game species, then the differences evident in these values must be due to age or condition differences. Comparing the two younger males with the mature bison, SAF, it appears that the male, SAM, is not quite mature in the partition of fat in the carcass. The late developing subcutaneous fat depot, is only 8.8 percent of total fat weight, and the early developing bone marrow fat is still a relatively large percent of total fat weight compared to that seen in the older females (5.6 versus 3.6 and 3.2 percent). Similarly, the early developing intermuscular fat depot in SAM is a slightly higher percent of total fat weight than that seen in SAF (30.9 versus 28.1 percent).

The age differences evident between the male, SAM, and the females, are more accentuated in the immature male, FYM. The proportion of total fat in the early developing depots is higher than that seen in the older male and in the females, and generally much lower in the late developing depots than that seen in the older bison. The fat depots (subcutaneous, intermuscular,

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Table 7.2. Fat Partition--Depot Fat Weight as a Percent of Total Side Fat Weight[a]

Depot Description	Percent of Total Side Fat Weight by Animal			
	FYM	SAM	SAF	FAF
subcutaneous fat	6.1	8.8	19.1	12.3
intermuscular fat	44.6	30.9	28.1	36.2
body cavity fat	14.7	10.3	9.7	8.9
intramuscular fat	12.9	31.8	28.2	25.6
marrow fat	7.7	5.6	3.6	3.2
bone grease fat	6.3	5.4	6.9	5.4
combined organs fat	7.6	7.2	4.5	8.4

[a] Total fat weight excludes the omental and mesenteric depots.

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cavity, marrow, and organ meat fat) that are higher proportions of total fat weight in the young male bison, FYM and SAM, than in the females are early developing depots. The older females had higher percentages of fat in the subcutaneous and bone grease fat depots. The latter should be an early developing depot, but perhaps is later developing due to the greater need for hemopoietic function. The intramuscular depot is proportionately largest in the male, SAM, but is smaller in the yearling, FYM, compared to the females. If sex differences do not exist in fat partitioning, then the magnitude of differences between SAM and the females must be insignificant.

Comparison of fat partitioning between the two females (Table 7.2) suggests that condition differences do exist between these animals, but the pattern of observed differences does not strictly follow the expectations given the general rule of depot growth and fat mobilization. The relative proportions of subcutaneous fat to total fat weight do behave as expected. The subcutaneous fat depot is 12.3 percent of total fat in the older female, FAF, thought to be in poorer condition, whereas, in the younger female, SAF, this depot represents 19.1 percent of total fat weight. Leat and Cox (1980:156) indicate that the normal ratio of subcutaneous to intermuscular fat, in cattle, is 0.6. The ratios for the two females, SAF and FAF, are 0.68 and 0.34. Assuming that cattle and bison have similar ratios of fat deposition in these depots, this suggests that the female, FAF, is in poor condition as previously suggested, and the female, SAF, is in good condition, and may be in slightly better than normal condition considering the magnitude of the ratio and the fact that she was shot in April. This ratio in the two younger males was much smaller, but the differences there, are attributed to age, rather than condition effects.

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The high percentage of fat in the intermuscular depot of FAF (Table 7.2) might be expected, given its early development and the expectation that it would be used later in the mobilization of fat. This difference may not be significant, however, given the relationship of SAM, FYM and the females in the relative proportion of this depot to total fat weight. The comparable, or slightly lower percentages of the marrow fat and bone grease fat weight compared to the values seen in the female, SAF, are somewhat unexpected. Higher values were expected given the depletion of other depots. An examination of total fat weights and the point at which skeletal fat is mobilized, may clarify this relationship.

Total fat weight (excluding mesenteric and omental fat depots) in this older female, FAF, is 9.4 percent of non-standard carcass weight (including head, tail, and shanks), compared to 10.2 percent for the younger female (Table 7.1). If omental and mesenteric fat were included, these percentages would be somewhat higher. Wright and Russel (1984:29) indicate that in mature cows, omental fat is approximately two percent of total fat weight in fat cows, and five to 10 percent in thin cows. Normal percent fat in cattle varies with breed, but was reported by Butler-Hogg and Wood (1982:255) in Friesian and Jersey steers, aged 507 days, to be 19.8 and 21.4 percent of liveweight, respectively, although the difference in their sample was not statistically significant. Wagner et al. (1988) report that the fat content of non-pregnant, non-lactating Hereford cows, determined as a percent of hot carcass weight, was 12.7 ± 5.83 percent (these values exclude the contribution of skeletal fat to total fat). Fat content figured as a percent of hot carcass weight should be higher than when figured as a percent of animal liveweight. Ledger (1968:307), however, found that carcass fat content in African ungulates was normally less than five

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percent, and Tyler (1987:205), in summarizing the work of others on this subject, found that temperate/sub-arctic species generally fall between 3.5 and 9.5 percent fat (relative to liveweight), whereas domestic cattle and sheep species range from 19.8 (c.f., Butler-Hogg and Wood 1982) to 45.5 percent fat. This indicates that a discrepency exists between domestic and wild game animals in normal fat content, with wild animals having smaller total fat weights and percent body fat than domestic animals that commonly are protected against overwintering food shortages. The bison in the current study show comparable fat content, as a percent of carcass weight (5.5, 5.7, 9.4, and 10.2 percent for FYM, SAM, FAF, and SAF) as Ledger's African ungulate sample.

Wright and Russel (1984) indicate that in mature female cattle, skeletal fat is not mobilized until total fat in the carcass falls below 10 percent. One might suspect that skeletal fat is mobilized at lower total fat levels in wild game and in bison, given their lower total fat content. As evidence of this, one may note that the skeletal fat in FAF appears to have mobilized. The fat content of the marrow of FAF was not excessively low, but did reflect the pattern of proximal to distal bone marrow mobilization expected for an animal in suboptimum condition. This suggests that perhaps some minor mobilization of fat from the skeletal depots might account for the slightly lower proportions the skeletal depots represent of total fat in FAF compared to SAF.

Alternatively one might suggest that FAF is in good condition and SAF is just in better condition, but this hypothesis does not fit the data. If this were true, one would expect the ratio of subcutaneous to intermuscular fat in the two animals to be comparable, because partitioning of fat does not change in mature animals that are healthy and get fatter with age--that

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is, fat is added to all the depots when animals gain under these circumstances, and not differentially (Truscott et al. 1983:268). The conclusion above, that FAF is in declining condition, and that SAF is in good condition (possibly better than one would expect given the spring season kill) appears to offer the best explanation of the available data.

The importance of these partition differences will not be evident until differences in fatty acid composition and the proportions of saturated and unsaturated fatty acids are considered. These differences, however, should be important only when total fat recovery is not critical and hunter diet is of high enough quality that selection decisions concerning fat depots might be made. During periods when fat recovery is critical, the relative quality of the fat depots should be irrelevant, because there is no evidence to indicate that the caloric value of the depots change with changes in fatty acid composition. Rather, it is differences in fat softness, and possibly flavor that appear to influence fat use when conditions permit differential recovery and use.

Studies of Fat Distribution

A study (Truscott et al. 1983) of differences in fat partitioning and distribution in steer carcasses demonstrated that major differences may occur in partitioning between breeds while only minor differences are present in distribution. This led Truscott et al. (1983:268) to conclude that the distribution of fat in the carcass is not controlled by the same factors that control its partition between depots. They did not indicate what factors control each aspect of fat quantities in the steer carcass, but for the purposes of the current discussion it is sufficient to know that the occurrence or absence of an age, sex, or condition difference in

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partitioning does not necessarily indicate that a like difference will be found in distribution.

Whereas, it is accepted that the partitioning of fat into depots is not affected by animal sex, researchers disagree concerning the effect of sex on the distribution of depot fat in the different parts of the carcass. Jones et al. (1980b:854) found distribution differences due to sex in cattle, but considered the differences to be relatively minor. In contrast, in an evaluation of sheep carcass composition, Jones (1982:384) indicates that distribution is unaffected by animal sex. The question remains, therefore, whether sex differences do occur in fat weight distributions in livestock and whether they may thus be expected to occur in bison. Bison are much more closely related to cattle, so one might anticipate that sex differences occur in bison fat distribution as reported by Jones et al. (1980b) for cattle.

It appears, however, that the sex differences reported by Jones et al. (1980b:852-854) in cattle, may be related to differences in animal maturity. They report that, at equal total side (i.e., half carcass) fat weight, heifers have more subcutaneous fat in the loin, ribs and flank than bulls, and bulls have more intermuscular fat in the chuck and round than heifers. The problem with this assessment, however, is that in many species with strong sexual dimorphism, males are larger than females and have larger fat weights at the same level of fattening. Therefore, at equal fat weight, the males should be at an earlier stage of maturity in the fattening process than the females, and the sex differences observed may be attributable to age or maturity differences, and not due to sex differences. If this is true, the supposed sex differences should be consistent with changes associated with growth and development.

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Jones et al. (1980a:847) report that intermuscular fat accumulates more rapidly in the forequarter compared to the hindquarter, and Leat and Cox (1980:163) indicate that the shift to fat development of the hindquarter occurs earlier in females than in males. At equal total side fat weight, therefore, males should be at an earlier stage of maturity than the females and the development of the hindquarter should be relatively smaller compared to the development of the forequarter in the bulls. It is not surprising, therefore, that males appear fatter in the chuck and and round (another moderately early developing location according to Butler-Hogg and Wood 1982:258) and females appear fatter in the loin and rib (late developing locations (Butler-Hogg and Wood 1982:258, Jones 1982:383).

Like sheep, therefore, it does not appear that the occurrence of sex differences in fat distribution has been unquestionably demonstrated in cattle. To evaluate sex differences in fat distribution at comparable maturity in animals that demonstrate dimorphism, the animals must be evaluated at equal relative fatness, not equal side fat weight (Kempster 1981:87). In the meat industry, differences in fat partitioning and distribution between sexes is often compared at equal fat weight because these measures are compared with estimates of total fatness used to evaluate carcass grade. The meat industry is interested in whether, at equal depth of back fat thickness, cows and bulls have similar carcass fatness. These studies, however, do not indicate whether at equal maturity, fat partitioning and distribution differ. Jones et al. (1980a) demonstrated that fat partitioning does not differ between the sexes when measured at equal maturity, but it is unclear whether fat distribution follows this pattern also. Truscott et al. (1983:268) note that partitioning and distribution appear to be controlled by different factors, so one cannot

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assume that the absence of sex differences in partitioning extends to distribution as well. It remains unclear, therefore, whether sex differences in fat distribution should be expected in bison, based upon cattle studies.

In addition to possible differences due to the age of the animals studied, animal condition must be considered as a potential factor influencing fat distribution in the bison carcass. Livestock studies of fat distribution that consider the effects of submaintenance diets are non-existent. Patterson et al. (1985) suggest that the distribution of fat in the male cattle carcass is not consistently affected by low versus high energy diet when measured at constant side subcutaneous fat weight--that is, the proportion of a fat depot found in a particular carcass unit remains relatively constant when growth is slowed by lowering the energy intake level. This, however, does not indicate what would occur when energy intake is reduced to a submaintenance level. If fat depletion operates in a manner similar to other body tissues, where the rate of depletion is most rapid in locations that are late to develop, and relatively slow in locations that develop early, one might expect that fat should be depleted more rapidly in the mid-carcass region, and more slowly in the medial and distal appendicular portions of the carcass, as well as in the skull.

Distribution of Fat in the Bison Carcass

The distribution of skeletal and intramuscular fat depots were discussed above in Chapters 5 and 6. Therefore, this discussion of fat distribution is limited to the subcutaneous, intermuscular, and body cavity depots, but also includes a discussion of the distribution of the combined weight of all fat depots analyzed. The distribution of fat is determined

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here by dividing the carcass unit fat weight by the total fat weight for that depot (e.g., by dividing the subcutaneous fat weight in the femur-patella carcass unit by the total weight of all subcutaneous fat), rather than dividing by total side fat weight. The exception to this is for the total fat weight distribution, where the combined totals in each carcass unit are divided by the total for all depots. These distribution data indicate which carcass unit provides the most fat for each of these three depots and for total recoverable fat (excluding omental and mesenteric fat).

Subcutaneous Fat Distribution

Table 7.3 presents the weights of rendered subcutaneous fat in each carcass unit and the proportions these weights represent of total subcutaneous fat weight. Butler-Hogg and Wood (1982:256) indicate that, in cattle, subcutaneous fat growth follows the same pattern as muscle development--in the appendicular skeleton, beginning in the distal portions of the legs and moving proximally, and in the axial part of the body, beginning at the head and rump, and culminating in the dorsal forequarter. They suggest that there is some debate over whether subcutaneous fat develops latest in the dorsal or ventral part of the thorax. Comparison of the thoracic and sternebrae units in these four animals (Table 7.3) indicates that although the dorsal unit (thoracic vertebrae unit) decreases as a percent of total depot fat with age, suggesting that it is early developing, it is farther from achieving the adult proportions of depot weight than is the sternebrae.

Age differences in subcutaneous fat weight distribution are suggested for the femur-patella (FEMP), humerus (HUM), sternebrae (STER), ribs, caudal vertebrae (CAUD), sacrum-pelvis (SPEL), lumbar (LUMB) and thoracic vertebrae

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Table 7.3. Weight and Distribution of Rendered Subcutaneous Fat in the Half Carcass

Carcass Unit	Fat Weight (gm)				Unit Weight as a Percent of Depot Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
CERV	13.9	48.7	122.9	70.6	4.5	5.0	5.5	4.0
THOR	180.9	504.2	796.3	558.9	59.0	52.1	35.5	31.6
LUMB	18.8	91.2	219.4	276.5	6.1	9.4	9.8	15.7
SPEL	3.7	0.0	144.9	95.0	1.2	0.0	6.5	5.4
CAUD	2.2	10.0	39.1	38.1	0.7	1.0	1.7	2.2
RIBS	31.5	94.3	404.2	184.5	10.3	9.8	18.0	10.4
STER	29.9	46.9	282.5	267.9	9.8	4.9	12.6	15.2
SCAP	17.4	0.0	T	46.7	5.7	0.0	T	2.6
HUM	0.0	0.0	115.1	19.3	0.0	0.0	5.1	1.1
RUL	0.0	0.0	0.0	5.8	0.0	0.0	0.0	0.3
CARP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MTC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FEMP	8.1	168.2	614.9	177.6	2.6	17.4	27.4	10.1
TIB	0.0	3.4	3.5	25.7	0.0	0.4	0.2	1.5
TARS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MTT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PPHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL[a]	306.4	966.9	2742.8	1766.6				

[a] Subcutaneous fat from the SKWOT unit was not separated from the intermuscular depot.

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(THOR) units. All of these, but the thoracic unit, appear to increase in proportion of total subcutaneous fat weight with age. The thoracic vertebrae unit shows a major decrease in proportion of total depot fat weight with age, dropping from a maximum 59 percent in FYM, to 31.6 percent in FAF.

These data also illustrate that fat development is not homogeneous throughout the carcass. The femur-patella (FEMP) unit in FYM is poorly developed, but in SAM is closer to the percent of total depot fat seen in the well-conditioned female, SAF, than to FYM. Conversely, the difference between the two males in the percent depot fat in the thoracic (THOR) unit, is much smaller than between SAM and the females. Apparently, the femur-patella (FEMP) unit develops earlier to adult proportions than does the thoracic unit, and SAM may be considered to be closer to maturity in subcutaneous fat development.

Sex differences in subcutaneous fat distribution are suggested for the carcass units of SAM whose values fall outside the range of distribution values determined for FYM and SAF. Other units may vary due to sex, but could not be distinguished from age differences in the analysis, given the small sample size. Carcass parts that may have smaller percentages of total subcutaneous fat weight in males than in females include the ribs and sternebrae (STER). A major difference is evident in the proportions of the total subcutaneous fat in the thoracic (THOR) unit, but this might be a reflection of age, rather than sex differences.

Condition differences in subcutaneous fat weight distribution are suggested for the following carcass units (comparing FAF with SAF, FYM, and SAM): the femur-patella (FEMP), ribs, sacrum-pelvis (SPEL), lumbar (LUMB), thoracic (THOR), and possibly cervical vertebrae (CERV) units. With poorer

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condition, all of these but the lumbar vertebrae unit decrease as a proportion of depot fat weight.

The significance of the age, sex and condition differences cannot be evaluated for such a small sample. Whether the magnitude of differences seen here might affect hunter selection decisions, however, may be considered by examining whether the distribution differences are of a large enough magnitude to change the rank order of carcass units for production of subcutaneous fat, and determining whether these units change in location within the rank orders enough that it might affect their use.

Rank Order Differences in Subcutaneous Fat Distribution. The occurrence of age, sex and possibly condition differences in subcutaneous fat weight distribution may be immaterial unless they affect carcass unit rank for fat production and are of a large enough magnitude to be noted by the people selecting animals and carcass units for further processing. In Figure 7.1, the carcass units of each animal are arranged in decreasing order of subcutaneous fat production. The weights of the unit subcutaneous fat are also listed. These weight comparisons help to indicate where the existence of rank differences may, or may not be particularly meaningful, where weights of adjacent units are similar. Clearly, this is not a measure of statistical significance, as even small differences in weight have the potential to be significant. It is suggested, however, that small differences may be beyond the levels of human perception.

Age differences in subcutaneous fat distribution were observed above for the femur-patella (FEMP), humerus (HUM), sternebrae (STER), ribs, caudal vertebrae (CAUD), sacrum-pelvis (SPEL), lumbar (LUMB) and thoracic vertebrae (THOR) units. Of these, the femur-patella and sacrum-pelvis are the only units that differ in the magnitude of subcutaneous fat production to a large

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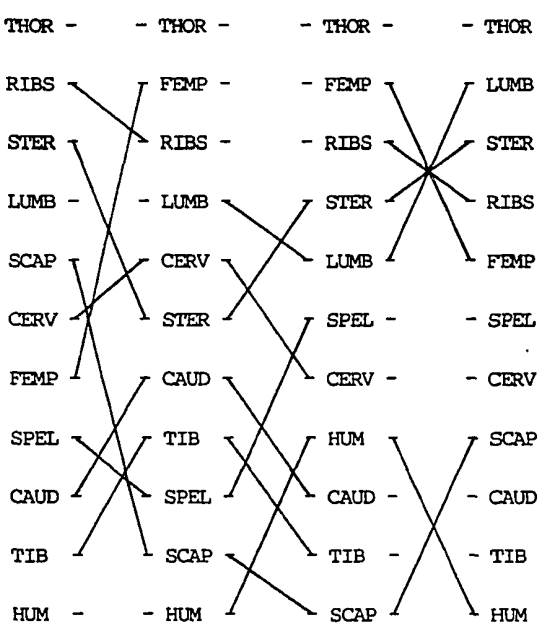
Figure 7.1. Rank Order of Carcass Units for Subcutaneous Fat Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
THOR	THOR	THOR	THOR	180.9	504.2	796.3	558.9
RIBS	FEMP	FEMP	LUMB	31.5	168.2	614.9	276.5
STER	RIBS	RIBS	STER	29.9	94.3	404.2	267.9
LUMB	LUMB	STER	RIBS	18.8	91.2	282.5	184.5
SCAP	CERV	LUMB	FEMP	17.4	48.7	219.4	177.6
CERV	STER	SPEL	SPEL	13.9	46.9	144.9	95.0
FEMP	CAUD	CERV	CERV	8.1	10.0	122.9	70.6
SPEL	TIB	HUM	SCAP	3.7	3.4	115.1	46.7
CAUD	SPEL	CAUD	CAUD	2.2	0.0	39.1	38.1
TIB	SCAP	TIB	TIB	0.0	0.0	3.5	25.7
HUM	HUM	SCAP	HUM	0.0	0.0	T	19.3
RUL	RUL	RUL	RUL	0.0	0.0	0.0	5.8
MTC	MTC	MTC	MTC	0.0	0.0	0.0	0.0
APHA	APHA	APHA	APHA	0.0	0.0	0.0	0.0
TARS	TARS	TARS	TARS	0.0	0.0	0.0	0.0
MTT	MTT	MTT	MTT	0.0	0.0	0.0	0.0
PPHA	PPHA	PPHA	PPHA	0.0	0.0	0.0	0.0

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enough extent that it substantially affects carcass unit rank order (Figure 7.1). As expected, the femur-patella unit shows this age difference only in the youngest animal, FYM, and not in SAM. The age difference in the sacrum-pelvis, conversely, applies to both of these younger animals.

Sex differences in subcutaneous fat distribution were suggested for the ribs and sternebrae (STER) units, and possibly for the thoracic (THOR) unit. Of these, only the sternebrae unit changes rank order between the male, SAM, and the female, SAF, being of higher rank (as expected) in the female.

Condition differences in subcutaneous fat distribution were suggested above for the femur-patella (FEMP), ribs, sacrum-pelvis (SPEL), lumbar (LUMB), thoracic (THOR) and possibly the cervical vertebrae (CERV) units. In Figure 7.1, the femur-patella (FEMP) and lumbar (LUMB) units change substantially in rank, with the lumbar (LUMB) unit increasing in rank with poorer condition, and the femur-patella (FEMP) unit dropping in rank. The ribs show a small, but conceivably significant difference in rank. The sacrum-pelvis (SPEL) and cervical vertebrae (CERV) unit do not change in rank order for subcutaneous fat production with the degree of condition change seen between SAF and FAF.

A substantial change in the rank of a carcass unit due to age or condition differences alone does not indicate that hunter selection decisions would be affected by this change. In the case of age differences, the femur-patella (FEMP) unit drops to near the bottom of the order for units that produce this fat in bison in FYM, compared to SAM and SAF. In this case, it does seem likely that the rank difference might affect selection decisions. This is also true for the sacrum-pelvis unit, but less so, as this unit in well-conditioned animals, is only moderately productive.

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The sex and condition differences in rank order are probably less important to selection decisions. The only unit showing a rank change due to sex (the sternebrae (STER)), is relatively highly ranked in both sexes. The three carcass units that show changes in rank order due to a change in condition (the femur-patella (FEMP), lumbar (LUMB), and ribs units), all ranked relatively high in the order for subcutaneous fat production. For example, although the femur-patella unit drops three positions to the fifth position in the order, this unit produces nearly twice as much fat as the next lower ranked unit, and this amounts to a difference of approximately 83 gm of fat.

Based on this analysis, it is suggested that age-, but probably not all sex- or condition-related fat distribution differences, influence selection decisions of carcass units for subcutaneous fat recovery. The location of subcutaneous fat beneath the skin and peripheral to the muscles, however, probably reduces the significance of the distribution and rank differences noted with respect to hunter practices of fat recovery. Ethnographic accounts often report that the subcutaneous fat layer was removed as one sheet, rather than being cut up and left with the associated carcass unit or muscle strip to be removed in later processing. The magnitude and ranking differences for carcass units for subcutaneous fat production have little meaning in animals where this fat is developed enough to allow sheet removal. In younger animals, or perhaps, in animals where nutritional condition has been poor for an extended period of time, and the back fat is not distributed as a continuous covering, these differences in distribution and carcass unit rank might be more meaningful. The presumed depletion of fat in the subcutaneous depot of FAF, however, representing a 36 percent decrease in fat weight compared to that seen in SAF, might not be large

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enough yet for this depot to be treated as part of the butchering units. In this older animal the subcutaneous fat layer was still well developed over the back and could have been removed as a unit.

Intermuscular Fat Distribution

Unlike subcutaneous fat, the distribution of intermuscular fat in the bison carcass demands a certain degree of processing for its recovery. Rather than occurring as a roughly continous layer overlying peripheral muscles, intermuscular fat is found in patches between muscles, dispersed throughout the carcass. Differences in distribution, therefore, are probably more relevant to hunter butchering decisions than they are in the subcutaneous depot.

In this section, intermuscular fat distribution is evaluated at two levels. First, the four TRNP bison are compared for the distribution of fat in the major segments of the carcass for comparison with cattle data. Second, the distribution of fat is compared between individuals at the smaller carcass unit level.

Distribution of Intermuscular Fat Between Major Carcass Divisions. The distribution of intermuscular fat between the major carcass divisions in the four TRNP bison appears to be similar to that reported by Jones et al. (1980a:847) in cattle. These authors reported that intermuscular fat accumulated more rapidly in the forequarter compared to the hindquarter. In the bison, the proportion of total intermuscular fat weight in the forequarter decreases with the advancing age of each animal (Table 7.4), although the differences are relatively small between the three youngest animals. The biggest difference in these proportions is seen between the youngest and oldest animals, but the values for the older female, FAF, might

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Table 7.4. Distribution of Intermuscular Fat Weight Between Major Divisions of the Carcass

Carcass Division	Fat Weight (gm)				Percent of Total Depot Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Forequarter[a]	1517.0	2301.4	2676.9	3076.1	68.1	67.6	66.1	59.3
Hindquarter[b]	710.2	1104.5	1370.3	2111.6	31.9	32.4	33.9	40.7
Side Total	2227.2	3405.9	4047.2	5187.7				

[a] Forequarter includes the following carcass units: SKWOT, CERV, THOR, RIBS, STER, and all foreleg units.

[b] Hindquarter includes the following carcass units: LUMB, SPEL, and all hindleg units.

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be attributable in part, to poorer condition. The differences between the other three animals are very small, but do show the expected pattern of development with growth. It is clear, however, that the magnitude of difference is not large enough to be influential in changing how major divisions of the carcass would be selected for fat recovery. In each animal, regardless of age, the forequarter was most productive. In these animals, condition did not change this rank either, but with a prolonged submaintenance diet, the possibility must be considered that the quarters may become more alike, or invert their positions for intermuscular fat production. The reduced percentage of total intermuscular fat found in the forequarter of the female, FAF, compared to SAF, suggests fat mobility may be more rapid in the forequarter than in the hindquarter. This is contrary to expectations given the usual relationship between development and mobility, and the report by Jones et al. (1980a:847) that intermuscular fat accumulates more rapidly in the forequarter than the hindquarter in cattle.

Distribution of Intermuscular Fat Between Carcass Units. Comparison of the distribution of intermuscular fat within the carcasses shows the possible influence of age, sex, and condition differences between the bison. The presence of age differences alone, however, does not indicate that they are of large enough magnitude to influence human selection decisions of carcass units. Consideration of the rank order of carcass units for production of fat is presented to address this issue.

Maturity and Intermuscular Fat Distribution. The intermuscular fat distribution data (Table 7.5) suggest that the immature bison, FYM, has appreciably larger percentages of total depot fat weight than the older bison, SAM and SAF, in the thoracic vertebrae (THOR), sacrum-pelvis (SPEL), scapula (SCAP), humerus (HUM), and radius-ulna (RULC). The carcass unit

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Table 7.5. Weight and Distribution of Rendered Intermuscular Fat in the Half Carcass

Carcass Unit	Fat Weight (gm)				Unit Weight as a Percent of Depot Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT[a]	81.4	235.4	238.5	311.9	3.7	6.9	5.9	6.0
CERV	297.6	594.0	657.4	680.6	13.4	17.4	16.2	13.1
THOR	464.5	524.9	642.3	723.3	20.9	15.4	15.9	13.9
LUMB	252.3	452.8	948.0	771.4	11.3	13.3	23.4	14.9
SPEL	146.7	178.6	157.4	248.4	6.6	5.2	3.9	4.8
RIBS	272.2	365.5	490.9	615.4	12.2	10.7	12.1	11.9
STER	199.2	486.3	553.5	484.9	8.9	14.3	13.7	9.3
SCAP	62.6	25.0[b]	0.0	40.1	2.8	0.7	0.0	0.8
HUM	103.3	67.6	79.0	133.1	4.6	2.0	2.0	2.6
RULC	31.5	0.0	9.3	54.3	1.4	0.0	0.2	1.0
MTC	2.2	0.0	0.1	13.1	0.1	0.0	T	0.3
APHA	2.5[b]	2.7	5.9	19.4	0.1	0.1	0.1	0.4
FEMP	270.9	411.3	239.6	917.6	12.2	12.1	5.9	17.7
TIB	18.5	49.3	16.9	107.2	0.8	1.4	0.4	2.1
TARS	3.2	10.0	5.2	23.6	0.1	0.3	0.1	0.5
MTT	16.7	0.9	0.6	29.8	0.7	T	T	5.7
PPHA	1.9	1.6	2.6	13.6	0.1	T	0.1	0.3
TOTAL	2227.2	3405.9	4047.2	5187.7				

[a] Weight for this unit includes fat associated with the eye orbit and the subcutaneous depot.

[b] Fat weight is estimated.

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contribution to total depot fat weight is smaller than that seen in SAM and SAF in the head (SKWOT), cervical (CERV), lumbar (LUMB), and sternebrae (STER) units. The lack of appreciable difference in the proportion of depot fat values between animals in the distal hindlimb elements suggests that fat development in these units do not change markedly in proportion to total depot fat weight with growth. This agrees with the pattern of development seen in other tissues of the body. The high percentage of total depot fat found in the sacrum-pelvis of the immature bison, FYM, conforms with the pattern of development that culminates in the mid-carcass area. Jones et al. (1980b:852) report that, in cattle, the impetus for growth is low in the limbs, neck and rump, and high in the mid-back, indicating early development in low impetus areas and late development in high impetus areas. The low values for the head (SKWOT) and cervical vertebrae (CERV) units do not follow this expected pattern of development. With age, therefore, one may expect that in bison, the proportion of intermuscular fat found in the thoracic vertebrae and sacrum-pelvis units should decrease as a proportin of the total as the proportion found in the lumbar and other late developing units increases.

Influence of Age on Rank Order of Intermuscular Fat Production. Figure 7.2 presents the intermuscular fat weight data for each carcass unit arranged in order of productivity. Examination of the rank order differences in carcass units for production of this resource, together with the comparisons of weights for adjacent units in each order, may indicate where the age differences noted above, might affect human perception of their importance.

Units showing differences in proportional weight between the yearling, FYM, and the older bison, SAM and SAF, that appear to substantially change

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Figure 7.2. Rank Order of Carcass Units for Intermuscular Fat Production

Unit Rank Order					Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	FYM	SAM	SAF	FAF
THOR	CERV	LUMB	FEMP	THOR	464.5	594.0	948.0	917.6
CERV	THOR	CERV	LUMB	CERV	297.6	524.9	657.4	771.4
RIBS	STER	THOR	THOR	RIBS	272.2	486.3	642.3	723.3
FEMP	LUMB	STER	CERV	FEMP	270.9	452.8	553.5	680.6
LUMB	FEMP	RIBS	RIBS	LUMB	252.3	411.3	490.9	615.4
STER	RIBS	FEMP	STER	STER	199.2	365.5	239.6	484.9
SPEL	SKWOT	SKWOT	SKWOT	SPEL	146.7	235.4	238.5	311.9
HUM	SPEL	SPEL	SPEL	HUM	103.3	178.6	157.4	248.4
SKWOT	HUM	HUM	HUM	SKWOT	81.4	67.6	79.0	133.1
SCAP	TIB	TIB	TIB	SCAP	62.6	49.3	16.9	107.2
RULC	SCAP	RULC	RULC	RULC	31.5	25.0[a]	9.3	54.3
TIB	TARS	APHA	SCAP	TIB	18.5	10.0	5.9	40.1
MTT	APHA	TARS	MTT	MTT	16.7	2.7	5.2	29.8
TARS	PPHA	PPHA	TARS	TARS	3.2	1.6	2.6	23.6
APHA	MTT	MTT	APHA	APHA	2.5	0.9	0.6	19.4
MTC	RULC	MTC	PPHA	MTC	2.2	0.0	0.1	13.6
PPHA	MTC	SCAP	MTC	PPHA	1.9	0.0	0.0	13.1

[a] estimated fat weight

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in rank, include the head (SKWOT) and sternebrae (STER) units. These units each change more than one rank position and if close in weight to an adjacent unit, the difference in rank remains a minimum of two positions. Although the proportion of total intermuscular fat weight in the ribs unit is similar in these animals, the magnitude of rank change in response to the changes in other units is quite large and equally important.

Other units also appear to be different in rank due to the age differences (Figure 7.2), but often these are limited to a difference of one rank position. Included in this group are the thoracic vertebrae (THOR), sacrum-pelvis (SPEL), scapula (SCAP), humerus (HUM), and the lumbar vertebrae (LUMB) units. Consistent differences were not evident in the radius-ulna (RULC) or cervical vertebrae (CERV) units. The rank difference of the lumbar vertebrae (LUMB) unit appears to be substantial between the two males, FYM and SAM, and the female, SAF.

Clearly, the difference in age between these bison are numerous. One might suspect, however, that unless the differences in carcass unit rank are large, and change a unit of high or medium rank to low rank, they might not have an effect on selection decisions. For example, although the difference seen in the thoracic vertebrae units might be significant and result in a rank change of two positions between FYM and SAF, it is a large fat producing unit in each of these animals, and therefore, may be expected to be used regardless of the change in rank (as long as a single individual carcass is being divided). Similarly, the rank changes in units that are at the lower end of the rank order and drop even further, or start at the bottom and rise to the lower levels of small producing units, probably would not affect selection decisions. Rather, it is the moderate or highly ranked unit that changes dramatically in rank that should affect selection practices.

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It appears that very few, if any, of the age-related differences in intermuscular fat distribution produce rank order changes that are potentially important to carcass unit selection decision. It is conceivable that the difference in the lumbar (LUMB) unit between FYM and SAF might be important, but even in FYM, this unit is relatively highly ranked. The difference in the head (SKWOT) unit might also influence selection. In FYM, this unit is ranked two positions below that seen in all three other bison, and it produces only 81 gm of fat. In the other bison, however, this unit produces 235.4 to 311.9 gm of intermuscular fat. It is possible that the magnitude of this difference would be substantial enough to influence human perceptions of the productivity of this unit in immmature animals.

Sex and Intermuscular Fat Distribution. Six carcass units appear to have appreciably different values for carcass unit fat production as a percent of total intermuscular fat production between the male, SAM, and the female, SAF (Table 7.5). Of these, the head (SKWOT), cervical vertebrae (CERV), sacrum-pelvis (SPEL), and femur-patella (FEMP) units are larger in the male than female, while the lumber vertebrae (LUMB) and ribs units are both smaller in the male. The lack of full maturity in the male, SAM, complicates the interpretations that can be made about these relationships. Comparison of the distribution values for SAM and SAF, with the immature bison, FYM, appear to suggest that the differences noted for the lumbar vertebrae (LUMB) and sacrum-pelvis (SPEL) units may be related to age, rather than sex. Sex differences, however, appear to be responsible for the differences noted in the head (SKWOT), cervical vertebrae (CERV) and ribs units, with males producing larger percentages of total intermuscular fat weight than females in the head and neck and smaller percentages in the

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ribs. The distribution difference of fat in the femur-patella units of these bison are difficult to interpret, and may represent an age- rather than sex-related difference.

Bison Sex and Rank Order of Intermuscular Fat Production. The largest rank order change of carcass units that produced substantial amounts of intermuscular fat in the TRNP bison, SAM and SAF, in Figure 7.2 was in the lumbar vertebrae (LUMB) unit. This difference is probably an age- rather than sex-related difference in fat distribution. None of the units in which sex-related distribution differences were noted (i.e., the head (SKWOT) and neck (CERV), ribs, and maybe the femur-patella (FEMP)), show substantial changes (i.e., more than one position) in rank. This suggests that the sex-related fat weight distribution differences probably are not of a large enough magnitude to influence priority of carcass unit selection in the processing of individual bull and cow carcasses.

Animal Condition and Intermuscular Fat Distribution. Comparison of the proportion of depot fat weight values from the older female, FAF, with those of the three younger bison, provides possible evidence of condition-related differences in fat distribution. As expected, given the assumption of poorer condition in FAF, the values noted for the female bison, SAF and FAF, are not always similar. When they differ, the values for the older female are more often like those of the younger males, FYM and/or SAM. The major exception to this pattern is in the thoracic vertebrae (THOR) unit, where the percent of depot fat weight is smallest in FAF (Table 7.5).

The carcass units showing possible differences between the two fully mature females in the distribution of intermuscular fat includes the cervical (CERV), thoracic (THOR), and lumbar vertebrae (LUMB), and the sternebrae (STER) units, all of which are a smaller percent of total depot

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fat weight in FAF. The sacrum-pelvis (SPEL), femur-patella (FEMP), and many limb units, as might be expected, contained proportionately more fat in the the older, poorer conditioned female, FAF, than in SAF. These data suggest that poor animal condition may be evident through differential distribution of intermuscular fat in the bison carcass with a greater proportion of intermuscular fat found in the limbs and sacrum-pelvis of animals in suboptimum condition. If the differences seen between these two females are representative of changes in distribution associated with differences in animal condition, then they suggest that depletion in this depot follows a pattern similar to the inverse of fat development.

Animal Condition and Rank Order of Intermuscular Fat Production. The largest apparent effect of the condition differences between FAF and SAF is in the higher rank position of the femur-patella unit in FAF (Figure 7.2). This change results from both an increase in its value in FAF, together with a drop in the value of the cervical, thoracic, lumbar and sternebrae units. This difference represents a large change, bringing this unit from a relatively moderate to a high rank. It is suspected that such a change would affect selection decisions.

It is interesting to note that in Figure 7.2 and Table 7.5 there is little difference between the intermuscular fat weights or rank positions between SAF and FAF for the major carcass units of the forelimb (the humerus (HUM) and radius-ulna (RULC)). This suggests that Binford's (1978) observation that the forequarters are depleted before the hindquarters in caribou, which also was evident in these bison in Table 7.4 in the comparison of forequarters and hindquarters, is probably the result of the reduced fat weights in the axial units of this division. As noted above, this is especially evident in the cervical (CERV), thoracic (THOR), and

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sternebrae (STER) units, in terms of intermuscular fat production, but in terms of its effect on the rank order of carcass units, the condition difference affects only the rank of the neck and sternebrae units (Figure 7.2). Both units are ranked lower in FAF.

Comparison of the rank order of carcass units for production of intermuscular fat indicates that although changes in fat distribution in the female FAF approached that of the younger males, in terms of the values in Table 7.5, the yearling, FYM, may be a better model for fat distribution than the female, SAF. This is illustrated in Figure 7.2. In this figure, the two females match best in carcass unit rank in the middle of the order, whereas, the older female, FAF, matches the young male, FYM, best in the lower third of the order. In the upper third of the rank order, both SAF and FYM differ somewhat from FAF. The major difference between the order for FYM and FAF is that the femur-patella (FEMP) and lumbar vertebrae (LUMB) units are ranked much higher in FAF. The other changes in order might be considered forced drops due to the rise of these units. The major difference between the two females, is in the higher rank of the femur-patella (FEMP) unit and the drop in the ranks of the neck (CERV) and sternebrae (STER) units in the older female, FAF. The remaining differences are small or occur in units which produce little intermuscular fat. In the comparison of rank orders for SAF and FAF three major carcass unit shift rank, while in the comparison of FAF with FYM only two units show major changes in rank. This suggests that the upper portion of the carcass unit rank order of FAF is best approximated by that of the young male. Given that the limb carcass units produce very little fat and the occurrence of variability between these units are of little consequence, and would do little to aid in carcass unit selection for recovery of intermuscular fat,

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it appears that it would be more useful to use the proportions of FYM as a model for FAF fat distribution. The biggest effect of such an approach would be that the importance of the femur-patella (FEMP) and lumbar (LUMB) units in FAF would be underestimated. Given that FAF still had more total intermuscular fat than SAF (despite the expectation that some fat loss had occurred), it might be expected that with continued reduction of the depot fat weight, the distribution of fat might eventually be approximated even more closely by the younger animal, FYM.

Comparison of Intermuscular and Subcutaneous Fat Distributions

Comparison of the rank order of carcass units for subcutaneous and intermuscular fat indicate that the same units are not necessarily similarly productive for both kinds of fat recovery. In all four bison, subcutaneous fat was most abundant in the thoracic vertebrae unit. Intermuscular fat distribution appears to be somewhat more variable. Both the thoracic and cervical vertebrae units ranked high in all four animals, although they were in the number one and two positions only in the two males. In the females, the lumbar vertebrae unit was higher ranked in both cases, and in the older female, FAF, the femur-patella unit was higher in the order as well. After these four units, the ribs and sternebrae units were the most productive carcass units for recovery of intermuscular fat.

Body Cavity Fat Distribution

The weights and relative distribution of fat from the body cavity, but associated with the carcass (i.e., excluding visceral depots), are listed in Table 7.6. In the four TRNP bison, only a small amount of cavity fat was found outside the lumbar-pelvic area. This fat was associated with the

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Table 7.6. Weight and Distribution of Rendered Body Cavity Fat in the Half Carcass

Carcass Unit	Fat Weight (gm)				Unit Weight as a Percent of Depot Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
LUMB	494.1	636.5	725.4	735.1	67.2	55.8	51.7	57.6
SPEL	190.4	327.1	527.7	379.0	25.9	28.7	37.6	29.7
STER	51.3	177.8	148.8	162.7	7.0	15.6	10.6	12.7
TOTAL	735.8	1141.4	1401.9	1276.8				
KKCF[a]	684.5	963.6	1253.1	1114.1	93.0	84.4	89.4	87.3

[a] KKCF (kidney knob and channel fat) is the combined fat weights of the LUMB and SPEL units.

sternebrae unit, located immediately anterior to the diaphragm, and in these bison accounted for only 7.0 to 15.6 percent of the total depot weight. No clear pattern of age, sex, or condition differences are evident from the mixed values of this part of the fat depot.

The body cavity fat from the combined lumbar and sacrum-pelvis units is equivalent to what is often referred to in the literature as the kidney-knob-channel-fat (KKCF), or as perirenal-retroperitoneal fat. In the bison, SAM, SAF, and FAF, the fat from these two units constituted from 84 to 89 percent of the carcass cavity fat, while in the immature bison, FYM, the KKCF fat represented a somewhat higher, 93 percent of the cavity total. The majority of this fat (ranging from 51 to 67 percent), in all four animals, is found in the lumbar unit, associated with the kidney.

Although there are small differences in the proportion of the total carcass cavity fat weight found in each carcass unit, these differences are relatively minor and do not change the rank of carcass units for fat production, regardless of the age, sex, and condition differences of these animals. In the two youngest bison, and in the oldest bison, FAF, in poor condition, it appears that the relative proportion of the weight of this depot fat found in the sacrum-pelvis (SPEL) unit is smaller than in SAF, who was in good, or better than normal condition. This difference may reflect age or sex differences between SAF and SAM, but probably reflects condition differences between SAF and FAF. The poor condition of FAF apparently has resulted in cavity fat distributions comparable to the male, SAM. The percent of total depot fat weight for the lumbar (LUMB) and sacrum-pelvis (SPEL) units in FAF are more like those of SAM than SAF.

These differences, however, should not affect hunter selection of carcass units for recovery of body cavity fat for two reasons. First, they

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do not affect the rank order of units for fat production. Second, and perhaps more importantly, as with subcutaneous fat, carcass cavity fat is not dispersed in body tissue requiring extra processing for its recovery, but is easily removed. One might expect that the KKCF and sternebrae unit cavity fat would be removed as two units during butchering, rather than being divided into smaller portions associated with meat units. This would be especially true under conditions where fat recovery is at a premium and the relative differences in fat softness do not reduce the desirability of fat from the internal, more saturated fat depots. Like subcutaneous fat, therefore, one might expect that use of the fat from this depot would vary little between different classes of animals, and would be controlled more by total fat weight of the depot, than by the minor differences in its distribution.

Total Fat Weight Distribution

Total fat weight distribution (Table 7.7, Figure 7.3) refers to the relative production in each carcass unit of the combined weights of the fat from the subcutaneous, intermuscular, intramuscular, body cavity, marrow fat, and bone grease fat depots. Total fat weight excludes omental, mesenteric, and organ fat weights. For the head (SKWOT) unit, it excludes all but the intermuscular fat weight, as mandible marrow, and intramuscular depots were not analyzed in some animals. In each bison, therefore, the weight and percent of total fat weight for the head unit is underestimated. The addition of the fat from these depots could conceivably increase the rank of the unit in the order of carcass unit fat production.

The data in Table 7.7 show that age, possibly sex, and animal condition all influence the distribution of total fat weight in the bison carcass. As

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Table 7.7. Weight and Distribution of Total Fat in the Half Carcass

Carcass Unit	Fat Weight (gm)				Unit Weight as a Percent of Total Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT[a]	81.4	235.4	238.5	311.9	1.8	2.3	1.7	2.4
CERV	399.1	1210.8	1186.4	1264.8	8.7	11.8	8.6	9.6
THOR	760.9	1540.0	2273.3	1899.7	16.5	15.0	16.5	14.5
LUMB	795.5	1468.5	2272.4	2220.9	17.2	14.3	16.5	16.9
SPEL	408.2	834.9	1233.9	1024.4	8.9	8.2	9.0	7.8
CAUD	6.1	13.9	54.7	56.6	0.1	0.1	0.4	0.4
RIBS	533.5	1469.4	2093.2	1667.1	11.6	14.4	15.2	12.7
STER	384.2	973.2	1259.9	1308.3	8.3	9.5	9.2	10.0
SCAP	125.3	223.4	199.3	348.4	2.7	2.2	1.4	2.7
HUM	214.1	416.1	653.9	467.1	4.6	4.1	4.8	3.6
RUL	129.0	152.3	204.6	197.5	2.8	1.5	1.5	1.5
CARP	14.8	5.4	10.7	3.4	0.3	0.1	0.1	T
MTC	39.0	36.8	48.8	59.9	0.8	0.4	0.4	0.5
APHA	19.1	14.3	35.5	52.6	0.4	0.1	0.3	0.4
FEMP	428.9	1259.5	1562.1	1712.6	9.3	12.3	11.4	13.0
TIB	158.2	282.5	290.7	359.5	3.4	2.8	2.1	2.7
TARS	34.2	35.6	42.1	45.3	0.7	0.3	0.3	0.3
MTT	57.1	46.0	62.8	85.8	1.2	0.4	0.5	0.7
PPHA	23.8	19.2	25.0	44.1	0.5	0.2	0.2	0.3
TOTAL	4612.4	10237.2	13747.8	13129.9				

[a] SKWOT units include only the combined intermuscular and subcutaneous fat depot.

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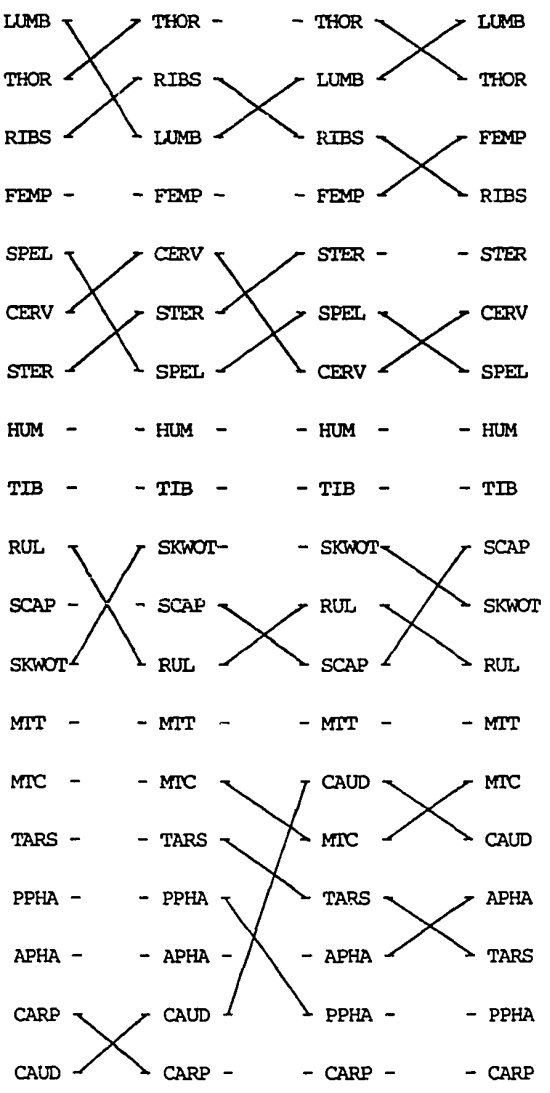
Figure 7.3. Rank Order of Carcass Units for Total Fat Weight Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
LUMB	THOR	THOR	LUMB	795.5	1540.0	2273.3	2220.9
THOR	RIBS	LUMB	THOR	760.9	1469.4	2272.4	1899.7
RIBS	LUMB	RIBS	FEMP	533.5	1468.5	2093.2	1712.6
FEMP	FEMP	FEMP	RIBS	428.9	1259.5	1562.1	1667.1
SPEL	CERV	STER	STER	408.2	1210.8	1259.9	1308.3
CERV	STER	SPEL	CERV	399.1	973.2	1233.9	1264.8
STER	SPEL	CERV	SPEL	384.2	834.9	1186.4	1024.4
HUM	HUM	HUM	HUM	214.1	416.1	653.9	467.1
TIB	TIB	TIB	TIB	158.2	282.5	290.7	359.5
RUL	SKWOT	SKWOT	SCAP	129.0	235.4	238.5	348.4
SCAP	SCAP	RUL	SKWOT	125.3	223.4	204.6	311.9
SKWOT	RUL	SCAP	RUL	81.4	152.3	199.3	197.5
MIT	MIT	MIT	MIT	57.1	46.0	62.8	85.8
MTC	MTC	CAUD	MTC	39.0	36.8	54.7	59.9
TARS	TARS	MTC	CAUD	34.2	35.6	48.8	56.6
PPHA	PPHA	TARS	APHA	23.8	19.2	42.1	52.6
APHA	APHA	APHA	TARS	19.1	14.3	35.5	45.3
CARP	CAUD	PPHA	PPHA	14.8	13.9	25.0	44.1
CAUD	CARP	CARP	CARP	6.1	5.4	10.7	3.4

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expected, more of the total body fat is found in the medial and distal limb units (i.e., the radius-ulna, tibia, and more distal elements) in the immature bison, FYM, than in the adult bison. In this young animal, the ribs and femur-patella (FEMP) units appear to have smaller amounts of the total fat weight than in the adults.

Comparison of the fat weight distributions of FAF and the other bison indicates that condition differences are evident in total fat weight, as might be expected, given the observance of possible differences in the separate fat depots. In Table 7.7 the distal limb units (metapodials and below) and the more proximal elements of the hindlimb (the femur-patella and tibia units) in FAF all show slight increases in the percent of total fat over the values seen in SAF. The differences are very small, but they are consistent and change in the expected direction for the interpretation of condition differences. The fact that these differences are most pronounced in the femur-patella (FEMP) and tibia (TIB) units suggests that the changes in fat distribution might be in the early stages of development. The ribs, sacrum-pelvis (SPEL), and thoracic vertebrae (THOR) units all are a smaller proportion of total fat weight in FAF than in SAF. The thoracic vertebrae unit was suggested above to be a relatively early developing unit for subcutaneous and intermuscular fat, so the reason for its suspected decrease in percent of total fat in FAF, is not clear. The ribs and sacrum-pelvis (SPEL) show larger differences from SAF than other units possibly indicating that they have lost a larger proportion of total fat weight. The increases in the values of the femur-patella (FEMP) and tibia (TIB) units are understandable, in that, by losing only minor amounts of fat and being relatively large producers of fat (especially the femur-patella unit), the percent of total fat in these units should show larger gains than in the

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smaller producing, more distal units. This might explain the perceived pattern of fat distribution changes suspected between SAF and FAF, but some inconsistences with the expected pattern of fat mobilization remain.

The presence of sex differences in the total fat weight distribution is questionable. In the axial skeleton and femur-patella units the occurrence of any sex differences should be masked by the large proportion that the carcass fat depots (subcutaneous and intermuscular) represent of the total. In the limb units, the occurrence of sex differences cannot be separated from possible effects of age differences in these animals.

Although age, and possibly sex and condition differences are evident in the total fat weight data, the question remains as to the importance of these differences. For example, does the fact that the limb units carry a higher porportion of total fat weight in the immature bison, FYM, than in the adults result in a change in the rank order of carcass units for fat production? The data in Figure 7.3 suggest they do not. Although some differences in rank order are evident, inspection of the accompanying fat weights suggest that where differences occur, the fat weights within each carcass are often quite similar in adjacently ranked units, and therefore, might not be influential in selection decisions. These data suggest that the order in which carcass units might be used for total fat recovery are essentially the same in animals of similar age, sex, and condition to these TRNP bison. It does not seem likely either that poorer conditioned animals would exhibit a markedly different rank order. Poorer condition is expected to result in fat weight distribution similar to that seen in young animals, but as can be seen (Figure 7.3), distribution in these animals does not differ markedly from that of the adults.

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Distribution of Total Selected Fat

Table 7.8 and Figure 7.4 present the total fat weight data from which the weight of the intramuscular and organ meat fat has been subtracted. This is designated as total selected fat weight. This was done in order to determine whether the deletion of the intramuscular fat depot changed the ranking of carcass units for fat production. The rationale for doing so is that during periods when protein intake levels must be limited, the presence of more fat in the intramuscular depot might not raise the value of any particular carcass unit, so its presence might cause one to overestimate the value of a carcass unit.

Examination of Figure 7.4 indicates that the carcass units in the rank orders that show the greatest between-animal differences are also the locations within each animal's rank of carcass units that show the greatest similarity in weights between adjacently ranked units. The sternebrae (STER) unit, for example, is ranked much lower in the immature bison, FYM, but the difference in fat weight between this unit and the cervical (CERV) unit, ranked two positions higher, is only 33.8 gm. Like total fat weight, therefore, it is suggested that total selected fat weight is essentially similarly distributed between animals of different age, sex and condition.

Comparison of Total and Selected Fat Weight Distributions

If the rank orders of total fat and total selected fat weight vary markedly within each individual, then one might anticipate that selection strategies would differ during periods of dietary stability and periods when protein poisoning is a potential threat. Figure 7.5 shows the two rank orders for each animal, comparing the order for total fat production with that for the total selected fat production. In the youngest animal, FYM,

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Table 7.8. Weight and Distribution of Total Selected Fat in the Half Carcass

Carcass Unit	Fat Weight[a] (gm)				Unit Weight as a Percent of Total Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT[b]	81.4	235.4	238.5	311.9	2.1	3.5	2.5	3.3
CERV	314.4	644.2	789.2	766.5	7.9	9.6	8.1	8.1
THOR	649.2	1044.2	1475.8	1316.8	16.4	15.5	15.2	13.9
LUMB	781.9	1203.3	1917.2	1807.1	19.7	17.9	19.8	19.1
SPEL	369.7	617.0	976.9	816.5	9.3	9.2	10.1	8.6
CAUD	4.4	10.6	45.9	42.8	0.1	0.2	0.5	0.5
RIBS	309.3	496.1	971.7	890.2	7.8	7.4	10.0	9.4
STER	280.6	715.9	985.6	925.4	7.1	10.6	10.2	9.8
SCAP	84.5	38.3	23.1	108.0	2.1	0.6	0.2	1.1
HUM	206.6	315.1	415.3	360.1	5.2	4.7	4.3	3.8
RUL	128.2	125.3	186.3	191.3	3.2	1.9	1.9	2.0
CARP	14.8	5.4	10.7	3.4	0.4	0.1	0.1	T
MTC	39.0	36.8	48.8	59.9	1.0	0.5	0.5	0.6
APHA	19.1	14.3	35.5	52.6	0.5	0.2	0.4	0.6
FEMP	411.2	861.9	1193.8	1336.0	10.4	12.8	12.3	14.1
TIB	158.2	264.8	250.7	298.4	4.0	3.9	2.6	3.2
TARS	34.2	35.6	42.1	45.3	0.9	0.5	0.4	0.5
MTT	57.1	45.8	62.7	85.2	1.4	0.7	0.6	0.9
PPHA	23.8	19.2	25.0	44.1	0.6	0.3	0.3	0.5
TOTAL	3967.6	6729.2	9694.8	9461.5				

[a] Selected fat weight equals total carcass unit fat weight minus intramuscular fat weight. Organ fat weight is also excluded.

[b] SKWOT units include only the combined intermuscular and subcutaneous fat depot.

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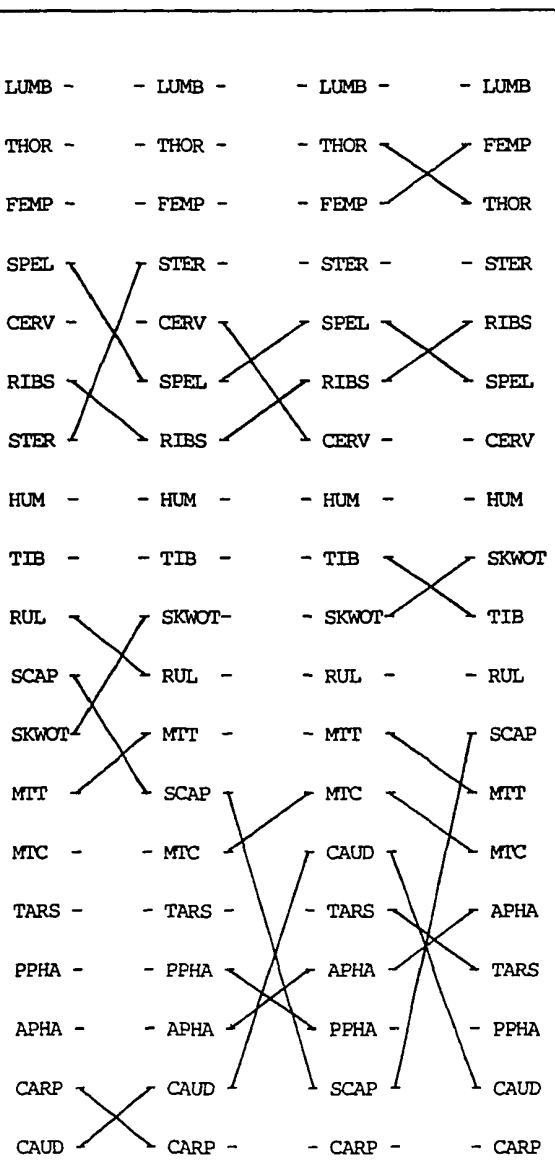
Figure 7.4. Rank Order of Carcass Units for Total Selected Fat Weight Production



Unit Rank Order				Unit Fat Weight (gm)			
FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
LUMB	LUMB	LUMB	LUMB	781.9	1203.3	1917.2	1807.1
THOR	THOR	THOR	FEMP	649.2	1044.2	1475.8	1336.0
FEMP	FEMP	FEMP	THOR	411.2	861.9	1193.8	1316.8
SPEL	STER	STER	STER	369.7	715.9	985.6	925.4
CERV	CERV	SPEL	RIBS	314.4	644.2	976.9	890.2
RIBS	SPEL	RIBS	SPEL	309.3	617.0	971.7	816.5
STER	RIBS	CERV	CERV	280.6	496.1	789.2	766.5
HUM	HUM	HUM	HUM	206.6	315.1	415.3	360.1
TIB	TIB	TIB	SKWOT	158.2	264.8	250.7	311.9[a]
RUL	SKWOT	SKWOT	TIB	128.2	235.4[a]	238.5[a]	298.4
SCAP	RUL	RUL	RUL	84.5	125.3	186.3	191.3
SKWOT	MTT	MTT	SCAP	81.4[a]	45.8	62.7	108.0
MTT	SCAP	MTC	MTT	57.1	38.3	48.8	85.2
MTC	MTC	CAUD	MTC	39.0	36.8	45.9	59.9
TARS	TARS	TARS	APHA	34.2	35.6	42.1	52.6
PPHA	PPHA	APHA	TARS	23.8	19.2	35.5	45.3
APHA	APHA	PPHA	PPHA	19.1	14.3	25.0	44.1
CARP	CAUD	SCAP	CAUD	14.8	10.6	23.1	42.8
CAUD	CARP	CARP	CARP	4.4	5.4	10.7	3.4

[a] weight includes only intermuscular fat

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Figure 7.5. Rank Order of Carcass Units for Total and Selected Fat Production

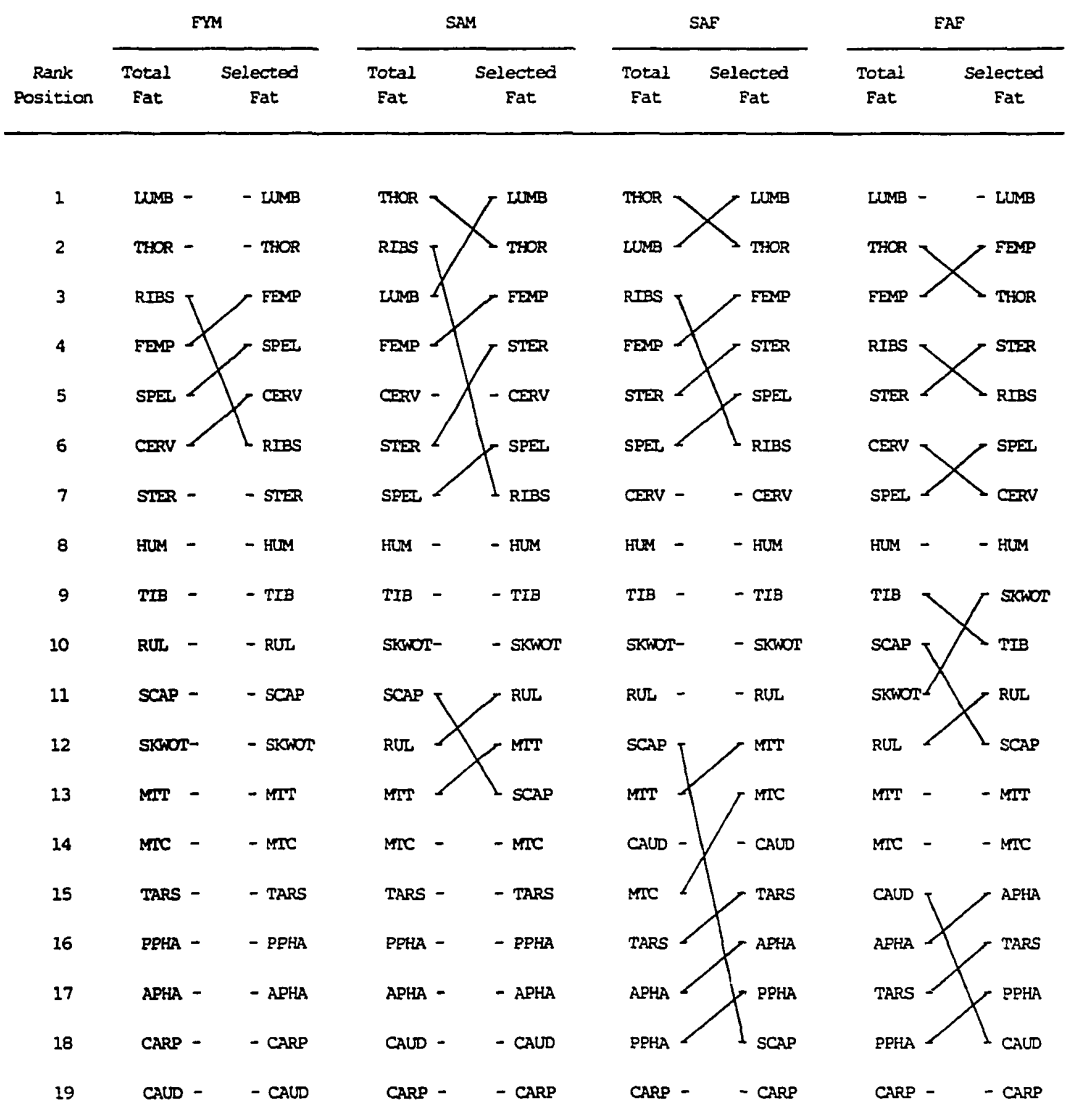

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Figure 7.5. (continued)

Rank Position	FYM		SAM		SAF		FAF	
	Total Fat Weight (gm)	Selected Fat Weight (gm)	Total Fat Weight (gm)	Selected Fat Weight (gm)	Total Fat Weight (gm)	Selected Fat Weight (gm)	Total Fat Weight (gm)	Selected Fat Weight (gm)
1	795.5	781.9	1540.0	1203.3	2273.3	1917.2	2220.9	1807.1
2	760.9	649.2	1469.4	1044.2	2272.4	1475.8	1899.7	1336.0
3	533.5	411.2	1468.5	861.9	2093.2	1193.8	1712.6	1316.8
4	428.9	369.7	1259.5	715.9	1562.1	985.6	1667.1	925.4
5	408.2	314.4	1210.8	644.2	1259.9	976.9	1308.3	890.2
6	399.1	309.3	973.2	617.0	1233.9	971.7	1264.8	816.5
7	384.2	280.6	834.9	496.1	1186.4	789.2	1024.4	766.5
8	214.1	206.6	416.1	315.1	653.9	415.3	467.1	360.1
9	158.2	158.2	282.5	264.8	290.7	250.7	359.5	311.9
10	129.0	128.2	235.4	235.4	238.5	238.5	348.4	298.4
11	125.3	84.5	223.4	125.3	204.6	186.3	311.9	191.3
12	81.4	81.4	152.3	45.8	199.3	62.7	197.5	108.0
13	57.1	57.1	46.0	38.3	62.8	48.8	85.8	85.2
14	39.0	39.0	36.8	36.8	54.7	45.9	59.9	59.9
15	34.2	34.2	35.6	35.6	48.8	42.1	56.6	52.6
16	23.8	23.8	19.2	19.2	42.1	35.5	52.6	45.3
17	19.1	19.1	14.3	14.3	35.5	25.0	45.3	44.1
18	14.8	14.8	13.9	10.6	25.0	23.1	44.1	42.8
19	6.1	4.4	5.4	5.4	10.7	10.7	3.4	3.4

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there is very little difference between the two orders of carcass unit fat production, which in part, is attributable to the small proportion of total fat that is intramuscular fat in this yearling. This is to be expected given the relatively late maturation of intramuscular fat. The only major difference visible in Figure 7.5 for FYM is in the rank position of the ribs unit. When intramuscular fat weight is excluded in the selected fat total, this unit drops three positions in rank order, representing a loss of 224.2 gm of fat which represents 42 percent of the total fat associated with this carcass unit. The loss in the other units is proportionately, much smaller.

Deletion of the weight of intramuscular fat in the carcass units of the other three bison results in a little more variability in the rank orders of units for fat production than was seen in FYM. In these older bison, the ribs unit drops from one to five rank positions when intramuscular fat is excluded in the calculation of the selected fat total. The drop in rank is greatest in the male, SAM (five positions), substantial in the immature male, FYM, and the female, SAF (three positions), and least in FAF (one position). It is not clear whether advanced age or poor condition are influential here in the minor magnitude of rank change in FAF.

The other unit that shows the largest drop in rank order position with the deletion of intramuscular fat from the total, is the scapula (SCAP). In the male, SAM, and the older female, FAF, the drop is relatively minor, but evaluation of adjacently ranked unit weights does not suggest the ranks would become closer. In the younger female, SAF, the drop in rank order in total selected fat rank is quite dramatic. Under circumstances where protein consumption must be limited and fat recovery maximized, one might expect that the ribs and scapula might be used differently than when total fat recovery is sought. It is doubtful, however, given the relatively high

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rank of the ribs units in both orders, that the ribs would be less used. The intermediate to low position of the scapula (SCAP) in this rank order figure, suggest that the scapula might show differences in its use under different dietary circumstances.

Other units that increase in rank by more than one position when intramuscular fat is excluded in the calculation of the selected fat total do not appear to show a consistent pattern between rankings for all four animals. For example, while the lumbar (LUMB) unit increases two rank positions in SAM in the selected fat rankings (Figure 7.5), there is only a one position increase in SAF and no increase in FAF or FYM. Similarly, the improvement in position seen for the metacarpal in SAF is absent in the other three animals. Therefore, although it would have to be verified with a much larger sample, it appears that the only major and consistent changes in the rank order of carcass units for fat production is for the ribs and scapula units. When intramuscular fat is excluded from the total, both of these units drop in rank.

As noted above, it seems doubtful that the archaeological record would reflect these changes under different strategies of fat recovery. The relatively high rank of the ribs, regardless of the rank position drops noted above, would probably insure its continued use, when collection is made from a single animal. The intermediate to low position of the scapula might result in changes in use, but in late prehistoric sites, where the scapula is often recovered and used as an agricultural tool, complications of interpretation would result from their absence from the kill and processing sites. Where multiple animals are killed, however, and differences in fat production between animals are large, the high rank of a unit and low rank of another may be immaterial if they are both from a low fat producer

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such as FYM. For example, if the carcass units from these four bison are arranged in descending order of total fat production, nearly 76 percent of the total available fat is recovered before the first carcass unit (the lumbar vertebrae) from the immature bison, FYM, appears in the order.

This problem with interpreting archaeological bone as indicators of selection, butchering, and processing decisions, leads one to wonder how the data presented above relates to what is seen in the archaeological record. Based upon total and selected fat values, the appendicular units appear to have relatively minor importance, and yet these units are often removed from kill sites in large proportions relative to their availability. This may be explainable in terms of the partitioning and distribution of fat and the amount of processing necessary to recover that fat.

It was previously shown (Table 7.2) that between 5.4 and 6.9 percent of total carcass fat weight (excluding omental and mesenteric fat) was found in the bone in the form of bone grease fat (as opposed to bone marrow fat from the medullary cavities). In Chapter 5 (Table 5.35), the partitioning of bone grease between Binford's (1978) categories of yellow and white grease was examined. It was found that yellow grease from the axial skeleton only constituted approximately 17.5 percent of skeletal fat for the immature male, FYM, and between 30 and 34 percent for the other three bison. As a portion of total fat weight, yellow bone grease fat represents from 1.8 to 2.2 percent of the total, while white bone grease fat represents from 3.9 to 5.6 percent of the total weight and bone marrow represents from 3.4 to 8.3 percent of the total weight. Due to differences in the processing efforts needed to recover bone marrow as opposed to bone grease, and due to the greater percent of total fat weight in marrow, it is not surprising that bone marrow was a frequently used fat source.

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Comparing white and yellow bone grease fat weights and percents of total fat, the cost of processing should be relatively similar given that bone must be broken up to facilitate its recovery. Differences in use, therefore, might be tied to either production or quality differences between these sources of bone grease fat. With one exception (FAF), yellow bone grease fat producing bones, however, were less that half as productive as white bone grease fat bones (Table 7.9) in these four bison. Furthermore, yellow grease represents no more than 2.2 percent of total fat weight in these animals. Perhaps this difference, in conjunction with differences in the softness of white compared to yellow bone grease fat, may have been large enough that axial skeleton elements were not as frequently processed for their fat content as appendicular elements.

Summary of Fat Distribution Differences in Bison

Fat is distributed differently in the bison carcass depending upon which fat depot is under consideration. Subcutaneous fat is most abundant in axial elements and in the femur-patella unit, and is scarce and sometimes non-existent in the medial and more distal appendicular elements. This distribution changes with the age of the animal from immaturity to maturity, with the yearling, FYM, having less of this fat in the femur-patella unit than the older animals. The possible effects of condition differences, illustrated by the comparison of the two females, include a depletion of subcutaneous fat that is large enough to drop the femur-patella unit several positions in rank order of fat production. It is not expected, however, that the femur-patella unit would be excluded from use, given its continued, relatively high ranking. One might expect that as condition deteriorates,

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Table 7.9. Skeletal Fat Depots as Proportions of Total Fat Weight[a] in the Half Carcass

Fat Depot	Fat Weight (gm)				Depot Weight as a Percent of Total Weight			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Marrow	385.5	618.1	514.1	451.8	8.4	6.0	3.7	3.4
Yellow Grease	54.6	187.3	298.2	267.3	1.2	1.8	2.2	2.0
White Grease	258.0	409.6	690.5	511.3	5.6	4.0	5.0	3.9
Total Carcass Fat	4612.4	10237.2	13747.8	13129.9				

[a] Total weight excludes fat from the organs, and the omental and mesenteric depots.

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fat weight distribution in mature animals may eventually approximate that seen in younger animals that have not yet reached maturity in terms of fattening.

The changes in intermuscular fat distribution between the immature bison, FYM, and more mature male, SAM, are abundant, but less significant than those seen for subcutaneous fat in terms of their effects on changing carcass unit rank. By four years of age, however, the ranking of carcass units for intermuscular fat production in the male bison (as represented by SAM) is quite similar to that of the females for the more productive units, with the exception that the lumbar unit does not rank as high. The other age- and sex-related differences in carcass unit rank are relatively minor, or occur between units that produce relatively little fat.

The major difference noted between the two females is the high ranking of the femur-patella (FEMP) unit and the lower ranking of the cervical (CERV) and sternebrae (STER) units in the older female, FAF. Although the female, FAF, had higher fat weights than the better conditioned female SAF in most carcass units, the effect of fat mobilization may be evident in differences in fat weight distribution between these animals. The intermuscular fat depot is an early developing fat depot, so the larger weights in the older female are understandable despite her decline in condition. Apparently, however, fat loss is most rapid in the forequarter and primarily in the neck (CERV) and sternebrae (STER) units. Intermuscular fat weight remained high in the femur-patella (FEMP) unit in FAF, which results in its representing a substantially higher proportion of total depot fat weight. This may be a result of lower rates of fat mobilization in the femur.

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Little variability was found in the distribution of body cavity fat in these four bison. In the youngest animal, FYM, the lumbar unit produced relatively more fat than in the other animals, but the differences noted between the animals were not large enough to affect the rank order of carcass units for carcass cavity fat production.

When all analyzed fat deposits were combined as total fat weight (excluding omental and mesenteric depots), the age, sex, and condition differences noted in each of the individual depots in previous discussions are masked by the combined weights of the deposits. These data indicate that for maximum recovery of fat, the lumbar and thoracic vertebrae units, along with the ribs and femur-patella units are the most productive, regardless of animal age or sex.

The ranking of carcass units by selected fat (total minus intramuscular fat) weight was quite similar to that for total fat weight. The rankings did not differ markedly except for two carcass units. When intramuscular fat is excluded, the ribs unit dropped substantially in rank, several positions in all bison except FAF. In all but the youngest bison, FYM, the scapula also dropped in rank when intramuscular fat was excluded. Neither change in rank is thought to be important in archaeological interpretations, first due to the continued relatively high rank of the ribs unit, which, it is assumed, would insure its continued use, and second, due to the intermediate to low rank of the scapula unit and the problem of confounding explanations for the absence of the scapula from sites when scapulae were procured for use as tools.

Due to the small amount, or absence of subcutaneous, intermuscular, and body cavity fat associated with the limbs elements, these units might be expected to be less heavily used than the axial units for the recovery of

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available fat. This expectation, however, ignores differences in fat quality, and how those differences might affect its selection and use by hunters.

Qualitative Analyses of Carcass Fat

During periods when maximum fat recovery is required, one might expect that differences in softness, or other factors that improve the desirability of a particular fat would be less important, and the presumed equally high caloric value of all fats would override the lower preferences for harder fats and all fats would be used. However, qualitative differences in the fat of different depots and between locations in the bison carcass are an important factor influencing carcass use during periods when dietary stability provides for some degree of choice in fat use and consumption. The caloric value of fat has not been reported to change substantially with its location or depth in the body, but there is evidence that the degree of saturation, and thus fat softness, varies with animal age, sex, and the location of the fat.

Binford (1978:23,32) suggested that the proportions of low melting point fatty acids in marrow and bone grease were the important factors influencing the quality of marrow and bone grease. He focused upon the relative amount of oleic acid present in the marrow and bone grease to indicate qualitative differences between locations, because it is the fatty acid with the lowest melting point and represents a relatively large proportion of total fatty acids. Other unsaturated, and thus, low melting point fatty acids also are found in these fats, but in smaller amounts. The literature that considers differences in the character of the depot fats, and differences in the fat of animals of different age or sex classes,

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however, is often much more generalized, focusing instead upon differences in the total proportions of saturated versus unsaturated fat. Recent studies have begun to characterize the fatty acid composition of fats, but have not yet examined differences between classes of animals.

Jones and Metcalfe (1988) argue convincingly that Nunamiut hunter preferences for caribou marrow bones were better predicted by an index primarily based on the quantity of marrow recovered, adjusted for efficiency of recovery, than by Binford's complex index that includes a measure of the amount of oleic acid available. This does not mean, however, that the degree of unsaturation in all fats is unimportant to their relative quality and hunter preferences. Rather, it suggests that perhaps the degree of difference was not large enough within the limb elements to override differences in fat quantity and efficiency of extraction. Difference in saturation between sources of fat may be an important factor in predicting preferences and use of fat resources. In this study, however, there was inadequate time to assay the fatty acid composition of the various fat depots of the bison carcass. Therefore, reference must be made to studies of the characterization of fat in other animals with the assumption that bison, with a relatively close genetic relationship to cattle, might show similar differences.

Saturation Differences in Fat

Leat (1976, 1977) and Leat and Cox (1980) discuss the general trends seen in fat saturation characteristics in sheep and cattle. The differences in fatty acid composition they discuss relate to differences due to (1) animal age and sex, (2) season of testing, (3) location of the fat depot within the body, and (4) fat location within the depot. Each of these

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differences are briefly reviewed and their potential effects upon hunting and butchering decisions evaluated.

Animal Age and Sex, and Fat Saturation

Leat and Cox (1980:170) indicate that, in cattle there is a progressive decrease in the saturation of animal fat with age. At birth, the percent stearic acid (a saturated fatty acid) in the perinephric fat depot is less than 10 percent, but by one year of age the percent of this fatty acid peaks in sheep and cattle at approximately 40 percent (Leat and Cox 1980:169). After one year of age, when the rumen becomes functional in young animals, the contribution of this fatty acid to the total begins to decline and the fat becomes less saturated with age. In addition to this direct age effect, Leat and Cox (1980:186) also suggest that the degree of unsaturation in cattle fat is probably related to the degree of fattening in the animal. As cattle advance in relative fatness, as commonly occurs with age, their fat becomes more unsaturated. This has implications for periods of reduced feed intake also, as discussed below.

If bison are like cattle in this aspect of their physiology, then one might expect the fat from a given depot of old and young mature animals of similar nutritional condition, to be softer in the older animal, and thus more desirable to hunters. The fat of calves and yearlings (non- or recently-functioning ruminants) with the highest stearic acid fat content are the most saturated, and therefore, least desirable when fat softness is the factor determining the characterization of quality. Given Leat and Cox's (1980) assessment that the degree of fattening is also related to the relative proportion of unsaturated fat present, an animal under submaintenance nutrition, in addition to having less fat than a healthy

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animal (due to the mobilization of fat to provide energy), might also have less unsaturated fat.

Sex differences have also been found in the saturation characteristics of cattle fat. Leat (1976:186) reports that in sheep and cattle, females have more unsaturated fat than males, a characteristic that one might assume to be related to differences in the degree of fattening generally seen between the sexes. If bison are like cattle in this aspect of physiology as well, then one might expect that the larger fat weights of females than males at the same age, together with the higher degree of unsaturation would lead to the preference of females over males, when choices are possible. At equal physiological maturity (equal proportional total fat weight), however, differences in animal size between males and females might enhance the perceived value of the male carcass.

Season of Testing

Leat (1976:188) also reports that, in cattle, unsaturation in fat is highest in the summer and lowest in the winter. This assessment is consistent with his argument that saturation is influenced by the degree of fattening. Apparently, in winter the decline in fat weight associated with the reduction in feed intake and quality, is associated with a decline in the degree of unsaturation of carcass fat. In summer, and conceivably in the fall as well, when feed is abundant and of high quality, animals are at their maximum annual fatness and the degree of unsaturation is high. If the decline in saturation is tied to restrictions in feed and submaintenance nutrition, then one might expect that in the fall, males should have substantially less saturated fat than females, due not only to the stated sex difference, but also due to poor nutrition in males associated with the rut.

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Fat Depot Location in the Carcass

In the animal carcass there is a gradient of saturation that runs from peripheral to central locations, that is thought to be influenced, in part, by the temperature of the site location (Leat 1976:185). Unsaturation is greatest in peripheral locations and least in internal depots, and is greater in fat from the limbs than from the axial part of the body. This gradient is evident in bone marrow and bone grease (e.g., Binford 1978), as well as in the non-skeletal fat depots of the carcass. Thompson et al. (c.f., Byers and Schelling 1988b:307) for example, note that fat in muscles of the distal limbs is more unsaturated than fat in the muscles found in warmer locations such as the longissimus dorsi muscle along the vertebrae.

Although this saturation gradient is generally accepted, the work of Turner (1979) raises some questions concerning its consistency in all animals at all seasons of the year, and illustrates the importance of temperature effects. Turner (1979) assayed the fatty acid composition of the marrow in desert bighorn sheep (Ovis canadensis cremnobates) in the summer and winter. In winter, these animals show the expected pattern of decreasing unsaturation as one moves from distal to proximal locations in the limbs. In summer, however, when land surface temperatures are high, unsaturation decreased significantly in the distal elements to levels comparable to the more proximal elements. Turner suggests this is an adaptation of desert bighorn sheep to potential heat stress that might result in the denaturing of the limb's low melting point fats. Although bison are not subjected to the extremes of land surface temperatures found in the habitat of these bighorn sheep, the general lack of summer season data in other animals, leads one to wonder if similar seasonal changes do not occur in other species, but have simply not yet been recorded.

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The peripheral to central gradient of decreasing unsaturation is present in the major carcass fat depots as well. Subcutaneous fat, which lies peripheral to the outermost muscles just under the skin, is the softest of the non-skeletal carcass fat depots (Leat 1976:185). Leat (1977) found that the order of decreasing saturation of depot fat in cattle, is as follows: subcutaneous, intermuscular, intramuscular, and internal organ fat. Although it cannot be proved, historic reports of the high value of subcutaneous fat, appear to be related to its softness as affected by the degree of unsaturation. One might expect that during periods when choice could be exercised in fat selection and consumption, the order of fat depot use might follow that noted above for decreasing saturation, with the exception that the intramuscular depot probably was not considered a separate resource, because it is not easily extracted from its associated muscle.

Location within the Fat Depot

Leat (1976:185-186) also demonstrated that the peripheral to central gradient of decreasing fat saturation applies to the fat within individual depots. That is, fat that is found farthest from the central core of the body tends to be more unsaturated. Within the subcutaneous fat depot for example, the fat closest to the skin is more unsaturated than the fat closest to the muscle. It is not clear what the temperature gradient within the body cavity would be like, or how it might influence the saturation of fat within the internal fat depots.

The differences in saturation within a fat depot do not intuitively seem to be important in terms of human selection of carcass products for use as food. If there are major differences in the internal depots in the

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degree of saturation, or in the intermuscular depots depending upon location (e.g., associated with the femur-patella rather than the cervical unit) then they might influence selection, but it is not known whether such differences occur, or if they do, whether they are large enough to be influencial in selection decisions.

Implications of Qualitative Differences in Fat Depots

A great deal remains to be learned concerning the quality of fat in the carcasses of bison and other animals. The information available concerning major patterns of changing fat saturation, however, do offer some expectations for how carcass fat might be used when selection of animals or carcass parts is an option. These studies suggest females are generally more desirable than males for fat production and softness, and that fall season kills would net greater fat recovery along with a greater degree of fat unsaturation than would late winter-early spring kills. In spring, females might still have greater, or possibly comparable fat unsaturation, given that they enter the winter with proportionately larger fat reserves than males. It is clear, however, that young, immature animals produce very little fat and that it is more saturated, and presumably less desirable than the fat of older animals.

Conclusions

In this chapter, quantitative and potential qualitative differences in dissectible bison carcass fat depots and total fat weight were examined. Excluded from these analyses were the omental (stomach) and mesenteric (intestinal) fat depots. Quantitative analyses included examination of fat production and partitioning differences between animals, and evaluation of

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the possible existence and importance of differences in fat distribution in the carcass. Qualitative analyses were limited to a review of available literature concerning the relative proportions of unsaturated fatty acids available in the fat of animals of different age, sex, and condition.

This study suggests that quantitative and qualitative differences in bison fat vary depending upon the age, sex, and condition of the animal examined. Absolute total fat production differences between the four TRNP bison are substantial. The yearling, FYM, produced only 35 percent of the fat weight found in the older females, and 45 percent of the fat weight of the older, but not fully mature bison, SAM. This older male produced 77 percent of the fat weight of the two fully mature females.

Fat partitioning between depots is markedly different with animal age and condition. The subcutaneous and intramuscular depots are late to develop, and therefore, are proportionately smaller in the young bison FYM. In SAM, who is older (approximately four years of age), but not fully mature, the intramuscular depot has reached adult proportions of total fat weight, but the subcutaneous depot is relatively underdeveloped. A decline in animal condition (as evidenced in FAF) results in a more rapid depletion of the subcutaneous depot. Studies of other species show that fat weight losses occur in other depots as well, but at slower rates of decline, resulting in less fat loss. The literature also indicates that the fat depots that are latest to develop are those most rapidly depleted, which suggests that declining condition in mature animals should result in fat partitioning comparable to immature animals.

Animal class differences in fat weight distribution within depots, also appear to exist, although the small number of animals studied, makes determination of the significance of these differences impossible.

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Distribution differences, however, sometimes do not result in changes in the ranking of carcass units for fat production. Furthermore, some differences that are large enough to change the rank of a carcass unit, occur in units that are so highly ranked that the change probably would not influence their use in the division of a single carcass. Low fat production in individual carcass units becomes important, however, when a multiple animal kill is made. Under these circumstances, a drop in rank may eliminate even a high to moderate ranking unit from use if it is from a young bison producing little fat compared to adults. For example, when the carcass units of these four bison are combined as one sample and ranked by total unit fat production, the lumbar unit of FYM, the highest ranked unit in this bison, is not reached until 76 percent of the total available fat has already been accounted for by higher ranked units from the other animals.

These fat distribution analyses of subcutaneous, intermuscular, and body cavity depots, as well as the combined total of these and previously evaluated skeletal and intramuscular fat depots, indicate that in terms of quantity alone, the axial units of the skeleton are the most productive segments of the bison carcass. The analyses of the skeletal fat depots (Chapter 5) on the other hand, indicate that the appendicular skeleton is more productive than the axial units for these depots. These differences, together with the results of the analysis of the meat resource, suggest that on the basis of resource quantity alone, the axial skeleton units are the most productive.

Quantitative differences alone, however, may not explain the archaeological evidence of differences in bison carcass selection and use. Qualitative differences in fat, measured by differences in the degree of

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unsaturation, also have potentially large influences on how animals are selected and their carcasses used. A review of the literature on this topic suggests that (1) fat from females and older individuals is more unsaturated, and thus, softer than fat from males or young individuals; (2) seasonal and conditional losses in fat weight reduce the degree of fat unsaturation, and reduce fat quality; (3) appendicular depots are more unsaturated than axial depots, and peripheral depots are more unsaturated than internal depots (e.g., subcutaneous versus KKCF); and (4) the peripheral to central gradient of decreasing unsaturation applies within depots as well. Given that the most unsaturated depots are the skeletal fats from the appendicular units and the subcutaneous depot, and that the location and continuity of the subcutaneous depot from the axial part of the carcass permits its removal independent of the skeletal units, one might suggest that, in terms of fat quality, the appendicular units are the most productive, in contrast to their lower value when total fat production is considered.

Without a more detailed breakdown of how depot versus location differences in saturation are related, and how these qualitative differences are influenced by quantitative differences in their availability, it is difficult to evaluate the importance of fat distribution differences within the carcass. Clearly, however, the nutritional condition of the hunter is also important. At this point, it is only possible to suggest that when qualitative differences in fat are important, the value of the appendicular units should increase relative to their value when qualitative differences are overridden by the demand for maximum fat recovery. If the bison are in relatively good condition, a maximized fat recovery strategy would give greater value to the axial skeleton units. Under circumstances where

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maximum fat recovery is important, but the bison are in very poor condition, the axial part of the skeleton and the upper limb units would be diminished, and the later depletion of the skeletal fats (especially the medullary cavity bone marrow) would increase the relative value of the appendicular units. In the bison studied here, it does not appear that the condition of the female, FAF, is to that point.

The relationship between these factors and the nutritional condition of the hunter was also touched upon in terms of the individual carcass units. During periods of poor human nutrition, when protein poisoning is a potential dietary threat, the changes in carcass unit value, depending upon whether or not intramuscular fat is excluded, are not substantial except in the ribs unit of the two young males and SAF. Under these conditions, the ribs unit in these animals drops in rank in the selected fat order of production. It is doubtful, however, that such differences would be important to hunter decisions concerning carcass use. If protein poisoning is a threat, the importance of fat is high regardless of perceptions of qualitative differences between depots, or between locations within the carcass. Under these circumstances, all available fat that is not part of the intramuscular depot should be recovered, and it is expected that the fatter organs and carcass cuts would also be used.

The differences in fat production, partitioning, distribution, and quality discussed here, as well as the differences in these characteristics found in meat and bone products are considered for their affect upon the composition of archaeological assemblages of bison bone in the next two chapters. Whereas the discussions in this and the previous two chapters have focused upon partition, production and distribution of individual carcass components, hunter selection decisions are more likely based upon

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how these differences are cumulatively reflected in bison carcasses of different age, sex and condition.

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CHAPTER 8. MODELING SELECTION

Three selection phases associated with bison hunting are considered in this chapter. In each case, an assumption is made that the package value (whether it represents a bison herd, an individual bison carcass, or a smaller subdivision of that carcass) is dictated by the quantity of the available carcass products. The first and second aspects of selection concern which bison--males, females, or immature animals--offer the largest quantities of individual or combined carcass products, such as meat and fat. This is a question of herd and animal selection. Bison are found primarily in bull groups and cow/calf herds, and during the breeding season, in mixed herds. This variability in herd composition allows hunters to focus their activities upon herd types that offer the greatest return for their efforts.

The selection process also involves choosing the order in which the bison are butchered after the kill. In the case of an arroyo trap such as the Olsen-Chubbuck site (Wheat 1972), this may be dictated, in part, by the accessibility of the carcasses. In other cases, however, the carcasses may have been equally accessible, and thus may have presented another selection option (assuming that the kill size was large, which thus prevented concurrent butchering of all carcasses). In many respects, the carcass composition factors which may have guided the selection of the herd type (not forgetting the influence of herd managability, however), might also be applicable to the order of priority for carcass processing.

The third aspect of selection, and a major focus of this chapter, is the division and processing of the available carcasses for recovery of meat

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and fat resources. Binford (1978) has effectively argued that there is a negative relationship between the frequencies of bones left at a kill site and the economic utility of the carcass units associated with those bones. Speth's (1983) analysis of the Garnsey Site (a late prehistoric site in New Mexico) bison assemblage suggests that animal age, sex, and condition influence the extent of the butchering of the carcasses of the different animal classes, because they affect the relative utility of the carcass units. In this section, several models are presented that are designed to link the economic anatomy of the carcass with selection and butchering processes. The construction of these models is evaluated, as is their capability of dealing with variability in carcass composition.

As noted above, in each case, the selection decisions made regarding herd, animal, and carcass unit utility should have been governed to some extent by the quantity of the desired product(s) available in the respective herds, individuals, or carcass units. The comparative evaluation of the worth of the carcasses depends, in part, upon the nutritional condition of the people using these resources (see Speth 1983). During the fall, when the human diet is likely to be nutritionally balanced with adequate proportions of protein, fat, and carbohydrate, and adequate calories are available to maintain a positive energy balance, then the total energy available in the bison carcass, whether in the form of fat or protein, may be used to guide selection decisions. During the late winter and early spring, Speth (1983) notes that the nutritional condition of the hunter may be low due to the combined effects of a carbohydrate-restricted diet following exhaustion of stored supplies, low caloric intake due to low food availability, and high proportions of lean protein in the diet which require more energy to convert to energy than either carbohydrate or fat. Speth

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(1988, 1989) also argues that humans are limited in their capacity to ingest diets with high proportions of lean meat and that protein poisoning may occur in a relatively short time if those limitations are exceeded. For assemblages from late winter-early spring sites, therefore, models that emphasize fat resources, rather than protein may provide better measures of selection.

This raises the question of how one models utility and whether the models are adequate to address all three aspects of selection. For example, what units of measure should one use and does one use the same measure to model selection at each of the three levels (i.e., herd, animal, and carcass unit)? When modeling selection at the level of the carcass unit, do the models for the individual bison differ significantly from models based upon averaged data? Where these differences occur, does it affect the application of averaged models to archaeological bone assemblage data? Finally, can differences between animals in their productivity at the carcass unit level be modeled as well? These are the primary questions that are addressed in the remainder of this chapter. In the next chapter several carcass utility models are applied to published archaeological bone assemblage data in order to evaluate their relative usefulness.

Herd and Animal Selection

The resource production totals, expressed in terms of their caloric yield, are summarized here in order to assess which animals provide the greatest quantities of energy in the form of protein and fat. It is assumed that, unless difficulties arise with herd management due to its size or composition (Frison 1970:41), due to the size of the available labor force, or due to some other constraint, hunter selection of the target herd should

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be determined, to a large extent, by the overall utility of the herd and its members.

Bison herd organization is somewhat fluid, changing seasonally in response to the reproductive cycle. Bison hunters have two, and sometimes three herd types to choose from (McHugh 1958:14-15, 1972:157): (1) small bull groups, which generally numbers from one to 12 members and which usually contains males, four years old or older, with the occasional inclusion of a female without a calf (Meagher 1973:46), (2) larger cow/calf group generally averaging around 23 members, and during the non-breeding season composed of mature cows, calves, yearlings, two year old bulls, some three year old bulls, and rarely bulls four years old or older, and (3) mixed herd which represents one or more cow/calf herds that have been joined by a number of adult males from bull groups during the breeding season, and which may average in size from small groups comparable in size to the cow/calf group to large herds averaging 175 members.

The appropriateness of the selection of each herd type is governed in part by seasonal patterns in the reproductive behavior of bison and their affect upon herd maneuverability by hunters. Frison (1970:41, 1978:250) argues that driving bison over long distances is difficult when cows have small calves in the spring and when bulls are present in the herd during the breeding season and for short periods thereafter. He suggests that herds containing mature bulls are difficult to drive at any time, because the bulls tend to break away, often leading other animals away with them. The best time to drive bison, according to Frison (1970), is in the fall when potentially disruptive factors are at a minimum. He (1978:229-230) also suggests that herd size strongly affects the maneuverability of bison; drives over jumps require large numbers of animals (100 or more) for success

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and drives into traps or corrals require smaller herds for proper handling.

On the basis of herd size and factors related to handling, one would suspect that bull groups would not be the focus of a drive over a jump, because of the difficulties of controlling bulls, and due to the larger number of animals needed to force the lead animals over a jump. Small bull groups could be trapped, corralled or surrounded, but probably would not be the focus of such operations during the early fall, due to their poorer condition following weight loss during the rut. They might be hunted in late fall, winter, or early spring, however, following a period of nutritional recovery in the fall.

Cow groups are in prime condition during the fall and may be found still in large groups, having recently coalesced for the rut. These groups could be driven over jumps, or if they had split again into smaller non-breeding-season-sized groups, they could be trapped, corralled or surrounded.

In the late winter and early spring, it is more likely that cow/calf groups were hunted prior to the calving period than after it, due to both the increased difficulty of handling these animals at this point in the reproductive cycle, and due to the increased nutritional stress on the cows associated with late gestation and lactation following the winter-early spring period of reduced feed quantity and quality. As both cow/calf groups and bull groups would be difficult to handle at this time of year, differences in carcass composition should be considered for their influence on herd selection. Speth (1983) has suggested that in the spring, bulls may be in superior condition relative to pregnant or lactating cows and hunting practices might focus on these male groups as was evident at the Garnsey Site in New Mexico. Carcass composition data from the bison used in this

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study provide some support for this assessment, but they also suggest that additional research, providing data from male bison older than those available in this sample, are needed to fully support his arguement. The available carcass composition data are examined below.

Comparative Carcass Composition and Nutritional Value

The bison carcass provides two primary sources of food energy: protein and fat. In order to compare carcass value, the differences in energy provided by each of these resources are computed separately, because their energy values are not equivalent. Guthrie (1975:83) indicates that one gm of protein and fat respectively provide 4 and 9 kcal of energy. In this analysis of the nutritional value of bison carcass meat, the 4 kcal/gm value is applied to the computed dry matter weight of the meat following extraction of the associated water and intramuscular fat. This slightly overestimates the energy value of the meat protein, because the dry matter weight includes both protein and ash. The effect of this difference is probably minimal as bone is not a component of the samples. The difference is given no further consideration here. The caloric value of the available fat is computed using the 9.0 kcal/gm conversion for all solvent-extracted fat weights (i.e., for the intramuscular, bone grease, and marrow fats). The caloric value of the combined weights of the carcass fat depots (the subcutaneous, intermuscular, and cavity depots) is estimated using an arbitrary conversion factor of 75 percent of the normal fat value (6.75 kcal/gm), because the fat weights include an unknown quantity of water recovered with the fat during the rendering process, and because solvent-extractions to determine the actual fat content were not carried out on these samples.

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Comparative Yields

The data presented in Table 8.1, Part A include summary calculations of the caloric yields of the protein, intramuscular fat, bone grease and marrow fat, and the combined carcass depot fats, as well as three sets of caloric totals, and computations of the percent each product represents of the total (all products) caloric production. These data do not include the organs, or the mesenteric and omental fat depots. Total Products (TP) includes the caloric yields of all protein and fat products, Total Fat (TF) includes only the caloric yield of the fats, and Selected Fat (SF) includes the caloric value of the fats, excluding intramuscular fat. Table 8.1, Part B presents the same data, based upon product weight.

Total Products (TP). The total, TP, includes the caloric yield of the meat protein and fat. It should be useful for evaluating carcasses under circumstances where protein poisoning is not a potential problem. Under these circumstances, the four bison are ranked as follows (from highest to lowest caloric yield): SAM, SAF, FAF, FYM. This is a slightly different order than that which results if the animals are ranked on the yield estimated by subtracting dry bone weight from the unit gross weight. When ordered by gross weight, the females change rank, but the males remain in the same positions: SAM, FAF, SAF, FYM. Apparently the differences between the males and females are large enough that consideration of caloric yield does not alter their ranking. Between the females, however, the differences are relatively small and in this case, when caloric yield is determined, it increases the rank of the fatter female over its position when rank is determined by weight. If product weight (Table 8.1, Part B) is evaluated, rather than caloric yield, the same ranking results as determined for gross weight. The caloric yield data, which considers the difference between the

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Table 8.1. Component Contribution to Productivity in the Half Carcass

Part A. Productivity Measured by Caloric Yield

Carcass Component	Side Caloric Yield (kcal)				Percent of Total Production (TP)			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Protein + Ash	52,710.8	113,592.0	81,328.0	86,382.4	60.5	58.6	43.4	46.3
Intramuscular Fat	6,104.2	32,131.0	37,252.2	33,607.0	7.0	16.6	19.9	18.0
Bone Grease Fat	2,813.4	5,372.1	8,898.3	7,007.4	3.2	2.8	4.7	3.8
Bone Marrow Fat	3,470.4	5,563.8	4,628.7	4,066.2	4.0	2.9	2.5	2.2
Carcass Fat[a]	22,069.2	37,221.4	55,295.4	55,560.5	25.3	19.2	29.5	29.8
Total Products (TP)	87,168.0	193,880.3	187,402.6	186,623.5				
Total Fat (TF)	34,457.2	80,288.3	106,074.6	100,241.1	39.5	41.4	56.6	53.7
Selected Fat (SF)	28,353.0	48,157.3	68,822.4	66,634.1	32.5	24.8	36.7	35.7
Animal Rank for TP	4	1	2	3				
Animal Rank for TF	4	3	1	2				
Animal Rank for SF	4	3	1	2				

[a] Includes the subcutaneous, intermuscular, and cavity depots.

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Table 8.1. (continued)

Part B. Productivity Measured by Weight Yield

Carcass Component	Side Weight Yield (gm)				Percent of Total Production (TP)			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
Protein + Ash	13,177.9	28,401.4	20,332.2	21,595.9	73.9	73.3	59.5	62.1
Intramuscular Fat	678.4	3,570.2	4,139.3	3,734.3	3.8	9.2	12.1	10.7
Bone Grease Fat	312.6	596.9	988.7	778.6	1.8	1.5	2.9	2.2
Bone Marrow Fat	385.6	618.2	514.3	451.8	2.2	1.6	1.5	1.3
Carcass Fat[a]	3,269.8	5,514.5	8,192.2	8,231.4	18.3	14.2	24.0	23.7
Total Products (TP)	17,824.3	38,701.2	34,166.7	34,792.0				
Total Fat (TF)	4,646.4	10,299.8	13,834.5	13,196.1	26.1	26.6	40.5	37.9
Selected Fat (SF)	3,968.0	6,729.6	9,695.2	9,461.8	22.3	17.4	27.7	27.2
Animal Rank for TP	4	1	3	2				
Animal Rank for TF	4	3	1	2				
Animal Rank for SF	4	3	1	2				

[a] Includes the subcutaneous, intermuscular, and cavity depots.

energy value of protein and fat, apparently has an affect on the ranking of animals of similar total product yield, as was expected, but the difference between protein and fat energy values are not large enough to override the differences in animal size between adult males and females, and between adult females and immature males. The change in female animal rank, however, suggests that caloric yield data which compensate for the energy differences of protein and fat may serve as a better predictor of the nutritional value of carcasses than measures based upon weight alone.

Given that the male, SAM, was collected in the spring, and was not fully mature and might be expected to produce smaller meat and fat weights than a fully mature male, it appears that in terms of total caloric yield, adult male bison, four years old or older are the most productive animals. It is clear, however, from the percentage breakdowns of the carcass products (Table 8.1, Part A), that the adult male bison (and the yearling male bison) yields a greater percentage of its total product energy (approximately two-thirds) from protein than do the females (who yield only a little over half their available energy through protein).

Lacking a fall-killed, adult male specimen comparable to SAM, it is difficult to determine whether the caloric yield for male carcasses would be higher, lower, or comparable to that reported for the spring-killed male, SAM. It is probable that both the protein and fat yield of fully mature male bison would be higher, and in such an animal that is not nutritionally stressed, the proportion of yield from fat would be higher than that seen in the male, SAM. In the late summer and early fall, during and following the rut, however, a decrease in fat and some protein weight is expected for sexually active males. As the largest proportion of weight loss is from fatty tissue, one might expect that, as with SAM, the majority of the

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immediate post-rut caloric yield of fully mature bison would probably arise from protein rather than from fat.

Total and Selected Fat (TF and SF). If fat is a particularly desirable product, and potential problems related to protein poisoning exist, then the caloric totals based on fat weights (Table 8.1, Parts A and B, TF and SF) may be more useful in determining selection than the total (TP) based upon all products. In Table 8.1, Parts A and B, Total Fat (TF) represents the caloric yield when all fats, including intramuscular fat, are combined. Intramuscular fat is directly associated with muscle and is not separable without extractive processing. If protein poisoning is a potential problem and maximum fat recovery is desirable, this fat could be separated and recovered from the carcass meat by boiling in a manner similar to the processing for bone grease. No explicit reports of such processing are available, although reports of soup or stew making with the addition of marrow or grease fat to improve it, are common (e.g., Binford 1978:145). If the value of the intramuscular fat is included with the other fats, but the caloric yield of the protein is excluded, then the caloric yield of TF would indicate the relative value of the different carcasses. When fat (TF) is considered without the caloric contribution of protein, the animals are ranked (from highest to lowest yield) as follows: SAF, FAF, SAM, FYM.

Selected Fat (SF, Table 8.1, Parts A and B) represents the caloric yield when both protein and intramuscular fat are excluded. In this case, the animals are evaluated for their caloric yield from carcass and skeletal fat alone. This might occur if the fat yield from the meat were not considered large enough to offset the costs of processing the meat. The ranking of animals in this case is like that for total fat: SAF, FAF, SAM, FYM. The spring-killed, four year old male, SAM, drops in rank behind both

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females compared to the total, TP, that includes protein energy yield. Before concluding that cow/calf groups should be the focus of selection when fat is a primary resource target, however, several factors concerning the sample animals (age and condition) and the season of kill need to be considered.

Changes in Carcass Energy Productivity

The data presented in Table 8.1, Parts A and B reflect differences in productivity for the bison studied at only one point in their annual cycles. Consideration must be given to how that productivity changes seasonally. As previously noted, the periods of increased energy requirements for male and female bison occur at different times of the year. Males are stressed during the breeding season in the late summer-early fall, whereas, breeding females are stressed most in late gestation and during lactation in early to late spring. There is evidence (Halloran 1968:24) as well, that the number of consecutive years that cows calve, affects their condition, potentially resulting in lighter weight in the fall. Lighter weights (and less fat) in the fall may lead also to greater stress in the late winter and spring. All bison, regardless of age or sex, experience a degree of nutritional stress over winter and in early spring in response to the lowered quality and quantity of available forage. One might expect mature, breeding females to be in poorest condition when these two conditions coincide, especially following multiple years of calving. In the fall, most adult females, unless individually impaired or exposed to severe and extended periods of submaintenance nutrition, should be in good condition. Fully mature males, on the other hand, may have a more complex cycle, with troughs in the condition cycle occuring in association with the rut and the winter-spring

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forage decline. One might anticipate, however, that the spring drop in male condition probably is not as marked as it is in pregnant and lactating cows. The question of which animals are fattest at this time of year remains, however, because factors of animal age and maturity determine how much fat is available prior to its mobilization.

Male Versus Female Productivity. Four year old, adult males probably do not produce a caloric yield in fat comparable to adult females, unless the unlikely event occurs where herd females alone are in conditions poorer than that seen in FAF. In Table 8.1, Parts A and B, Total Fat and Selected Fat are both smaller for SAM than for SAF. These bison were killed on the same day in the spring, but the male, SAM, produced only 81 to 84 percent of the caloric yield from fat as SAF (Table 8.2). It was suggested above that SAF might be in better than normal condition, but comparison of SAM with FAF, who was in poorer condition when killed, shows SAM is also less productive than that female. One might argue that this is not a fair comparison, because older animals should carry more fat than a younger animal of similar condition due to the longer period of fattening in older animals. The FAF value (Table 8.1, Part A) might be higher than a comparable value for an animal of similar age to SAF, if she were in poor condition like FAF.

In order to examine this issue and the possible relationship between a normal four year old male, such as SAM, and a female like SAF, but in poorer condition comparable to that seen in FAF, I calculated the caloric yields for a hypothetical SAF (Table 8.3). In Table 8.3, the smaller relative yields of the fat depots in FAF compared to SAF are evident in all depots except carcass fat where they are comparable. The lower FAF values are evidence of her poorer condition. In the last column of this table are the

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Table 8.2. Comparative Production Between Bison Based Upon Caloric Yield

Protein + Ash (PRO)

	FYM	SAM	SAF	FAF
FYM	----	46.4	64.8	61.0
SAM	----	----	139.7	131.5
SAF	----	----	----	94.1
FAF	----	----	----	----
kcal	52,710.8	113,592.0	81,328.0	86,382.4

Total Fat (TF)

	FYM	SAM	SAF	FAF
FYM	----	42.9	35.9	34.4
SAM	----	----	83.6	80.1
SAF	----	----	----	95.8
FAF	----	----	----	----
kcal	34,457.2	80,288.3	96,074.6	100,241.1

Selected Fat (SF)

	FYM	SAM	SAF	FAF
FYM	----	58.9	48.2	42.6
SAM	----	----	81.9	72.3
SAF	----	----	----	88.3
FAF	----	----	----	----
kcal	28,353.0	48,157.3	58,822.4	66,634.1

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Table 8.3. Approximations of Component Yield for SAF in Poor Condition

Product	Production (kcal)		Product:Protein Proportion		Caloric[a] Yield for Hypothetical SAF
	SAF	FAF	SAF	FAF	
Protein + Ash	81,328.0	86,382.4	100.0	100.0	81,328.0
Intramuscular Fat	37,252.2	33,607.0	45.8	38.9	31,636.6
Bone Grease Fat	8,898.3	7,007.4	10.9	8.1	6,587.6
Bone Marrow Fat	4,628.7	4,066.2	5.7	4.7	3,822.4
Carcass Fat[b]	55,295.4	55,560.5	68.0	64.3	52,293.9
Total Products (TP)	187,402.6	186,623.5			175,668.5
Total Fat (TF)	106,074.6	100,241.1			94,340.5
Selected Fat (SF)	68,822.4	66,634.1			62,703.9

[a] Value calculated by multiplying SAF protein total by the product:protein proportion for FAF for each product.

[b] Includes the subcutaneous, intermuscular, and cavity depots.

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caloric yields for the products, derived by using the protein value for the female, SAF, as the stable variable and the relative yields for the fat depots from FAF as the reducing variables. The three totals, including total products (TP), total fat (TF), and selected fat (SF) are also listed. These data indicate that if SAF were in a condition comparable to FAF, her total caloric yield based on either fat total (Table 8.3, TF and SF) would be reduced, but would remain substantially higher than those seen in the male, SAM (Table 8.1, Part A). Depending upon how good FAF is as a representative of cows in poor condition (there is reasonable evidence that she is in poor, but not extremely poor condition, and is far from the point of starvation), this suggests that in the spring, males four years of age and younger would probably rarely be the deliberate target of hunter selection.

Older males that are fully mature and have comparable fat content in the body as adult females, would be reasonable targets at this time of year, as their larger body size should yield larger total fat weights. It is not known, however, how many years past the four year age mark the males would have to be to have a fat content similar to mature females. It was reported in Chapter 7 that, at four years of age, the fat content of the carcass of SAM was 5.7 percent compared to the 9 to 10 percent fat reported for FAF and SAF. As long as adult male growth involves the significant addition of protein weight, male fat content should remain below that seen for mature females. The growth curves for bison in Chapter 2 suggest that after perhaps six years of age, growth in male bison slows. Although some protein growth probably continues after this age, it is seems likely that fat growth and depletion are the primary factors in weight changes after six years of age in male bison. Males over six years of age, being larger than mature

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females, and probably having reached maturity, would make good targets for selection in the late winter-early spring. By this age, their larger size and attainment of maturity might assure larger fat weight recoveries per animal killed. However, due to the smaller herd sizes of bull groups compared to cow/calf groups, as well as the possible inclusion of males in the herd that are not fully mature, total fat recovery might be smaller.

The taking of bull groups rather than cow/calf groups, although optimal in terms of package size and handling time, and suboptimal in terms of herd size, could also be considered a conservation measure. Removal of a cow/calf group reduces both current and future producers, whereas removal of a bull group affects a smaller segment of the potential reproductive population. However, the logic of such an argument applied to prehistoric peoples who killed large numbers of bison during the fall and early winter, focusing primarily on cow/calf herds seems minimal.

Conclusions Regarding Herd and Animal Selection and Carcass Productivity

The carcass composition data, together with expectations concerning changes in yield associated with the attainment of full maturity in the male bison, suggest that prehistoric patterns of herd selection focusing on cow/calf groups in the fall and early winter and primarily on bull groups composed of older males in the spring are consistent with the expectation that selection is dictated by productivity. It is also apparent that the relative productivity of fat versus protein differs for animals of different age, sex, and condition classes, and that the relative value of a given herd or animal is best evaluated by reference to energy yield. Once a kill has been made, the priority of butchering should be highest for animals yielding the largest amounts of the desired product(s). It is not expected that

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lower yielding carcasses would have been completely discarded, but that evidence for incomplete carcass use would be highest among the remains of such animals. This was demonstrated by Speth (1983) at the Garnsey Site, a spring season kill site. Here, male carcasses were processed to a greater extent than what were thought to be poorer conditioned female carcasses. Detailed sexing data from archaeological bison bone assemblages is practically nonexistent, which makes it difficult to evaluate selection after the kill in most cases. Sexing bones is quite time consuming, requiring multiple measurements of each bone. This makes it doubtful that it would be included as a regular component of bone assemblage analyses. Epiphyseal fusion, on the other hand, is readily determined, suggesting that at least some analyses of young versus adult selection is possible.

Carcass Unit Selection

After a bison kill, just as the whole carcasses of animals are evaluated for productivity, parts of individual or multiple carcasses may be evaluated with respect to each other for their relative productivity of carcass products. In Chapters 5, 6, and 7 the effects of age, sex, and condition differences on the production of individual carcass products were evaluated. It is doubtful, however, that recovery of a single product was ever the objective of a bison kill (except under the effects of the economic influences of American culture during historic times). Therefore, the combined influence of the relative productivity of multiple products in individual carcass units must be evaluated to determine whether selection, as represented by the bone remains of bison at kill and processing sites, reflects differences in the economic value of the associated carcass units. In order to do this, utility models are constructed that evaluate carcass

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units by their productivity and the likelihood of their being removed from a kill site.

The remainder of this section is devoted to consideration of (1) the history of the development and subsequent simplifications of carcass unit utility model construction; (2) the development and presentation of new models of carcass unit utility for bison that are significant with respect to both their construction (including single class, averaged, and mixed class models) and the combinations of carcass products utilized in their construction; (3) whether the previously described product distribution variabilities (Chapters 5 through 7) that are attributable to the influences of age, sex or condition are masked by averaged data model constructions; and (4) where the lack of fit between models and archaeological assemblages might occur due to variability in carcass composition. Table 8.4 provides a list of the acronyms and descriptions of the utility models discussed or presented in this dissertation.

Development of Archaeological Models of Carcass Utility

Lewis R. Binford (1978) first addressed the relationship between the economic utility of carcass parts and the presence and absence of their associated bone at archaeological sites in his book, Nunamiut Ethnoarchaeology. His models of utility were constructed based upon the assumption that the selection of carcass parts for transport to other locations for processing or consumption should reflect their value, modified to some extent in the appendicular units by their proximity to parts of higher value. Carcass units of high value should be removed from a kill site with greater frequency than parts of low value, and conversely, the

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Table 8.4. Glossary of Utility Model Names and Acronyms

Part A. Utility Models from Other Sources

Model Acronym	Description
MUI	Meat Utility Index (Binford 1978:21)
(S)MUI	Standardized Meat Utility Index (Binford 1978:21,23)
MI	Marrow Index (Binford 1978:27)
WGI	White Grease Index (Binford 1978:34)
GUI	General Utility Index (Binford 1978:73)
(S)GUI	Standardized General Utility Index (Binford 1978:73)
MGUI	Modified General Utility Index (Binford 1978:74)
MJ-MUI[a]	Meat Utility Index (Metcalfe and Jones 1988:489)
(S)MJ-MUI[a]	Standardized Meat Utility Index (Metcalfe and Jones 1988:489)
FUI	Food Utility Index (Metcalfe and Jones 1988:492)
(S)FUI	Standardized Food Utility Index (Metcalfe and Jones 1988:489)

[a] MUI and (S)MUI used by Metcalfe and Jones (1988); MJ- used to distinguish from Binford's MUI and standardized MUI.

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Table 8.4. (continued)

Part B. Utility Models for Bison

Model Acronym	Description
MJ-MUI	Gross Weight Model; equivalent to Metcalfe and Jones's (1988) MUI model construction
(S)MJ-MUI	Standardized Gross Weight Model; equivalent to Metcalfe and Jones's (1988) MUI model construction
(S)AVGMUI	Averaged (S)MJ-MUI model
(S)FUI	(S)MJ-MUI model modified for riders
(S)AVGFUI	Averaged (S)FUI model
TP	Total Products model; kcal production of all carcass resources
(S)TP	Standardized TP model
(S)MTP	(S)TP model modified for riders
(S)MAVGTP	Averaged (S)MTP model
(S)MMCTP	Mixed Class (S)MTP model
(S)M9PBTP	Nine Percent Bulls (S)MTP model
PRO	Protein model; kcal production based on weight of protein plus ash and 4 kcal/gm energy conversion
(S)PRO	Standardized PRO model
(S)MPRO	(S)PRO model modified for riders
(S)MAVGPRO	Averaged (S)MPRO model
(S)MMCPRO	Mixed Class (S)MPRO model

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Table 8.4. (continued)

Part B. Utility Models for Bison (continued)

Model Acronym	Description
MAR	Marrow Fat model; kcal production based on weight of marrow fat and 9 kcal/gm energy conversion
(S)MAR	Standardized MAR model
(S)MMAR	(S)MAR model modified for riders
(S)MAVGMAR	Averaged (S)MMAR model
(S)MMCMAR	Mixed Class (S)MMAR model
WG	White Grease Fat model; kcal production based on the weight of white grease fat and 9 kcal/gm energy conversion
(S)WG	Standardized WG model
(S)MWG	(S)WG model modified for riders
(S)MAVGWG	Averaged (S)MWG model
(S)MMCWG	Mixed Class (S)MWG model
YG	Yellow Grease Fat model; kcal production based on the weight of yellow grease fat and 9 kcal/gm energy conversion
(S)YG	Standardized YG model
(S)AVGYG	Averaged (S)YG model
(S)MCYG	Mixed Class (S)YG model

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Table 8.4. (continued)

Part B. Utility Models for Bison

Model Acronym	Description
TF	Total Fat model; kcal production of the following fat depots: skeletal, intramuscular, intermuscular, subcutaneous, and body cavity; excludes visceral depots
(S)TF	Standardized TF model
(S)MTF	(S)TF model modified for riders
(S)MAVGTF	Averaged (S)MTF model
(S)MMCTF	Mixed Class (S)MTF model
SF	Selected Fat model; kcal production of the following fat depots: skeletal intermuscular, subcutaneous, and body cavity; excludes intramuscular, and visceral depots
(S)SF	Standardized SF model
(S)MSF	(S)SF model modified for riders
(S)MAVGSF	Averaged (S)MSF model
(S)MMCSF	Mixed Class (S)MSF model
GRE	Grease Fat model; kcal production based on the weight of the yellow and white grease fat and 9 kcal/gm energy conversion
(S)GRE	Standardized (S)GRE model
(S)MGRE	(S)GRE model modified for riders
(S)MAVGGRE	Averaged (S)MGRE model
(S)MMCGRE	Mixed Class (S)MGRE model

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Table 8.4. (continued)

Part B. Utility Models for Bison (continued)

Model Acronym	Description
SKF	Skeletal Fat model; kcal production on weight of marrow and grease fat and 9 kcal/gm energy conversion
(S)SKF	Standardized SKF model
(S)MSKF	(S)SKF model modified for riders
(S)MAVGSKF	Averaged (S)MSKF model
(S)MMCSKF	Mixed Class (S)MSKF model

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bones left behind at a kill site should include greater frequencies of units of low productivity.

To model the general utility of different carcass parts, Binford first constructed component models of utility for the production of (1) marrow, (2) bone grease, and (3) all carcass products except dry bone. The marrow and grease indices were constructed to include the influence of product quantity as well as quality, and in the case of the marrow index, to include a measure of the efficiency of processing bone to recover this product. Binford combined the three indices into one index, the General Utility Index (GUI), and subsequently modified it (yielding the Modified General Utility Index or MGUI) in order to account for the effect of riders. This refers to the fact that parts of low utility are often transported away from the kill site in frequencies higher than would be expected given their utility values. These appendicular units act as riders, being removed from the site due to their proximity to, or location between parts of higher utility. Metcalfe and Jones (1988) suggest that this is a reflection of the costs of removing these low utility parts. Their presence at the kill site, they argue, reflects the trade off between butchering and transportation costs.

Simplifications of Binford's Models

Metcalfe and Jones (1988) argue that Binford's models of general utility (GUI and MGUI) are unnecessarily complex. They present a simplified model (which they also designated MUI--designated MJ-MUI here to distinguish it from Binford's model) based upon Binford's caribou data, which is derived by subtracting the dry bone weight from the gross weight of each part, thus representing the weight of all edible tissue. Some non-edible tissue, such as cartilage and ligament, is included in these values as well. Metcalfe

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and Jones show that this MJ-MUI is essentially equivalent to Binford's MUI, and is quite similar to his derived GUI. They argue that their simplified model permits greater understanding of the effects of data manipulations than Binford's GUI model which depends upon multiple data manipulations.

As with Binford's GUI, MJ-MUI cannot deal with the problem of riders. Therefore, they apply Binford's rider averaging routine to their standardized, simplified model, (S)MJ-MUI, to calculate a new model, (S)FUI (the standardized Food Utility Index), which is basically a simplified version of Binford's MGUI. To construct FUI, the gross weight data (MJ-MUI) are first standardized by expressing the value of each carcass unit as a percent of the value of the unit having the highest value, yielding (S)MJ-MUI. Metcalfe and Jones's practice of using a preceding (S) to indicate the model is standardized is followed here. An averaging routine is applied to the (S)MJ-MUI values of the appendicular units to account for the effect of riders, yielding a standardized Food Utility Index ((S)FUI).

It should be noted that both Binford's and Metcalfe and Jones's models deviate from being direct reflections of relative carcass unit value in two ways. First, whole and bone group weights are used to determine the MUI and MJ-MUI values for some appendicular units and for the atlas and axis, apparently because specific data for each unit were not available. For example, the weight of the whole femur is used as a substitute for the actual weights of the proximal and distal ends in the computation of MUI and MJ-MUI. Similarly, the group weight of the carpals plus the metacarpal is substituted for the actual weights of each end of the metacarpal and for the carpals in the derivation of the MUI and MJ-MUI values for these units. Metcalfe and Jones (1988:495-496) suggest this model construction procedure may account for the absence of a stepped or threshold function in the

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relationship between economic utility and abandoned elements, but they duplicate the practice in the construction of their simplified MJ-MUI and FUI models. The result is that the values of the appendicular and the atlas-axis units are artificially inflated relative to those of the axial units. It is not clear why one would want to do this, so the practice is not continued in this study, except in the construction of the bison (S)FUI model presented here for comparative purposes.

The second deviation from direct reflection of carcass unit value is in the application of the averaging routine used to account for the effect of riders. This modification also increases the value of most appendicular units. Together, these two model construction procedures work to increase the value of the appendicular units relative to the axial units. Although this increase in an understandable modification when used to account for riders, the initial doubling of unit values by use of the whole or group unit value is not. In my opinion this should be avoided, because it tends to mask differences between axial and appendicular use. This is illustrated in the next chapter.

Carcass Unit Selection Models for Bison

Speth's (1983, 1988) work and Metcalfe and Jones's (1988) discussions of the lack of direct linear correspondence between the MGUI and FUI models of economic utility and bone abandonment at kill sites suggest that the construction of these models may not adequately reflect differences in the economic value of the body parts. Speth (1983) indicates this is probably due to differences in animal condition between the sexes which result in variability in productivity for the same unit in different animals, which is not reflected in Binford's MGUI model. Metcalfe and Jones (1988) agree that

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age, sex and condition differences between animals could contribute to the disparity between economic value and bone abandonment, but also suggest that it could be accounted for in the construction of FUI models, if the anatomical data were available.

In this study of bison anatomy and selection modeling, the differences in productivity between animals of different age, sex and condition classes are considered important, and changes in utility model constructions have been incorporated to account for these differences. The first involves changing the unit of measure used to compare productivity. The models of body part utility presented in this chapter are based upon measures of caloric yield rather than product weight yield, unless so specified. This is done in order to account for differences in the energy value of protein and fat, and in recognition of the importance of fat in the hunter-gatherer diet during periods of low calorie and carbohydrate intake.

The second change involves using different methods of model construction to produce different types of utility models (single class, averaged, and mixed class models) which vary in their capability of dealing with differences in animal class variability, but which are all needed due to differences in the detail of analysis of archaeological bone assemblage composition (e.g., indicating the numbers of male and female bones).

The third change in model construction presented in this study of the economic anatomy of bison involves the addition of models that incorporate caloric yield data for new combinations of carcass products. Several models reflecting the importance of fat are presented, including for example, a total fat (TF) model.

All of the changes in construction incorporated into the bison models presented here are based upon quantitative differences alone. Although

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qualitative differences or differences in processing costs (e.g., Jones and Metcalfe 1988) may have important influences on utility value, it is important to determine whether quanitative differences alone can account for selection priorities. Lacking specific data of qualitative differences between carcass units or on the relative costs associated with recovering products, it is currently not possible to incorporate measures of these differences into the carcass utility models presented here.

Measuring Productivity

Binford's (1978) models and Metcalfe and Jones's (1988) simplifications of these models, assess the value of a carcass unit based upon differences in the weights of the parts, or based upon some proxy of the relative differences in productivity. No distinction is made in the relative value of fat over protein for the production of energy--that is, a unit weight of protein is considered of equal, and sometimes greater value to a unit weight of fat, despite the higher energy value of fat. In Binford's (1978:72) construction of the standardized General Utility Index ((S)GUI) for example, the contributing value of the marrow and grease fractions from each unit are reduced by multipling each value of the contributing indices (meat, marrow, and white grease) by constants said to represent the relative proportions of the products as components of carcass gross weight minus dry bone weight. The effect of this modification is to further reduce the importance of the two fat components he includes in the derivation of the standardized GUI. As a result, meat weight is the dominant component of utility, and as Metcalfe and Jones (1988) note, the GUI is essentially identical to Binford's MUI in the relative ranking of the carcass parts.

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Speth's (1983) argument that fat plays an especially important role in the diet of hunters during the spring, and his discussion (1988, 1989) of the possible effects of protein poisoning and the importance of fat in the diet when carbohydrates are few or absent, and calories are low, both suggest that determination of the relative value of carcass units based solely on weight production (which equates protein value with fat value) may not adequately express unit value variability.

Weight Versus Caloric Yield Models. The comparison between weight and caloric yield is examined here in two respects: first, as it relates to measures of gross weight and second, as it relates to total products weight. The distinction is in what is included in the weight variable, which is specified in the discussion of each weight to caloric yield comparison.

Caloric yield is compared first with the value of gross weight minus dry bone weight, which is designated GWT. The GWT values are not identical to the MJ-MUI values (Appendix C, Table 1, Part A) because grouped bone data is substituted for the actual weights of some units in the construction of the latter model. Evaluating whether caloric yield provides a different unit ranking than weight yield, demands that comparable units be used in the analysis. It is expected that recognition of the differences in the energy yield of protein and fat may result in changes in the rank order of body parts. If no differences are registered, then GWT data should be adequate to model selection.

Figure 8.1 illustrates rank comparisons based on GWT and caloric yield. It shows that the rank of the caudal unit (CAUD) increases when expressed in terms of calories rather than weight, and the rank of the head (SKWOT, the skull and mandible without the tongue) decreases. Many of the other changes in rank appear to occur in response to the changes in the rank of the caudal

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Figure 8.1. Rank Comparison of Carcass Units Based Upon GWT and Caloric Yield

FYM				SAM			
GWT[a] (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)	GWT[a] (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)
33,160.6	FEMP	FEMP	18,135.0	64,750.6	FEMP	FEMP	37,228.0
17,338.7	RIBS	RIBS	10,757.4	43,462.9	RIBS	RIBS	28,939.3
14,299.8	THOR	THOR	10,044.8	32,218.8	THOR	THOR	21,678.9
12,704.2	LUMB	LUMB	9,756.6	31,303.5	C3C7	LUMB	19,384.8
10,871.0	STER	SPEL	6,730.6	27,552.7	LUMB	C3C7	18,298.6
10,448.9	C3C7	STER	6,381.7	23,393.1	SPEL	SPEL	14,298.3
10,444.6	SPEL	C3C7	5,930.0	20,549.8	STER	STER	13,367.9
8,577.1	HUM	HUM	4,744.3	19,809.6	SCAP	HUM	11,143.6
8,279.4	SKWOT	SCAP	4,342.9	19,259.8	HUM	SCAP	9,577.2
7,948.2	SCAP	TIB	3,070.7	17,988.5	SKWOT	TIB	5,888.7
5,911.7	TIB	RUL	2,489.8	9,946.3	TIB	SKWOT	4,006.7
3,908.6	RUL	SKWOT	1,521.3	7,511.7	RUL	RUL	3,865.9
1,345.9	AXIS	AXIS	819.8	4,183.6	AXIS	AXIS	2,521.4
1,048.3	ATLAS	ATLAS	678.4	3,273.2	ATLAS	ATLAS	2,061.6
937.4	MTT	MTT	487.0	1,506.8	MTC	MTT	425.4
850.9	MTC	MTC	345.3	1,380.2	MTT	MTC	332.1
811.4	TARS	TARS	300.6	1,170.0	APHA	TARS	297.9
602.1	PPHA	PPHA	209.9	1,064.4	TARS	CAUD	223.0
583.5	APHA	APHA	166.3	1,003.5	PPHA	PPHA	169.2
341.2	CARP	CARP	133.2	597.5	CARP	APHA	122.6
274.8	CAUD	CAUD	122.4	484.1	CAUD	CARP	48.6

[a] GWT equals unit gross weight minus the dry bone weight.

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Figure 8.1. (continued)

SAF				FAF			
GWT[a] (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)	GWT[a] (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)
51,765.4	FEMP	FEMP	34,946.5	51,641.6	FEMP	FEMP	34,119.5
31,307.3	RIBS	RIBS	28,085.2	35,803.9	RIBS	RIBS	25,784.9
25,701.7	LUMB	THOR	24,374.9	25,662.3	LUMB	LUMB	23,396.0
24,330.4	THOR	LUMB	23,380.8	25,569.4	THOR	THOR	21,548.8
19,330.1	SPEL	SPEL	15,779.2	22,273.7	C3C7	C3C7	16,479.5
16,306.5	C3C7	STER	13,289.7	18,799.8	STER	STER	15,120.8
14,927.3	STER	C3C7	12,415.5	17,458.6	SPEL	SPEL	13,016.6
14,696.5	HUM	HUM	11,147.3	13,300.7	HUM	HUM	8,719.9
12,104.2	SKWOT	SCAP	6,095.3	13,235.5	SCAP	SCAP	8,053.9
11,320.5	SCAP	TIB	4,870.5	12,870.4	SKWOT	TIB	6,039.5
6,393.2	TIB	SKWOT	3,838.4	8,298.8	TIB	SKWOT	3,899.9
4,942.0	RUL	RUL	3,518.2	5,140.4	RUL	RUL	3,362.4
2,151.2	AXIS	AXIS	1,729.1	2,962.5	AXIS	AXIS	2,264.6
1,712.7	ATLAS	ATLAS	1,410.4	2,316.1	ATLAS	ATLAS	1,869.3
903.5	MTC	MTT	574.5	1,027.5	MTT	MTT	717.2
866.8	MTT	CAUD	519.1	961.5	MTC	CAUD	538.9
759.8	TARS	MTC	439.1	745.2	APHA	MTC	510.5
707.0	APHA	TARS	367.2	655.3	TARS	APHA	429.8
601.0	PPHA	APHA	306.2	631.8	PPHA	PPHA	366.3
558.2	CAUD	PPHA	219.2	544.5	CAUD	TARS	354.6
340.0	CARP	CARP	96.3	380.5	CARP	CARP	30.6

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and head units, but each of the animals exhibit some other minor changes in unit rank positions, as well. In general, however, it appears that with the major exceptions of the head and tail, the GWT and caloric yield data provide similar, though not identical results in body part ranking.

This comes as a surprise, because the difference in caloric yield for protein (4 kcal/gm) and fat (9 kcal/gm) represents an increase of 125 percent. A difference of this magnitude was expected to be evident through rank order changes. It is possible, however, that the differences in what is included in the measure GWT and caloric yield is partly involved in the small number of rank changes. As the weight of the unit minus the weight of the associated dry bone, GWT includes the weight of several products that are not included in the evaluation of caloric yield. These include ligament, tendon, fasciae, cartilage, and water associated with muscle and adipose tissue. It is impossible, therefore, to determine why some units change rank and others do not, and whether or not the difference in the caloric yield of fat and protein is important.

For this reason, the caloric yield data are compared with a second set of weight data for the four TRNP bison (Figure 8.2). In this figure, product weight is used instead of GWT. Product weight includes the weight of the protein and fat for each unit. It differs from GWT in the exclusion of the water weight associated with muscle and adipose tissue as well as ligament, tendon, and cartilage weight.

Once again, very few units increase or decrease in rank when order is determined on the basis of caloric yield rather than product weight (Figure 8.2). The caudal unit (CAUD) continues to demonstrate a change in rank, but decreases in value relative to the surrounding units when caloric yield is the determinant of rank order. In Figure 8.2 only protein and fat are used

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Figure 8.2. Rank Comparison of Carcass Units Based Upon Product Weight and Caloric Yield

FYM				SAM			
Product Wt (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)	Product Wt (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)
4,154.6	FEMP	FEMP	18,135.0	8,058.8	FEMP	FEMP	37,228.0
2,193.3	RIBS	RIBS	10,757.4	5,656.7	RIBS	RIBS	28,939.3
1,923.1	THOR	THOR	10,044.8	4,073.6	THOR	THOR	21,678.9
1,875.2	LUMB	LUMB	9,756.6	3,674.6	LUMB	LUMB	19,384.8
1,364.1	SPEL	SPEL	6,730.6	3,654.0	C3C7	C3C7	18,298.6
1,272.9	STER	STER	6,381.7	2,815.4	SPEL	SPEL	14,298.3
1,225.3	C3C7	C3C7	5,930.0	2,525.4	STER	STER	13,367.9
976.7	HUM	HUM	4,744.3	2,304.0	HUM	HUM	11,143.6
974.1	SCAP	SCAP	4,342.9	2,129.1	SCAP	SCAP	9,577.2
580.5	TIB	TIB	3,070.7	1,149.1	TIB	TIB	5,888.7
479.0	RUL	RUL	2,489.8	776.1	RUL	SKWOT	4,006.7
282.6	SKWOT	SKWOT	1,521.3	762.2	SKWOT	RUL	3,865.9
169.0	AXIS	AXIS	819.8	503.0	AXIS	AXIS	2,521.4
139.1	ATLAS	ATLAS	678.4	411.4	ATLAS	ATLAS	2,061.6
59.8	MTT	MTT	487.0	49.4	MTT	MTT	425.4
38.9	MTC	MTC	345.3	44.0	CAUD	MTC	332.1
34.2	TARS	TARS	300.6	36.9	MTC	TARS	297.9
24.2	CAUD	PPHA	209.9	35.6	TARS	CAUD	223.0
23.8	PPHA	APHA	166.3	19.2	PPHA	PPHA	169.2
19.1	APHA	CARP	133.2	14.3	APHA	APHA	122.6
14.8	CARP	CAUD	122.4	5.4	CARP	CARP	48.6

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Figure 8.2. (continued)

SAF				FAF			
Product Wt (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)	Product Wt (gm)	Carcass Unit	Carcass Unit	Caloric Yield (kcal)
7,264.9	FEMP -	- FEMP	34,946.5	7,005.3	FEMP -	- FEMP	34,119.5
4,908.3	RIBS -	- RIBS	28,085.2	4,812.3	RIBS -	- RIBS	25,784.9
4,069.4	LUMB -	- THOR	24,374.9	4,075.8	LUMB -	- LUMB	23,396.0
4,061.3	THOR -	- LUMB	23,380.8	3,733.8	THOR -	- THOR	21,548.8
2,869.3	SPEL -	- SPEL	15,779.2	3,194.8	C3C7 -	- C3C7	16,479.5
2,301.5	STER -	- STER	13,289.7	2,659.8	STER -	- STER	15,120.8
2,272.6	C3C7 -	- C3C7	12,415.5	2,380.0	SPEL -	- SPEL	13,016.6
2,078.7	HUM -	- HUM	11,147.3	1,681.9	HUM -	- HUM	8,719.9
1,274.7	SCAP -	- SCAP	6,095.3	1,626.8	SCAP -	- SCAP	8,053.9
865.7	TIB -	- TIB	4,870.5	1,135.5	TIB -	- TIB	6,039.5
688.0	SKWOT -	- SKWOT	3,838.4	678.3	SKWOT -	- SKWOT	3,899.9
629.2	RUL -	- RUL	3,518.2	627.6	RUL -	- RUL	3,362.4
314.9	AXIS -	- AXIS	1,729.1	439.1	AXIS -	- AXIS	2,264.6
257.2	ATLAS -	- ATLAS	1,410.4	361.1	ATLAS -	- ATLAS	1,869.3
83.4	CAUD -	- MTT	574.5	88.8	MTT -	- MTT	717.2
65.5	MTT -	- CAUD	519.1	85.4	CAUD -	- CAUD	538.9
48.9	MTC -	- MTC	439.1	60.1	MTC -	- MTC	510.5
42.1	TARS -	- TARS	367.2	52.6	APHA -	- APHA	429.8
35.5	APHA -	- APHA	306.2	45.3	TARS -	- PPHA	366.3
25.0	PPHA -	- PPHA	219.2	44.1	PPHA -	- TARS	354.6
10.7	CARP -	- CARP	96.3	3.4	CARP -	- CARP	30.6

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to rank body parts, whether the order is determined by caloric yield or weight. Apparently the drop in caudal unit rank below other more subordinate units when rank is based on caloric yield rather than weight is due to the smaller proportion of total yield that is derived from fat, in conjunction with the relatively comparable total weights of the products.

Clearly the difference in total yield between adjacent units is important in determining whether a change in measurement can affect rank. For a lower ranked unit (based on weight) to increase in rank (when caloric yield is determined) above a heavier, higher ranked unit, the proportion of fat in the lighter weight unit must be greater. The fat proportion must be large enough to match the fat yield in the heavier unit, and be still large enough to account for more than the difference in calories determined by the protein yields of the units. Only then can the lighter unit outrank the heavier unit when caloric yield is determined. Apparently this does not happen often in these bison.

The general lack of major changes in rank order when product weight is used rather than caloric yield, suggests that in wild animals that have relatively low fat content, weight values may be an adequate substitute for the more detailed caloric yield values when they are not available. When fat content increases as a proportion of yield, due either to better animal condition or to a greater species tendency to accumulate fat, the potential for a change in rank order increases when caloric yield is used instead of weight. Caloric yield always provides the best measure of energy value, but it may not always be possible to gather this data, and in some cases, it appears that weight data are adequate to meet modeling data needs. From comparisons of Figures 8.1 and 8.2, and because it is easier to understand why changes in rank occur when they do, the more difficult to gather,

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product weight and caloric yield data are preferred. In the absence of these data, gross-weight-based data provide a better measure of economic utility than data from substitute species. In this study, I have used the caloric yield data to construct the models of carcass unit utility, because the data are available and no judgements are necessary on how to modify units that change rank.

New Model Development

Speth's (1983) analysis of the treatment of male and female carcasses at the Garnsey Site demonstrates that variability in carcass composition between animals of different age, sex and condition, and its influence on selection cannot be modeled adequately by the existing MGUI (Binford 1978) and FUI (Metcalfe and Jones 1988) models. Nevertheless, not all archaeological bone assemblages have been analyzed for differences in the treatment of the carcasses of males and females or adults and juveniles. This suggests that there is need for different types of models to handle the variability in analytical needs. The existing caribou MGUI and FUI models developed by Binford (1978) and Metcalfe and Jones (1988) are based upon the carcass composition data from one animal. Binford's (1978) sheep MGUI model, however, is derived from the data provided by two carcasses. He averaged the data from each sheep, with some modifications, to produce a single model to represent sheep in general. In the present study, data are available for four bison that are used as representatives of animals in different age, sex and condition classes. These data may be averaged, as in Binford's sheep example, to indicate general economic utility. Models based upon this type of construction are referred to in this dissertation as averaged models. They differ somewhat in construction from Binford's MGUI

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and Metcalfe and Jones's FUI, as discussed shortly, but the intent is the same--to serve as a general model of economic utility.

In previous chapters, differences in the production and distribution of various carcass products were noted and the influences of age, sex and condition on these differences were considered. The data from each of the bison individuals (in the absence of larger samples) may be used to construct separate models, here referred to as single class models, that would be useful in analyzing bone assemblages dominated by immature males (represented by the FYM-based models), young adult males (represented by SAM), adult females in good condition (represented by SAF), or older females in declining condition (represented by FAF). Like averaged models, these single class models are not adequate to investigate differential use of carcass parts related to variable productivity.

A new model type, referred to as mixed class models are developed here in order to deal with selection that involves the concurrent evaluation of the body parts of individuals of different age, sex or condition classes. Its development was suggested by the work of Speth (1983) who demonstrated differential treatment of male and female body parts at the Garnsey Site, and by Metcalfe and Jones (1988) who suggested that weight differences in body parts due to age or sex, could be incorporated into a FUI model, if available.

Mixed class models use data from at least two classes of animals (for example, males and females). Unlike averaged models, the construction of mixed class models permits the maintained separation of the class representatives--that is, there are model values for male ribs and female ribs, for example. Mixed class model applications differ from overlayed applications of single class models for males and females, continuing the

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example, because the data for each class are expressed according to the same scale. If, for example, the male ribs unit is the highest yielding part from either class, then all other male and female body parts are standardized by expressing them as a proportion of this yield. By expressing all parts relative to one scale, differences in unit value are incorporated into the model and differences in the treatment of male and female units may be understood with reference to the differences in their relative economic value. The MGUI and FUI models, as constructed, do not do this.

In order to understand the difference between the types of models presented here (i.e., single class, averaged and mixed class models), as well as the significance of the differences between the models when applied to archaeological assemblages, it is first necessary to understand how they are constructed. The construction of single class models are described in detail. Averaged and mixed class model constructions employ similar procedures with some modifications which are described below.

Single Class Model Construction. Single, averaged and mixed class model construction starts with a basic data set which represents the weight or caloric yield of the product(s) associated with each carcass unit. For example, the total products models (TP) list the combined caloric yields of the protein, and the marrow, grease, and carcass fats (TP models for each of the animal class representatives are presented in Table 8.5, Part A).

In most cases, the second step in model construction is to standardize this data by expressing the value of each unit as a percent of the highest yielding unit. Thus, each carcass unit has a value ranging between zero and 100. The standardized data does not differ from the original data except for a change in the expression of scale. In our example, TP becomes (S)TP

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Table 8.5. Single Class, Total Products Model (TP)

Part A. Model TP (kcal production)

Anatomical Unit	Total Products (TP)			
	FYM	SAM	SAF	FAF
SKWOT	1,521.3	4,006.7	3,838.4[a]	3,899.9
ATLAS[b]	678.4	2,061.6	1,410.4	1,869.3
AXIS[b]	819.8	2,521.4	1,729.1	2,264.6
C3C7[b]	5,930.0	18,298.6	12,415.5	16,479.5
THOR	10,044.8	21,678.9	24,374.9	21,548.8
LUMB	9,756.6	19,384.8	23,380.8	23,396.0
SPEL	6,730.6	14,298.3	15,779.2	13,016.6
CAUD	122.4	223.0	519.1	538.9
RIBS	10,757.4	28,939.3	28,085.2	25,784.9
STER	6,381.7	13,367.9	13,289.7	15,120.8
SCAP	4,342.9	9,577.2	6,095.3	8,053.9
PHUM	2,462.6	5,939.0	5,728.0	4,595.3
DHUM	2,281.7	5,204.6	5,419.3	4,124.6
PRUL	1,291.7	1,922.6	1,838.3	1,705.5
DRUL	1,198.1	1,943.3	1,679.9	1,656.9
CARP	133.2	48.6	96.3	30.6
PMTC	137.1	172.8	210.1	264.7
DMTC	208.2	159.3	229.0	245.8
APHA	166.3	122.6	306.2	429.8
PFEM	9,020.7	18,661.7	17,325.2	17,086.3
DFEM	9,114.3	18,566.3	17,621.3	17,033.2
PTIB	1,639.3	3,248.7	2,761.5	3,129.1
DTIB	1,431.4	2,640.0	2,109.0	2,910.4
TARS	300.6	297.9	367.2	354.6
PMTT	216.5	204.6	262.5	328.9
DMTT	270.5	220.8	312.0	388.3
PPHA	209.9	169.2	219.2	366.3

[a] Caloric yield of protein estimated.

[b] Estimated subdivisions of the larger cervical unit, based upon the following proportions: ATLAS = 9 % CERV, AXIS = 11 % CERV, and C3C7 = 80 % CERV.

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Table 8.5. (continued)

Anatomical Unit	Part B. (S)TP				Part C. (S)MTP			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	14.1	13.8	13.7	15.1	14.1	13.8	13.7	15.1
ATLAS	6.3	7.1	5.0	7.2	6.3	7.1	5.0	7.2
AXIS	7.6	8.7	6.2	8.8	7.6	8.7	6.2	8.8
C3C7	55.1	63.2	44.2	63.9	55.1	63.2	44.2	63.9
THOR	93.4	74.9	86.8	83.6	93.4	74.9	86.8	83.6
LUMB	90.7	67.0	83.2	90.7	90.7	67.0	83.2	90.7
SPEL	62.6	49.4	56.2	50.5	62.6	49.4	56.2	50.5
CAUD	1.1	0.8	1.8	2.1	1.1	0.8	1.8	2.1
RIBS	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
STER	59.3	46.2	47.3	58.6	59.3	46.2	47.3	58.6
SCAP	40.4	33.1	21.7	31.2	40.4	33.1	21.7	31.2
PHUM	22.9	20.5	20.4	17.8	40.4	33.1	21.7	31.2
DHUM	21.2	18.0	19.3	16.0	30.8	25.6	20.5	23.6
PRUL	12.0	6.6	6.5	6.6	21.4	16.1	13.5	15.1
DRUL	11.1	6.7	6.0	6.4	16.3	11.4	9.8	10.8
CARP	1.2	0.2	0.3	0.1	9.1	6.0	5.4	6.2
PMTC	1.3	0.6	0.7	1.0	5.5	3.3	3.3	4.0
DMTC	1.9	0.6	0.8	1.0	3.7	2.0	2.2	2.8
APHA	1.5	0.4	1.1	1.7	2.6	1.2	1.6	2.3
PFEM	83.9	64.5	61.7	66.3	84.7	64.5	62.7	66.3
DFEM	84.7	64.2	62.7	66.1	84.7	64.4	62.7	66.2
PTIB	15.2	11.2	9.8	12.1	50.0	37.8	36.3	39.2
DTIB	13.3	9.1	7.5	11.3	31.6	23.4	21.9	25.2
TARS	2.8	1.0	1.3	1.4	17.2	12.2	11.6	13.4
PMTT	2.0	0.7	0.9	1.3	9.9	6.5	6.3	7.4
DMTT	2.5	0.8	1.1	1.5	6.2	3.7	3.7	4.5
PPHA	2.0	0.6	0.8	1.4	4.1	2.1	2.3	2.9

Note: (S)TP values calculated from data in **Part A.**

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(Table 8.5, Part B) when the value for each carcass unit is divided by the value for the ribs (which in this model is the highest yielding part in each of the four bison studied).

The third step in model construction is to modify the standardized data (the unaltered data could also be modified in this manner with similar results), in order to account for the effect of riders, yielding (S)MTP (Table 8.5, Part C). As for all models developed here (except for the MUI and FUI models) the initial M serves as an indicator that the data were modified to account for the effect of riders. This modification is performed only on the appendicular units (the axial unit values remain unchanged from (S)TP and in all other models). The rider averaging routine is described by Binford:

> I reasoned that the probability of a given part being assimilated to a part of higher value will increase as a function of the mean value between the two parts. Where a given part has a low value but is anatomically between two parts of higher value, it would be assimilated to the part of highest value as a function of the mean of the general utility value for the adjacent parts of higher value [1978:74].

The specific application of this rule is somewhat complex, and my evaluation of how it works differs slightly from the assessment of Metcalfe and Jones (1988). A more detailed explanation is needed.

In most cases, the more proximal units of the limb are ranked higher than the more distal units (see the raw data or standardized models, Tables 8.5, Parts A or B, or similar models in Appendix C), and the decrease in value follows down the limb, with perhaps one or two units in the distal portion of the limb having higher value than a more intermediate unit. When

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this occurs, the averaging routines described by Binford (1978) and Metcalfe and Jones (1988) are easily understood. For example, the (S)MTP value of a unit (the proximal metatarsal (PMTT) of SAF, for example) that has a lower (S)TP value than the surrounding units (Table 8.5, Part B), increases in value as a function of the average of the modified value ((S)MTP, Table 8.5, Part C) of the higher unit (the tarsals (TARS) in this example) and the standardized value ((S)TP, Table 8.5, Part B) of the next unit (the distal metatarsal (DMTT)). Occassionally, however, two other situations occur which are not addressed by Binford's or Metcalfe and Jones's discussions of the rider averaging routine.

Sometimes more than one or two intermediate units are lower in value than a more distal unit, and sometimes the highest valued part in a limb occurs somewhere besides the most proximal unit. When the first of these occurs, and a part has an unmodified index value ((S)TP) that is lower than any part more proximal and distal to it, its value is determined by averaging the previously modified index value ((S)MTP) of the higher valued part immediately adjacent to it and the unmodified index value ((S)TP) of the next highest valued unit in the limb that lies in the same direction (i.e., toward the distal end if that is the direction of the determination), regardless of whether it is immediately adjacent to the part in question. Thus, two or more units may lie between the two units used to determine the value for the unit in question. This routine is followed for each subsequent low valued unit lying between the units of higher value. That is, each successive (S)MTP value is averaged with the more distal high valued ((S)TP) unit until the (S)MTP value has been determined for the high valued (S)TP unit itself. An example may help to clarify how this works.

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Examination of the (S)TP data for the foreleg of the female, FAF (Table 8.5, Part B), shows that the values of the units decrease in magnitude as one moves from the proximal toward the distal end, until one reaches the carpal-proximal metacarpal (CARP-PMTC) unit junction. Units lower than the carpal unit all have higher values than this unit, and the anterior phalanges (APHA) unit has the highest value of these four more distal units. The (S)MTP values for the carpal and proximal metacarpal units are as follows:

$$\text{(S)MTP (CARP)} = \frac{\text{(S)MTP (DRUL)} + \text{(S)TP (APHA)}}{2}$$

$$\text{(S)MTP (PMTC)} = \frac{\text{(S)MTP (CARP)} + \text{(S)TP (APHA)}}{2}$$

Had the distal metacarpal (DMTC) unit had the highest value rather than the anterior phalanges (as seen in the data for FYM, Table 8.5, Part B), then the value for the distal metacarpal (DMTC) would be substituted in the equations above for the (S)TP value of the anterior phalanges (APHA), through the determination of the (S)MTP value for the distal metacarpal. The (S)MTP value for the phalanges (APHA) would then be determined by averaging the (S)MTP value for the distal metacarpal and the (S)TP value for the anterior phalanges.

Exceptions to this pattern of averaging unit values of the appendicular units include the proximal humerus (PHUM) and proximal femur (PFEM) units. Binford's practice is to raise the value of the proximal humerus to that of the scapula (SCAP) and the proximal femur (PFEM) to that of the distal femur

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(DFEM), if they are lower. This practice is followed in the construction of the utility models for bison unless the highest valued unit of the limb is not in the most proximal units. For example, the distal radius-ulna (DRUL) unit in the (S)MGRE model of FYM (Appendix C, Table 8, Part C) is the highest valued unit of the limb and the more proximal units decrease in value as they increase in distance from that unit.

Averaged Model Construction. Construction of averaged models, where the data from all four bison are used, is similar to that described above. The averaging of values for the four animals takes place at the level of the standardized data. For example, the mean of the four (S)TP values for the bison are determined for each unit, yielding (S)AVGTP (Table 8.6). The rider averaging routine is then applied to these values, yielding the standardized, modified averaged TP model ((S)MAVGTP, Table 8.6). In the construction of these models, the determination of the mean is performed on the standardized data, rather than on the caloric yield data, in order to reduce the influence of the variability in productivity that relates to animal size rather than differences in distribution. For example, the caloric production of the proximal humerus (PHUM) in FYM and SAM is substantially different (Table 8.5, Part A), but the difference in the proportion this unit represents of the caloric output of the highest valued unit (the ribs unit) for each animal (Table 8.5, Part B) is not particularly large. Using the standardized data reduces the influence of size differences while maintaining the recognition of distribution differences.

When the highest valued unit in the individual models is not the same for each animal, the averaged model does not have a unit valued at 100. When this occurs, the averaged values are standardized by dividing each unit by the unit with the maximum value and multiplying by 100. The protein

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Table 8.6. Averaged Total Products Model ((S)MAVGTP)

Anatomical Unit	Model (S)AVGTP	Model (S)MAVGTP
SKWOT	14.2	14.2
ATLAS	6.4	6.4
AXIS	7.8	7.8
C3C7	56.6	56.6
THOR	84.7	84.7
LUMB	82.9	82.9
SPEL	54.7	54.7
CAUD	1.5	1.5
RIBS	100.0	100.0
STER	52.9	52.9
SCAP	31.6	31.6
PHUM	20.4	31.6
DHUM	18.6	25.1
PRUL	7.9	16.5
DRUL	7.6	12.1
CARP	0.5	6.6
PMTC	0.9	3.9
DMTC	1.1	2.6
APHA	1.2	1.9
PFEM	69.2	69.4
DFEM	69.4	69.4
PTIB	12.1	40.8
DTIB	10.3	25.5
TARS	1.6	13.6
PMTT	1.2	7.5
DMTT	1.5	4.5
PPHA	1.2	2.9

Note: (S)TP data from Table 8.5 are used to calculate the unit averages for Model (S)AVGTP.

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model (PRO, Appendix C, Table 11) provides an example of this model construction procedure. The averages of the (S)PRO values for the four bison for each unit are listed in the first column. The ribs unit has the highest average, so in the second column, the (S)AVGPRO values are listed, which represent the value in the first column divided by the ribs value (97.0) and multiplied by 100. This standardized average model, (S)AVGPRO, is then modified to account for riders, yielding (S)MAVGPRO (Appendix C, Table 11).

Mixed Class Model Construction. Construction of the mixed class models (e.g., (S)MMCTP, Table 8.7) begins by expressing the carcass unit caloric yields (e.g., TP) of all animals included in the model as a percent of the unit of highest value in any of the animals, yielding (S)MCTP (Table 8.7). This ranks all units to the scale of this maximum valued unit, regardless of animal origin. The standardized values ((S)MCTP) are then modified by individual animals to account for the effect of riders. Applying the rider averaging routine to each animal takes into account the fact that the butchering process begins with complete carcasses that are subdivided into smaller units for processing. The resulting model ((S)MMCTP) has a value for each carcass unit for each animal class represented. For example, using SAM and FAF as representatives of males and females, the final model has values for male carcass units and for female units.

Animal Selection for Use in Model Construction. In this study, the mixed class models use the male, SAM, and the female, FAF, as representatives for model construction, because they are later applied to a spring season kill site and this adult male and poor condition female are the best representatives for use in this situation. It should be understood, however, that other models may also be constructed from the

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Table 8.7. Mixed Class, Total Products Model ((S)MMCTP)

Cows[a]				Bulls[b]			
Anatomical Unit	Model TP	Model (S)MCTP	Model (S)MMCTP	Anatomical Unit	Model TP	Model (S)MCTP	Model (S)MMCTP
SKWOT	3,899.9	13.5	13.5	SKWOT	4,006.7	13.8	13.8
ATLAS	1,869.3	6.5	6.5	ATLAS	2,061.6	7.1	7.1
AXIS	2,264.6	7.8	7.8	AXIS	2,521.4	8.7	8.7
C3C7	16,479.5	56.9	56.9	C3C7	18,298.6	63.2	63.2
THOR	21,548.8	74.5	74.5	THOR	21,678.9	74.9	74.9
LUMB	23,396.0	80.8	80.8	LUMB	19,384.8	67.0	67.0
SPEL	13,016.6	45.0	45.0	SPEL	14,298.3	49.4	49.4
CAUD	538.9	1.9	1.9	CAUD	223.0	0.8	0.8
RIBS	25,784.9	89.1	89.1	RIBS	28,939.3	100.0	100.0
STER	15,120.8	52.3	52.3	STER	13,367.9	46.2	46.2
SCAP	8,053.9	27.8	27.8	SCAP	9,577.2	33.1	33.1
PHUM	4,595.3	15.9	27.8	PHUM	5,939.0	20.5	33.1
DHUM	4,124.6	14.3	21.1	DHUM	5,204.6	18.0	25.6
PRUL	1,705.5	5.9	13.4	PRUL	1,922.6	6.6	16.1
DRUL	1,656.9	5.7	9.5	DRUL	1,943.3	6.7	11.4
CARP	30.6	0.1	5.5	CARP	48.6	0.2	6.0
PMTC	264.7	0.9	3.5	PMTC	172.8	0.6	3.3
DMTC	245.8	0.8	2.5	DMTC	159.3	0.6	2.0
APHA	429.8	1.5	2.0	APHA	122.6	0.4	1.2
PFEM	17,086.3	59.0	59.0	PFEM	18,661.7	64.5	64.5
DFEM	17,033.2	58.9	59.0	DFEM	18,566.3	64.2	64.4
PTIB	3,129.1	10.8	34.9	PTIB	3,248.7	11.2	37.8
DTIB	2,910.4	10.1	22.5	DTIB	2,640.0	9.1	23.4
TARS	354.6	1.2	11.9	TARS	297.9	1.0	12.2
PMTT	328.9	1.1	6.6	PMTT	204.6	0.7	6.5
DMTT	388.3	1.3	3.9	DMTT	220.8	0.8	3.7
PPHA	366.3	1.3	2.6	PPHA	169.2	0.6	2.1

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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caloric yield data and such models might be more useful for some site types than those presented here. For example, a mixed class model using the data of SAF and FYM, or an averaged model based on data from the females and FYM might be useful for site assemblages representing cow/calf groups, and a model incorporating the male, SAM, as well, might be useful for applications to early fall season assemblages where some bulls linger on after the breeding season. There are many options for model construction and one should not be limited by those presented here, especially if data from additional bison specimens increase the sample size. One should also keep in mind which animals have been included in the model construction when applying the models presented.

Differences in Model Focus

In addition to the differences in how models may be constructed, thus yielding the three basic model types, there is also variability in the focus of the models. Models of carcass utility may be generalized, or focus on specific carcass products in the same way that Binford's Marrow, White Grease, and Yellow Grease Indices are models of specific carcass resources, and his General Utility Index and Modified General Utility Index are models of general utility. The generalized models presented here for bison include variations on a Total Products (TP) model (Tables 8.5, 8.6, and 8.7) which incorporate data for protein, and marrow, grease and carcass fats, and a gross weight model which is constructed in the same manner as Metcalfe and Jones's (1988) FUI (Appendix C, Tables 1 and 10). Two slightly more specific, but still generalized, models include the Total Fat (TF) and Selected Fat (SF) indices (Appendix C, Tables 6, 15, and 23, and Tables 7, 16 and 24 respectively). These two indices model carcass utility when meat

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protein is not included in the calculations. Utility models based upon caloric yield with modifications for riders (when appropriate), are also presented in Appendix C for the following individual and grouped carcass products: protein (PRO, Tables 2, 11, and 19), marrow fat (MAR, Tables 3, 12, and 20), white grease fat (WG, Tables 4, 13, and 21), and yellow grease fat (YG, Tables 5, 14, and 22), and the combined product models of grease fat (GRE, Tables 8, 17, and 25) which groups the yellow and white grease data, and a model for the combined skeletal fats including marrow and both grease fat types (SKF, Tables 9, 18, 26). No modifications have been made in the construction of these models for differences in quality or for differences in the efficiency with which the product may be recovered from each unit.

Model Construction and Product Distribution Variability

Given the construction procedures for the three model types, the question arises as to whether or not variability between animals in the production and distribution of carcass products (as detailed in the previous three chapters) is evident in these models. Clearly the single class models cannot account for either production or distribution differences unless they are directly compared with one another. To compare production differences between classes, the unmodified and unstandardized yield data could be compared. The standardized and modified models express carcass unit yield in relation to the highest yielding unit. This is an expression of relative distribution, but it is difficult to know how to evaluate differences in values for the same body part between animals (and models), because distribution is not expressed relative to the same highest yield value.

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Production and distribution differences between animals are potentially addressed in the mixed class models. Expression of all carcass units, relative to the maximum valued unit, regardless of animal origin, accounts for differences in productivity between animals while at the same time maintaining a scale of distribution differences, as long as the comparison is made only within each animal and not between them. These combined animal data models seem to have the greatest potential for improving the conformity between site assembalge data and utility models, because they account for production differences, as well as distribution differences, in kills including more than one class of animal.

As noted above, however, due to the only recent development of analytical methods for sexing most post-cranial bone (Speth 1983) and probably due to the large time investment required to do so, very few sites have been analyzed to the detailed extent required to use such mixed class models. Application of single class models to sites lacking this detail is potentially worthwhile, if the site is dominated by members of one class--if large bone size suggests a bull group is represented, for example. An alternative is the application of averaged models to sites including multiple animal classes, but for which there is no individual bone counts for the represented classes. Averaged models include data from multiple classes, averaging the relative value of the body parts. It seems, therefore, that differences between animals in their distributions of products are probably masked by the averaged models. If so, the body locations where these differences occur, are likely to be locations where utility models fail to predict rates of bone abandonment.

To determine whether differences between individuals are evident in single class models, but hidden in averaged models, scatterplots and

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regressions of the single class and the averaged models are compared for each of the product(s) models. White and yellow grease fat models are compared with the averaged models only between units producing those products. Marrow fat models are compared to the averaged model that includes the sacrum-pelvis and the appendicular units. The summary data for this analysis are presented in Table 8.8. Significant linear patterns were found in the scatterplots between the single class and averaged models, modified to account for riders, for all comparisons. Most of the comparisons were significant at the 0.0001 level. The exceptions to this were all significant at the 0.0005 level, indicating that each of the single class models was quite similar to the averaged model, as might be expected.

Studentized residuals are presented as well in Table 8.8 for each single class-averaged model comparison. Residuals that exceed ± 2.0 indicate where the index value for a carcass unit of the single class model is substantially greater or less than that of the averaged model. There is not a one to one correspondence between the variability from the distribution analyses (i.e., age, sex, and condition influences on variability) and the units of the single class model that differ substantially from the regression of the single class and averaged model data. The studentized residuals indicate where the single class model unit value differs from the line describing the relationship between the single class and averaged model. The averaged model includes all four bison, and the regression analyses indicate where a carcass unit differs from that average. The distribution analyses, on the other hand usually compared paired sets of data in order to consider age, sex, or condition influence differences. It is probable, therefore, that some differences that were evident in the distribution analyses may not be evident in the regression

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Table 8.8. Summary of Regression Analyses of Single Class and Averaged Models

Independent Variable	Dependent Variable	Regression Equation	Probability > F	R^2	Studentized Residuals ≥ 2.0		Studentized Residuals ≤ -2.0	
(S)MAVGTP	FYM(S)MTP	Y = 2.02 + 1.08 X	0.0001	0.9863	PFEM DFEM	2.1 2.1	C3C7 RIBS	-2.2 -3.1
	SAM(S)MTP	Y = 0.31 + 0.93 X	0.0001	0.9844	C3C7 RIBS	3.1 2.3	LUMB	-3.2
	SAF(S)MTP	Y = -2.09 + 0.98 X	0.0001	0.9854			SCAP PHUM C3C7	-2.0 -2.0 -2.6
	FAF(S)MTP	Y = -0.18 + 1.01 X	0.0001	0.9922	LUMB C3C7 STER	2.8 2.6 2.0		
(S)FUI	FYM(S)FUI	Y = 0.09 + 0.97 X	0.0001	0.9861			C3C7 RIBS	-2.0 -2.9
	SAM(S)FUI	Y = 1.12 + 1.00 X	0.0001	0.9926	C3C7	3.8		
	SAF(S)FUI	Y = -0.94 + 1.00 X	0.0001	0.9936	LUMB	2.7	C3C7	-3.0
	FAF(S)FUI	Y = -0.11 + 1.02 X	0.0001	0.9947	RIBS	3.0		

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Table 8.8. (continued)

Independent Variable	Dependent Variable	Regression Equation	Probability > F	R^2	Studentized Residuals ≥ 2.0		Studentized Residuals ≤ -2.0	
(S)MAVGSF	FYM(S)MSF	Y = 0.45 + 0.94 X	0.0001	0.9784	THOR	2.2	STER	-3.5
	SAM(S)MSF	Y = 0.85 + 1.05 X	0.0001	0.9890	STER	2.6	RIBS	-2.7
							LUMB	-2.7
	SAF(S)MSF	Y = -1.14 + 1.02 X	0.0001	0.9949	RIBS	3.5	THOR	-2.0
	FAF(S)MSF	Y = 0.14 + 0.99 X	0.0001	0.9916	RIBS	2.4	THOR	-3.0
(S)MAVGTF	FYM(S)MTF	Y = 0.99 + 0.91 X	0.0001	0.9828	LUMB	2.6	RIBS	-3.2
					THOR	2.2		
	SAM(S)MTF	Y = 0.40 + 0.98 X	0.0001	0.9835	C3C7	3.2	LUMB	-3.5
					RIBS	2.4		
	SAF(S)MTF	Y = -1.43 + 0.99 X	0.0001	0.9935	RIBS	3.3	C3C7	-3.2
	FAF(S)MTF	Y = 0.69 + 0.94 X	0.0001	0.9918	LUMB	2.7	RIBS	-2.3
					STER	2.1	THOR	-2.4
(S)MAVGSKF	FYM(S)MSKF	Y = 2.22 + 0.90 X	0.0001	0.8700			SPEL	-2.7
							RIBS	-2.7
	SAM(S)MSKF	Y = -4.95 + 0.95 X	0.0001	0.9748	PHUM	3.0	RIBS	-2.0
	SAF(S)MSKF	Y = -1.45 + 0.91 X	0.0001	0.9580	SPEL	2.6	PHUM	-2.9
	FAF(S)MSKF	Y = 4.82 + 0.91 X	0.0001	0.9442	RIBS	4.1		

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Table 8.8. (continued)

Independent Variable	Dependent Variable	Regression Equation	Probability > F	R^2	Studentized Residuals ≥ 2.0		Studentized Residuals ≤ -2.0	
(S)MAVGGRE	FYM(S)MGRE	Y = 9.52 + 0.88 X	0.0001	0.6116			RIBS	-2.2
	SAM(S)MGRE	Y = -6.25 + 0.86 X	0.0001	0.9244	SPEL PHUM	3.4 2.0		
	SAF(S)MGRE	Y = -5.76 + 1.00 X	0.0001	0.9655	PTIB	2.0		
	FAF(S)MGRE	Y = 4.36 + 0.95 X	0.0001	0.8293	RIBS	3.5		
(S)MAVGPRO	FYM(S)MPRO	Y = 0.36 + 0.99 X	0.0001	0.9860			C3C7 RIBS	-2.9 -3.3
	SAM(S)MPRO	Y = 0.52 + 0.93 X	0.0001	0.9860	C3C7 RIBS	2.7 2.3	PFEM DFEM	-2.1 -2.1
	SAF(S)MPRO	Y = -0.94 + 1.02 X	0.0001	0.9854			C3C7	-3.4
	FAF(S)MPRO	Y = 0.10 + 0.95 X	0.0001	0.9861	C3C7	4.0		
(S)MAVGMAR[a]	FYM(S)MMAR	Y = 1.88 + 0.90 X	0.0001	0.9765			PFEM	-2.9
	SAM(S)MMAR	Y = -1.62 + 1.03 X	0.0001	0.9654	PHUM	2.9		
	SAF(S)MMAR	Y = -0.89 + 0.97 X	0.0001	0.9839	PRUL	2.0		
	FAF(S)MMAR	Y = 1.17 + 0.95 X	0.0001	0.9898	PFEM	2.1	PHUM	-2.2

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Table 8.8. (continued)

Independent Variable	Dependent Variable	Regression Equation	Probability > F	R^2	Studentized Residuals ≥ 2.0		Studentized Residuals ≤ -2.0	
(S)MAVGWG[a]	FYM(S)MWG	Y = 28.88 + 0.66 X	0.0045	0.3868			PHUM	-2.1
	SAM(S)MWG	Y = -14.94 + 1.23 X	0.0001	0.9392	PHUM	2.8		
	SAF(S)MWG	Y = -13.58 + 1.11 X	0.0001	0.9695	PTIB	2.4	PHUM	-2.8
	FAF(S)MWG	Y = 6.18 + 0.93 X	0.0001	0.7733	PHUM	2.4		
(S)AVGYG[a]	FYM(S)YG	Y = 1.84 + 0.94 X	0.0007	0.7822	LUMB	2.3		
	SAM(S)YG	Y = -4.12 + 0.95 X	0.0001	0.9595	SPEL	2.8	RIBS	-2.0
	SAF(S)YG	Y = -2.10 + 0.99 X	0.0001	0.9706			LUMB	-2.7
	FAF(S)YG	Y = 4.37 + 1.10 X	0.0002	0.8465	RIBS	2.6	SPEL	-2.0

[a] Regression analyses exclude those units that do not produce the product.

analyses. It is possible as well, that not all units with outlying studentized residuals are exceptional due to only distribution variability, but in most cases, this appears to be true as will be shown.

Models for single carcass products, such as protein or marrow fat, are easier than multiple product models to evaluate for matches between deviations in distributions and regressions, because the units with significant studentized residuals may be compared directly with the distribution data to determine if they register either age, sex or condition differences in productivity. All units with outstanding residuals for the single product models did show variability in the same units for distribution, due to age, sex or condition (compare Tables 8.8, 8.9).

If the data are for a multiple product model, however, then to fully understand why the exceptional units (those with studentized residuals greater than or equal to ± 2.0) are so different, one must first examine each multiple product model for the contribution of the component products to the caloric total for the exceptional carcass unit (Table 8.10 for the (S)MTP model, Appendix C, Table 27 for all other models), and then examine the distribution data from the chapters above to determine whether the direction of the model variability follows the expected direction of distribution variability (if it exists). For example, if the studentized residual is positive and greater than 2.0, this indicates that its value in the single class model is much higher than would be expected given the relationship between the single class and averaged models. One would expect the distribution data to similarly show that a greater proportion of the product(s) was found in this unit of this animal than in the others. Similarly a negative studentized residual should be matched with lower individual distribution than in the other animals. If the exceptional unit

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Table 8.9. *Summary of Carcass Product Distribution Differences*

Carcass Product	Age Differences		Sex Differences		Condition Differences	
	FYM > SAM	FYM < SAM	SAM > Females	SAM < Females	FAF > SAF	FAF < SAF
Meat	FEMP STER	CERV RIBS HUM	CERV SCAP	FEMP LUMB SPEL	TIB SCAP	HUM RUL
Marrow Fat	RUL MTC TIB MTT PELV	FEM HUM	HUM FEM	RUL MTC TIB MTT	MTC MTT	RUL FEM
White Grease Fat	CARP MTC TARS MTT PPHA	HUM RUL FEM TIB	HUM	RUL	SCAP HUM APHA	FEM TIB TARS
Yellow Grease Fat	LUMB CAUD	THOR SAC PELV RIBS	PELV LUMB	RIBS THOR	RIBS	SAC PELV
Intramuscular Fat	RIBS STER	FEMP	CERV	THOR		
Subcutaneous Fat[a]	THOR	FEMP HUM RIBS STER LUMB SPEL CAUD	THOR	STER RIBS	LUMB	FEMP CERV THOR SPEL RIBS

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Table 8.9. (continued)

Carcass Product	Age Differences		Sex Differences		Condition Differences	
	FYM > SAM	FYM < SAM	SAM > Females	SAM < Females	FAF > SAF	FAF < SAF
Intermuscular Fat[a]	THOR	SKWOT	SKWOT	LUMB	SPEL	CERV
	SPEL	CERV	CERV	RIBS	FEMP	THOR
	SCAP	LUMB	SPEL			LUMB
	HUM	STER	STER			STER
	RUL		FEMP			
Cavity Fat[a]	LUMB	STER	LUMB	SPEL	LUMB	SPEL
		SPEL	STER			

[a] Literature for livestock studies suggests that sex differences in distribution for these carcass fat depots may not be significant.

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Table 8.10. Percent of Caloric Contribution to Products Total for Carcass Units with Studentized Residuals Greater than ± 2.0 for Regressions of Averaged and Single Class Models

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Component Percent of Unit kcal Total for Single Class Model[a]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGTP	FYM(S)MTP	PFEM	2.1	82.6	0.9	1.5	4.6	0.3	10.2	0.0
		DFEM	2.1	81.8	0.9	3.8	3.3	0.3	10.0	0.0
		C3C7	-2.2	61.2	10.3	0.1	0.0	1.3	27.1	0.0
		RIBS	-3.1	61.7	18.8	0.5	0.0	2.0	17.1	0.0
	SAM(S)MTP	C3C7	3.1	58.7	22.3	0.0	0.0	1.4	17.5	0.0
		RIBS	2.3	57.9	30.3	1.1	0.0	2.2	8.5	0.0
		LUMB	-3.2	45.5	12.3	1.1	0.0	3.2	15.8	22.2
	SAF(S)MTP	C3C7	-2.6	42.7	23.0	0.3	0.0	5.3	28.6	0.0
		SCAP	-2.0	70.6	26.0	3.0	0.4	0.0	0.0	0.0
		PHUM	-2.0	49.7	18.7	13.0	7.0	6.8	4.7	0.0
	FAF(S)MTP	C3C7	2.6	53.0	21.7	0.6	0.0	2.3	22.3	0.0
		LUMB	2.8	31.7	15.9	0.9	0.0	8.0	22.3	21.2
		STER	2.0	35.8	22.8	0.6	0.0	12.0	21.6	7.3

[a] Intram. (intramuscular fat), Subcut. (subcutaneous fat), Interm. (intermuscular fat).

Note: Component contribution data for other model comparisons are presented in Appendix C, Table 27.

has a positive residual and the distribution data suggest that unit production is smaller in this animal than in the others (i.e., not matching), then that product is not responsible for the deviation of the individual from the single class to averaged model relationship.

Comparison of the data in Tables 8.10 and 8.11 indicates that the products which show matching residual signs and direction of variability in the distribution data, are not always the most predominate product in the multiple component model. It is clearly evident, as well, that not all units showing distribution differences between animal classes appear as exceptional units through the studentized residuals in the individual and averaged model comparisons. In Table 8.11, all model comparisons show some correspondence between the residual signs and at least one of the product component distribution analyses. It is evident, therefore, that some consideration needs to be given to how carcass unit utility values from averaged data models may deviate from the actual unit value if applied to a mixed animal class assemblage. Clearly, differences in productivity do affect these models. Therefore, one must consider where one might expect to see deviations in the bone assemblage data caused by averaged model applications where variability is a factor.

Predicting Carcass Unit Deviations for Averaged Model Applications

If an averaged model is applied to an assemblage that is characterized by animals comparable to one of the individual animal classes used in this analysis (i.e., FYM--yearling male; or SAM--young adult male; or SAF--well conditioned, fully mature female; or FAF--poorly conditioned, old female), then the deviations attributable to poor model fit may be predicted, if one knows the frequency with which parts of high, moderate, or low value were

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Table 8.11. Identifying Distribution Variability that Might Account for Units with Large Studentized Residuals (Greater than ± 2.0) for Regressions of Averaged and Single Class Models

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison[b]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGTP	FYM(S)MTP	PFEM	2.1	2	0	0	0	0	1	-
		DFEM	2.1	2	0	0	2	0	1	-
		RIBS	-3.1	3	0	3	-	1	0	-
		C3C7	-2.2	2	2	1	-	2	2	-
	SAM(S)MTP	C3C7	3.1	2	3	0	-	2	3	-
		RIBS	2.3	2	1	1	-	0	0	-
		LUMB	-3.2	3	2	1	-	2	2	2
	SAF(S)MTP	C3C7	-2.6	3	3	2	-	0	1	-
		SCAP	-2.0	3	3	1	0	2	3	-
		PHUM	-2.0	0	0	2	3	0	2	-

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Table 8.11. (continued)

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison[b]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
	FAF(S)MTP	C3C7	2.6	3	2	3	-	0	0	-
		LUMB	2.8	2	3	1	-	3	2	2
		STER	2.0	2	2	3	-	3	1	2

[a] see Table 8.4 for glossary of model acronyms and Appendix C, Table 28 for other model comparisons.

Note: 0 indicates the distribution value for the individual was smaller (if the residual sign is positive) or larger (if the residual sign is positive) than the other bison. 3 indicates the distribution value for the individual was smaller (if the residual sign is negative) or larger (if the residual sign is positive) than the other bison. Values 1 and 2 indicate partial agreement between the sign and the occurrence of distribution differences. Product components that were not present are so indicated with a "-".

removed from the site. This is referred to as the recovery strategy employed at the site. This is examined in more detail below, but some explanation of what recovery strategies are is needed first.

Recovery Strategies

Carcass parts are generally removed from a kill site according to some decision that relates to unit value and other factors including transport cost, and available labor. The graphed relationship between unit value (as determined by the chosen model) and the numbers of bone elements abandoned at the kill site may take many forms. Binford (1978:81) defines and illustrates three such strategies, and Metcalfe and Jones (1988:494-496) eleaborate on his discussion. Speth (personal communication) notes that these are arbitrary categories within a continuum of the relationship between economic utility and body part use. An understanding of what these categories of recovery strategies represent is needed in order to interpret the influence that using an inappropriate model type for a particular assemblage has on our assessments of carcass unit use. This is explained in more detail below.

The three major strategies, reproduced here in Figure 8.3, include: (1) the unbiased strategy, where carcass units are removed in direct relation to their utility, (2) the bulk strategy, where units of moderate and high value are removed in greater frequencies than parts of low value which are abandoned at high rates, and (3) the gourmet strategy, where units of high value are removed from the site in high frequencies and moderate and low utility units are abandoned at the site at increasing rates. Two bulk and gourmet strategy curves are illustrated in Figure 8.3 in order to illustrate, as Binford (1978:81) and Speth note, that a great deal of

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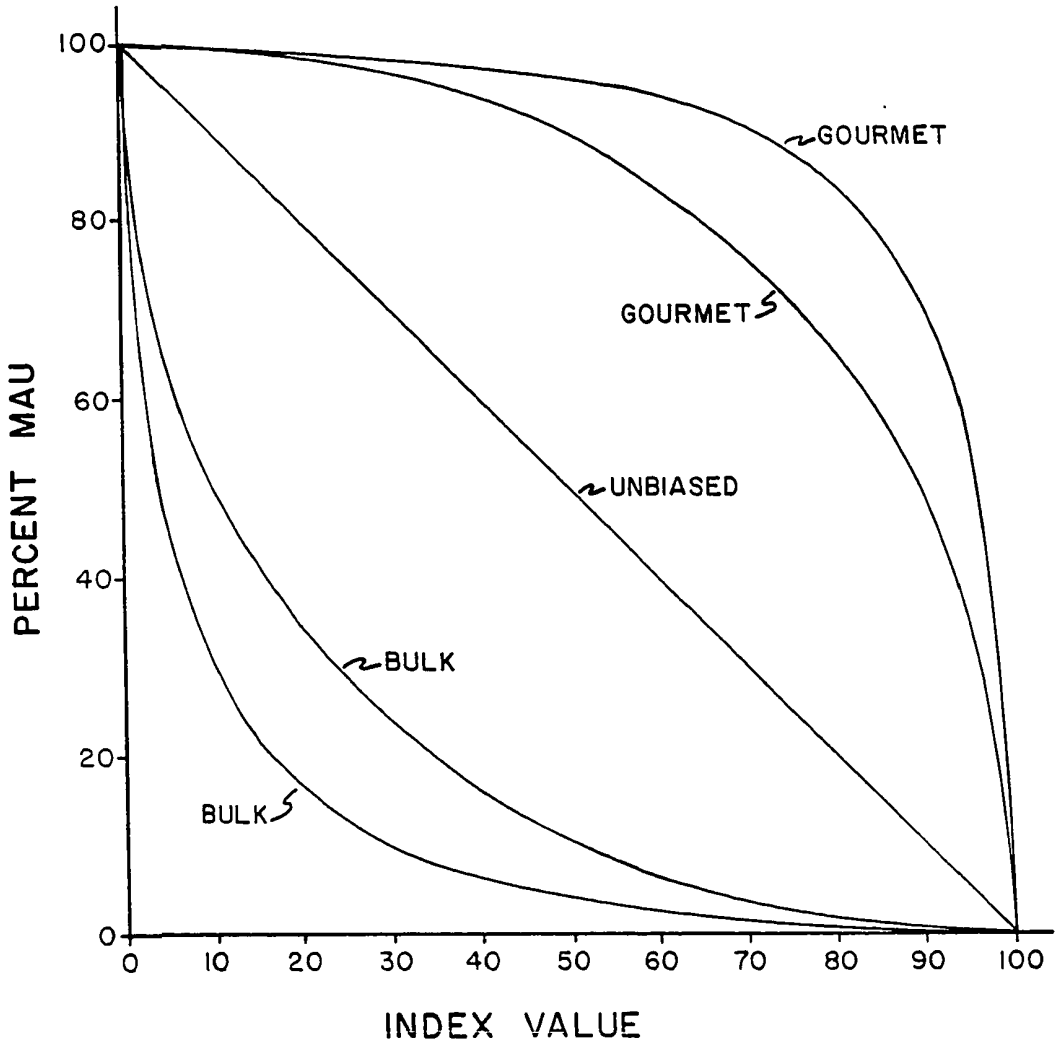

Figure 8.3. Relationship Between Model Values and Percent MAU's for Kill Site Assemblages with Different Carcass Unit Recovery Strategies. Redrawn from Binford (1978:81:Figure 2.18) and Metcalfe and Jones (1988: 496:Figure 6b).

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variability exists in how this may be expressed in the archaeological record. It should be noted that this figure illustrates the proportion of the available units that were abandoned at the kill site, rather than those taken away from the site for processing or consumption elsewhere. Therefore, units of high value are generally found in low proportions and conversely, units of low value are usually found in high proportions.

Predicting Deviations

In order to determine whether application of the averaged data models to assemblages dominated by members of a particular animal class would have a major effect upon the percent MAU (the percent present of the number possible, or minimum animal units (Binford 1984:50-51)) present for specific carcass units, several sets of data are needed. First, one must determine which units deviate between the averaged and single class models, and select those units which have studentized residuals that exceed ± 2.0. Second, it is important to know the magnitude of the difference between a unit's values in the two models and the direction of change, that is, whether an increase or a decrease in value is recorded and how large that change is. It is also imperative that the model values for that unit be known, because the effect of that change may or may not be important, regardless of its magnitude, if it falls within a particular range on the recovery strategy curves. A particularly crucial piece of information that is needed to predict whether the units with exceptional studentized residuals should deviate from the expected percent MAU, if the averaged data model is used rather than the single class model, is what kind of recovery strategy was employed at the site. As is evident in the summary of the data, presented in Table 8.12, the effect of the change in unit value differs depending upon whether a

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Table 8.12. The Effect of Using Averaged Models on Kill Site Assemblages Dominated by Single Animal Classes Under the Influence of Different Recovery Strategies

Part A. Data Needed to Determine the Effect

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value			Averaged Model Over- or Underestimates Single Class Model Value		
				Averaged Model	Single Class Model	Absolute Difference	Same Value	Over-estimates Value	Under-estimates Value
(S)MAVGTP	FYM(S)MTP	PFEM	2.1	69.4	84.7	15.3			X
		DFEM	2.1	69.4	84.7	15.3			X
		C3C7	-2.2	56.6	55.1	1.5		X	
		RIBS	-3.1	100.0	100.0	0.0	X		
	SAM(S)MTP	C3C7	3.1	56.6	63.2	6.6			X
		RIBS	2.3	100.0	100.0	0.0	X		
		LUMB	-3.2	82.9	67.0	15.9		X	
	SAF(S)MTP	C3C7	-2.6	56.6	44.2	12.4		X	
		SCAP	-2.0	31.6	21.7	9.9		X	
		PHUM	-2.0	31.6	21.7	9.9		X	
	FAF(S)MTP	C3C7	2.6	56.6	63.9	7.3			X
		LUMB	2.8	82.9	90.7	7.8			X
		STER	2.0	52.9	58.6	5.7			X

Table 8.12. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGMTP	FYM(S)MTP	PFEM			XV-S			XV-M			XV-S
		DFEM			XV-S			XV-M			XV-S
		C3C7		I-M			I-M			I-M	
		RIBS	I			I			I		
	SAM(S)MTP	C3C7			V-M			V-M			V-M
		RIBS	I			I			I		
		LUMB		XV-S			XV-M			XV-S	
	SAF(S)MTP	C3C7		X-S			X-M			X-M	
		SCAP		V-M			V-S			V-M	
		PHUM		V-M			V-M			V-M	
	FAF(S)MTP	C3C7			V-M			V-M			V-M
		LUMB			V-M			V-M			V-S
		STER			V-M			V-M			V-M

[a] see Table 8.4 for glossary of model acronyms and Appendix C, Table 29 for other model comparisons.

Note: The effect of the change in index value has two parts to it. The first part shows the magnitude of the index value change and the second part show the magnitude of the difference in the percent MAU expected. I = 0 to 4.9, V = 5 to 9.9, X = 10 to 14.9, ect.; -M indicates less than 10 percent MAU change, and -S indicates more than 10 percent MAU change when using the outside curves in Figure 8.4; -M/S indicates minor change for the outside curve and substantial change for the inside curve in Figure 8.4.

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bulk, unbiased, or gourmet strategy is used, and whether the unit is of high, medium or low value in the model.

Table 8.12 presents the results of the analysis for the averaged Total Products model ((S)MAVGTP) and the single class models (FYM(S)MTP, SAM(S)MTP, SAF(S)MTP, and FAF(S)MTP). Similar procedures are carried out on the other models developed in this study and the results of those analyses are presented in Appendix C, Table 8.29. In these tables, two levels of change are noted in addition to the direction of that change. Units that show a change in percent MAU of greater than 10 percent are marked with an "S" (indicating a substantial change) following the indicator of the magnitude of the unit value change between models. Units that show a change in the percent MAU of less than or equal to 10 percent are marked with a "M" indicating a minor effect. The 10 percent level selected, is an arbitrary designation. For data that closely lie around a line, 10 percent may be too large, excluding all of the outlying data points, and in other cases where data points are loosely described by the line, a 10 percent change may include too many points. It should be noted that the shape of the bulk and gourmet curves also is influential in determining whether the effect is substantial or minor. This is evident where both M and S designations are listed together.

To determine the M and S values in this particular analysis, the curves illustrated in Figure 8.3 are used. Figure 8.4 is a reproduction of that figure, which illustrates the magnitude of index value change required to exceed the 10 percent MAU change. For example, a change in index value from 100 to less than 29 would be required to produce a percent MAU change of greater than 10 percent for the bulk strategy curve that lies closest to the x and y axes (Curve 1). (Note that the x-axis value where the horizontal

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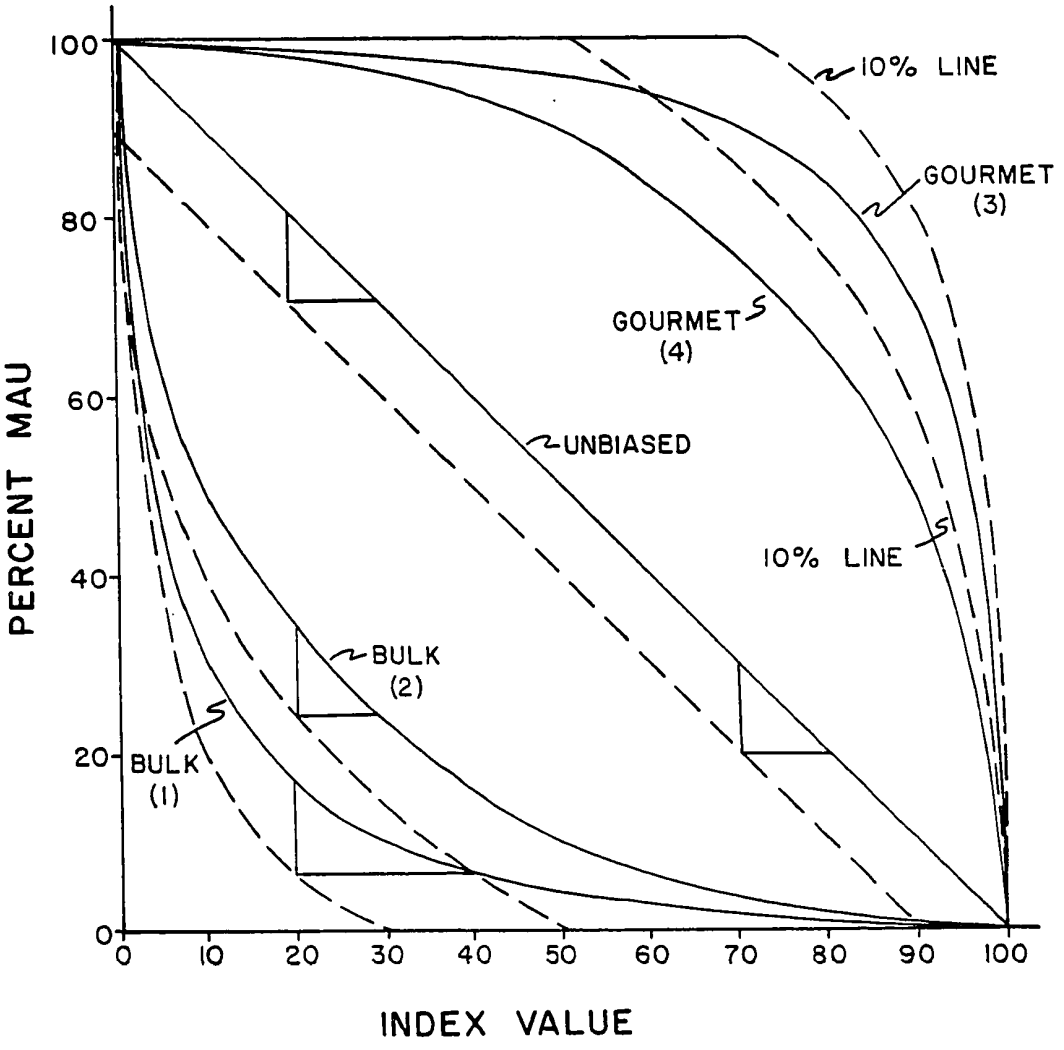

Figure 8.4. Effect of Model Value Differences for a Series of Recovery Strategies. Horizonatal and vertical projections from the dashed lines to the nearest strategy or straight line identify the range of the model value change needed to produce a ten percent change in the expected percent MAU under different recovery strategies.

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and vertical lines intersect is the point that must be passed to exceed the 10 percent change in percent MAU.) At the lower index values, however, it takes much smaller changes in unit value between models to produce a substantial change in the percent MAU expected. For example, a change in model value from 40 to less than 20 is all that is needed to exceed the 10 percent change in percent MAU, and this magnitude declines rapidly as one approaches the lowest index values, where the change in index value required is fractional.

The bulk curve that lies farther from the x-y axes (Curve 2) differs from the previously described bulk curve (Curve 1) in the magnitude of change needed to produce a substantial change in the percent MAU. For this curve (Figure 8.4), at the upper end of the index values, a unit need only change value from 100 to less than 50 to exceed the 10 percent MAU change. For the middle range of the curve, smaller changes in unit value are needed than in Curve 1 to produce the 10 percent change in percent MAU.

Curves 3 and 4 in Figure 8.4 represent gourmet strategy curves. For these curves, the effect of index value changes are opposite those seen for the two bulk strategy curves. That is, at the higher index values, it takes only very small changes in the index value to produce large differences in the percent MAU, and at the lower index values, large differences in model values are needed to produce a substantial change in the percent MAU.

The two gourmet curves behave similarly to the two bulk strategy curves in the changes needed to produce similar changes in the percent MAU. That is, Curve 4 requires a smaller magnitude of index value change than Curve 3 to produce the 10 percent MAU change.

The unbiased strategy differs from the bulk and gourmet strategies, because it is a straight line rather than a curved line. The effect of this

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characteristic is that regardless of where the unit lies along the index range, the magnitude of model value change needed to produce the 10 percent MAU change is constant, and in this case, requires a change in index value of 10 because the slope of the line is negative one. An unbiased strategy (straight line relationship) with a different slope would also have a constant magnitude of change needed to produce a substantial change in the percent MAU. As the slope gets smaller and the line flatter, relative to the x-axis, the magnitude of change in index value needed to produce a substantial change in the percent MAU increases. Conversely, steeper lines, representing unbiased strategies require smaller magnitudes of index value change to affect percent MAU.

Archaeological assemblages sometimes show a different pattern of bulk, unbiased, and gourmet curves, with the lowest percent MAU falling much higher on the curve, and other units lying higher than in the ideal models presented in Figure 8.3. In Figure 8.5, a hypothetical example, the lowest percent MAU is 30. The dashed lines illustrate the 10 percent MAU value change resulting from index value changes. When Figure 8.5 is compared with Figure 8.4 one may see that increasing the abandoned percent MAU increases the magnitude of change in model values needed between the averaged and individual model before a substantial (greater than 10 percent) change in the percent MAU is registered.

The point of this discussion is that one cannot determine whether the change in index value when using an averaged or a single class model is going to be important until one knows the recovery strategy and the minimal rate of abandonment. Once these have been determined, it is then possible to establish whether points (carcass units) lying off of the curve might be there because an averaged model was used rather than another, perhaps more

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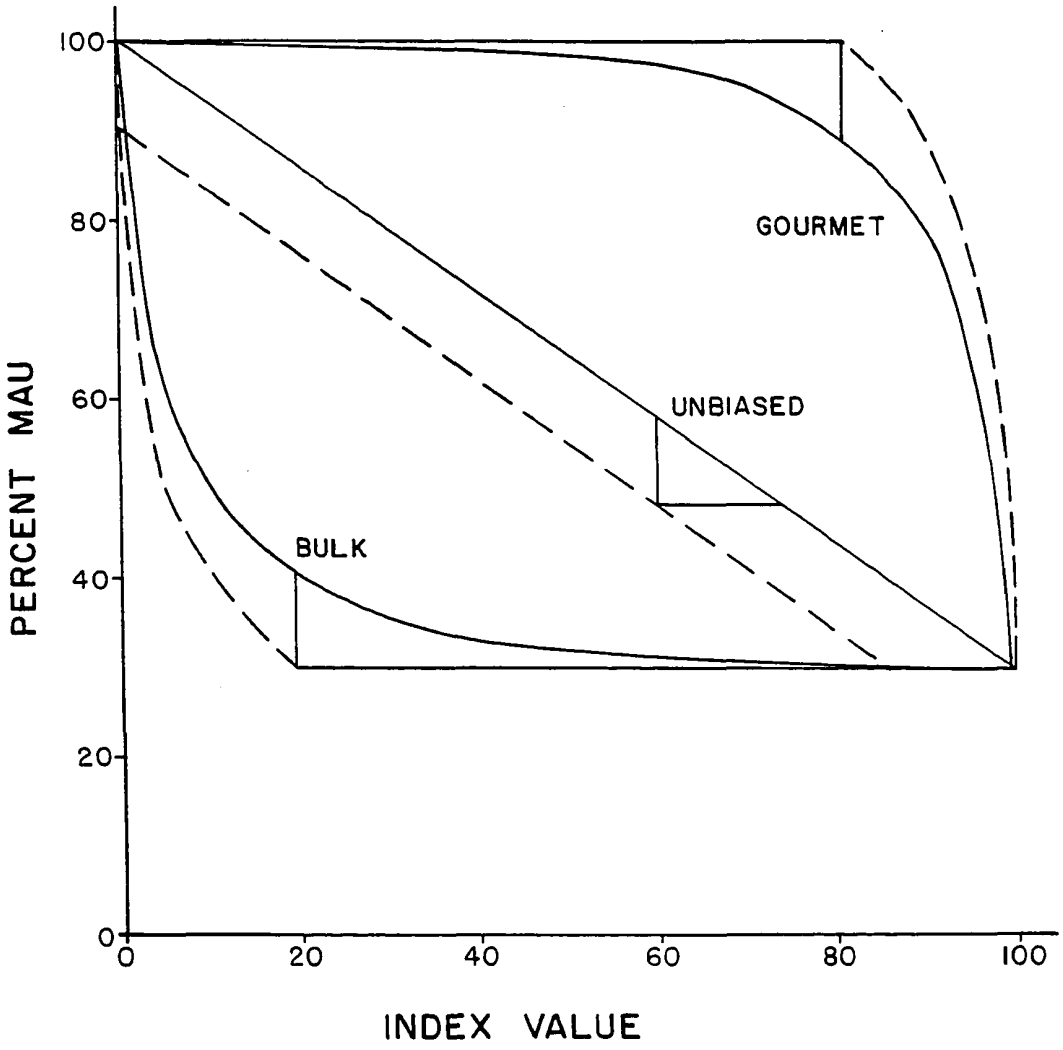

Figure 8.5. Effect of Model Value Differences for a Series of Recovery Strategies when the Minimum Abandonment Rate is High. Dashed line indicates ten percent MAU change for index value changes under different recovery strategies.

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appropriate, single class model for that assemblage analysis. In Table 8.12 and Appendix C, Table 29, only those units with studentized residuals exceeding ± 2.0 are listed, but one would not be restricted to these units when investigating outlying units in model applications to archaeological assemblages. They are merely indicators of units most likely to deviate from the curve due to model differences. It might be worthwhile, for example, to examine units with studentized residuals that are somewhat smaller, but approaching the ± 2.0 values as well. Appendix C, Table 30 presents the studentized residuals greater than ± 1.5, as a reference for such analyses.

Discussion and Conclusions

Three phases of selection that occur in bison hunting have been examined in this chapter. Selection decisions are made when a hunting group determines which type of herd to pursue, which carcasses to butcher, and which carcass units to take from or leave behind at the kill site. In each case, I suspect that selection is largely guided by the quantity of products available in the herd, carcass, and carcass unit. Although variability in single carcass resource production and distribution was considered in previous chapters, it is assumed that the quantity of multiple, rather than single resources available from the carcasses of animals from specific age and sex classes, modified by changes in animal condition, determine which types of herds, animals and carcass units are most frequently selected.

Some modifying factors probably alter the direct relationship between resource value and selection at each level of selection, and these factors were discussed as well. Herd selection is potentially affected by the nutritional needs of the hunter population as well as by herd size,

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composition and maneuverability. Based upon carcass productivity and these modifying factors, it is concluded that the fall and early winter focus on cow/calf groups (Speth 1983:1) is not surprising. It was also concluded that fully mature males are reasonable targets for selection in the spring when cows are at their lowest levels of productivity, especially if calves have already been born. Cow/calf and bull groups are both difficult to manage at this time of year. The potentially larger body size, and thus, larger fat yield of fully mature male bison would make them a primary target for use at this time. Prior to the calving period, however, the larger size of cow/calf herds and the potentially greater ease with which they might be maneuvered to the kill location, might make the cow/calf herds attractive targets as well, although many of the females are probably in poorer condition than the fully mature males. The spring season might see a mixed focus on herd selection, therefore.

Selection of carcasses for processing after the kill is governed by many of the same productivity factors as herd selction, except that the carcasses available to choose from may have been limited by the selection of the herd. As with herd selection, the purpose of the kill, whether to provide food for storage and immediate consumption, or whether to provide primarily for immediate food needs, affects how selection decisions are made. For example, at fall kills young, low-fat animals might be used to provide dried meat for the production of pemmican. While the low intramuscular fat content of the meat of young animals enhances rapid drying without spoilage, rendered fat is subsequently added to the powdered meat in the production of this product. This necessitates the recovery of fat as well. At fall kills, where carcasses are processed for winter food storage, young animals low in fat content may, therefore, be used more extensively

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than at spring season kills where fat, rather than meat, may be the primary target of selection.

Animal carcass selection may also be modified by herd size and the type of kill. At a small kill, all animal carcasses may be processed, despite the lower productivity of some carcasses, unless they are too poor to be useful (e.g., Speth 1983). At a large kill, selection may be governed to some extent by the accessibility of the carcasses. At the Olsen-Chubbuck Site, for example, carcasses wedged into the bottom of the arroyo were abandoned (Wheat 1972). One would expect, however, that productivity guides the selection order of those carcasses that are processed.

Selection at the level of the carcass unit was examined as well. Utility models specify the relative values of each carcass unit, recognizing that while each unit has a value based upon its productivity, it is recovered as part of a larger package (the carcass or some subdivision of it), and its value may be influenced by that association. Basically, the modifications dictated by this fact recognize that the selection that occurs at a kill site is not characterized by the independent selection of individual carcass units regardless of animal origin, but is characterized instead by selection that occurs in larger anatomical divisions.

Carcass unit selection models developed by Binford (1978) and simplified by Metcalfe and Jones (1988) were examined and criticized on two counts. These models undervalue the importance of fat as a resource separate from protein (except for skeletal fats), and their construction artificially inflates the value of the appendicular and atlas-axis units relative to the axial units beyond that needed to account for the effect of riders. The utility models developed in this study, therefore, include fat resources as separate products and modify relative productivity only to

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account for the effect of riders. The measurement of relative component contribution was also refined by recognizing the differences in the caloric yield of a unit weight of protein and fat. It was found, however, that the measurement of caloric yields, distinguishing between protein and fat, did not significantly alter unit values except in a limited number of carcass units, particularly the tail. Product weights apparently are adequate to determine relative unit value in bison, possibly due to the relatively minor contribution of fat to carcass yield. Although this finding did not affect model construction here (caloric yields are used in most model constructions), it suggests that any future carcass composition analyses of bison might not require such detail. This analysis, however, does not include an investigation of the affects of qualitative differences in fat on the relative value of carcass units. Speth (personal communication) suggests that fatty acid composition may be important and adds a dimension to selectivity that needs to be considered.

The remainder of the chapter concentrated upon model development and consideration of how variability in carcass composition is or is not reflected in these models. Three carcass unit utility model types were defined and their constructions specified: single class, averaged, and mixed class models. Single class models, developed for each of the bison studied here, are presented as representatives of their age, sex and condition classes. These models may be applied to assemblages characterized by similar animal class representation. These models also provide the basic data for the construction of averaged and mixed class models.

Averaged models are based upon the means of the carcass unit values for all four bison. These averaged models are suitable for application to assemblages of mixed age and sex composition, where detailed sex and age

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analyses of the bone assemblage have not been carried out. A detailed discussion was also presented concerning how averaged models mask age, sex, and condition differences in product distributions that were described in earlier chapters by averaging their values. It was also found that carcass units with large studentized residuals (when single class and averaged models are compared), showed distribution differences due to age, sex, or condition in earlier chapters. This indicates that application of an averaged model to an assemblage that is characterized by bison of a single animal class, results in under- or overestimation of the value of the carcass units that show distribution differences due to age, sex, or condition. It was predicted that these units might show up in applications to archaeological assemblages as units that do not fit model expectations. Depending upon the recovery strategy, an averaged total products model applied to an assemblage dominated by cows may overestimate the value of the neck, proximal humerus, and scapula. This averaged model applied to a bull dominated assemblage may underestimate the value of the neck and overestimate the value of the lumbar unit. Clear examination of this problem showed that this was not always the case, however. The recovery strategy, indicated by the relationship between the model and the percent MAU data for the assemblage, was found to profoundly affect whether the error in unit index value estimation would be expected to affect the proportions of bone recovery. Generally, if a bulk strategy is exhibited, the over- or underestimation of a unit's real value (given the animal class dominance of the assemblage) should have only a minor effect on bone distribution, because high and moderate valued units are removed in higher proportions than their value suggests anyway. The low valued units show the greatest risk of over- or underestimation with respect to expected use in

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the bulk strategy, but this may be of little importance. The greatest risk of erring in unit value estimation when using averaged models occurs in assemblages characterized by unbiased strategies and in the higher valued units in assemblages characterized by gourmet strategies.

The third model type described, the mixed class model, represents a new approach to modeling carcass unit selection. Mixed class models incorporate the data from two or more animal classes--in the models presented here, reasonably good conditioned males and poorly conditioned females--and scale the values of the units from both groups to the same maximum. By doing so, differences in productivity between the units of animals of different classes are recognized. Two potential problems, however, are evident with this model type. First, application of such models requires time consuming, detailed analyses of the archaeological bone assemblage to determine bone counts for the animal classes represented. Such analyses have only recently been developed (Speth 1983) and are time consuming. Second, these models are suitable for use primarily when major differences in class productivity, and thus, use, are expected. In this study, the animals used in the mixed class model, SAM and FAF, may not adequately represent the degree of difference in productivity (due to condition differences) needed to characterize the differences in some archaeological assemblages. Although the female, FAF, was found to be in poor condition, it might be characterized more fairly as suboptimum condition. Despite some apparent prolonged mobilization of fat resources, this female was not yet approaching starvation. Her productivity, therefore, may overestimate the frequencies of carcass unit bone present for females at the Garnsey Site. This is examined in more detail in the next chapter.

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In the next chapter, applications of the models developed in this study are compared with applications using models based upon gross weight ((S)FUI construction), in order to evaluate whether the developments presented here offer an improvement to modeling carcass unit selection. It is possible that these bison models are no more useful in the analysis of archaeological bone assemblages than bison models constructed according to the patterns described by Binford (1978) or Metcalfe and Jones (1988). It is this author's expectation, however, that eliminating unnecessary construction modifications and producing models that include measures of fat productivity, should offer improved results of model applications.

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CHAPTER 9. APPLYING CARCASS UNIT UTILITY MODELS

Three models types--single class, averaged, and mixed class models--all of which are constructed somewhat differently from those developed by Binford (1978) and simplified by Metcalfe and Jones (1988), were presented in the previous chapter and in Appendix C. Below, these models, as well as a gross-weight-based (S)FUI model (based upon the simplified construction outlined by Metcalfe and Jones 1988), are applied to two archaeological assemblages of bison bone, the Glenrock Buffalo Jump (Frison 1970) and the Garnsey Site (Speth 1983). These models are applied in order to evaluate their relative strengths in the analysis of carcass unit utility and prehistoric patterns of selection. In addition to these two general utility models, other models, presented in Appendix C, are applied to both archaeological assemblages in order to further investigate their usefulness in assemblage composition analyses. Before beginning these analyses, however, brief reviews of pertinent information concerning the sites and their assemblages are presented. A brief discussion of the potentially negative aspects of utility model applications follows presentation of the model evaluations.

Descriptions of Sites and Assemblages Used in the Analyses

Two late prehistoric period sites, the Glenrock Buffalo Jump (Frison 1970) and the Garnsey Site (Speth 1983) provide bison bone assemblages with which the carcass unit utility models may be evaluated. The Glenrock Jump is a kill site in central Wyoming. Frison (1970:7) reports that a hearth in

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the bottom of the bone-filled arroyo produced a radiocarbon date of A.D. 1740 (210 ± 100 B.P.). Its position below the bone level suggests the site assemblage is somewhat younger than this date. The Garnsey Site, located in southeast New Mexico, is reported by Speth (1983:48) to date between A.D. 1450 and 1500 (500 to 400 B.P.). Both sites predate the use of horses and guns by Native Americans in their respective regions.

These two sites were chosen for this analysis, in part, because the seasonality of the sites differ. Analyses of the dentition of the bison and the relative ages of the fetal remains indicate that the Glenrock Jump represents a fall kill (Frison 1978:294) and the Garnsey Site (Speth 1983:70) represents an early spring kill (possibly late March-early April, based upon the calving period of modern Southern Plains bison).

Multiple kill events are represented by the bone assemblages at both sites. Speth (1983:22-23,49) suggests that the Garnsey Site bone clusters represent quasi-contemporary kill events, and he treats the combined clusters as one assemblage. Two major bone levels are described for the Glenrock Jump, and the bottom level, which Frison notes is the larger of the two, is used in the analyses below.

A total of 35 animals is estimated as the minimum number of individuals (MNI) for the Garnsey Site (Speth 1983:53) and a total of 111 bison (based upon the count of the axis) is suggested by the bone count data presented by Frison (1970:10, Table 2) in his report. Speth suggests the Garnsey Site total might be increased by the separate analyses of the bone clusters, as well as age differentiation and other analytical techniques. Sexing of individual bones from the Garnsey Site assemblage, producing minimum numbers of individuals by sexes, did not increase this number. Speth (1983:75, 97) indicates the observed proportions of male and female elements for his

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analyses are based upon MNI estimates of 18 bulls and 13 cows. The assemblage appears to be the remains of one or more cow/calf groups and several bull groups (Speth 1983:72).

Sexing of individual bone elements was used by archaeologists only to a limited extent as an analytical tool at the time the Glenrock Jump assemblage was reported. Reher's (1970:52) analysis of the mandibles from this site (Reher 1970:52) produced bimodal distributions of mandible measurements. Reher concluded that, on the basis of these data, only 9 to 14 percent of the animals in the kill were mature bulls. There is no indication that the mandibles from each bone level were separated in his analysis. If this total assemblage percentage is applicable to the bottom level, which is used in the analysis below, then this would indicate the presence of 10 to 15 bulls in this cow/calf assemblage. Following the rut, mature bulls generally leave the herd, but may drift back for short periods of time during the non-breeding season, as herd grazing areas overlap (McHugh 1958:15-16, Lott 1974:383). Reher also concludes that immature bison are underrepresented at the Glenrock Jump and suggests that many were removed to a nearby processing site. Both the Glenrock Jump and Garnsey Site assemblages, therefore, include mature bison of both sexes, as well as immature animals.

The remaining site assemblage characteristic that is important to applications of carcass unit utility models is the effect of post-depositional taphonomic disturbances. Speth (1983:53-69) clearly demonstrates that disturbance of the Garnsey Site assemblage composition due to differential preservation, carnivore activity, or fluvial displacement is minimal. Based upon the relative numbers of proximal and distal humeri at the Glenrock Jump, the bottom level assemblage of the Glenrock Jump also

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appears to fall within a "zone of no destruction" as described by Binford (1981:219) and illustrated by Todd (1987a:151). Bone frequencies, for the most part, therefore, are assumed to represent selection decisions by the prehistoric hunters using these sites.

In the application of carcass unit utility models to archaeological bone, bone assemblage composition is expressed as the percent of the total number of animals each bone count represents, taking into account the number of each found in the body. This has been expressed as fractional MNI (Binford 1978) and more recently as the percent Minimal Animal Units (MAU, Binford 1984:50-51). In the Glenrock Jump assemblage from the bottom level (Frison 1970) for example, it was determined that a total of 111 bison are represented by the axis vertebra count. The bone count data also show that there are 136 scapulae. The scapula count is divided by two to account for the fact that there are two of these bones in the body, thus yielding a MAU value of 68. This is divided by 111, the maximum MAU value for all units, to indicate the percent of the minimum number of individuals represented, which in the case of the scapula is 61.3 percent. That is, 61.3 percent of a minimum of 111 bison are represented by one scapula. Speth (1983:86,97) provides these data for the Garnsey Site assemblage as a whole and for the assemblage when male and female bone elements are identified. The Garnsey Site data are reproduced in Table 9.1. The percent MAU data are calculated and presented in Table 9.2 for the Glenrock Buffalo Jump bottom level assemblage, based upon bone counts presented by Frison (1970:10), but these do not include counts based upon sex. It should be noted that these are best estimates of the minimum number of animals represented by each unit based upon the bone counts presented and that some error might occur due to the fact that (1) neither animal age nor sex were used to determine the bone

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Table 9.1. Garnsey Site Bone Assemblage Data

Anatomical Unit	Percent MAU Total[a]	Percent MAU Males[b]	Percent MAU Females[b]	Anatomical Unit	Percent MAU Total[a]	Percent MAU Males[b]	Percent MAU Females[b]
SKWOT	100.0	100.0	92.3	CARP	35.7	--	--
ATLAS	82.9	38.9	100.0	PMTC	44.3	16.7	61.5
AXIS	60.0	50.0	69.2	DMTC	35.7	16.7	61.5
C3C7	49.1	33.3	55.4	APHA	35.7	33.3	30.8
THOR	31.0	15.3	44.2	PFEM	24.3	5.6	38.5
LUMB	25.7	14.4	40.0	DFEM	38.6	5.6	38.5
SPEL	68.6	66.7	61.5	PTIB	42.9	11.1	38.5
CAUD	15.7	--	--	DTIB	31.4	16.7	38.5
RIBS	18.7	--	--	OTAR	28.6	--	--
STER	16.7	11.1	30.8	AST	28.6	11.1	61.5
SCAP	31.4	22.2	61.5	CALC	31.4	11.1	53.8
PHUM	45.7	11.1	46.2	PMTT	34.3	16.7	61.5
DHUM	41.4	16.7	46.2	DMTT	34.3	16.7	61.5
PRUL	32.9	27.8	38.5	PPHA	35.7	27.8	38.5
DRUL	34.3	16.7	30.8				

[a] Source: Speth (1983:86:Figure 28).
[b] Source: Speth (1983:97:Table 13).

Table 9.2. Skeletal Data for Lower Level of the Glenrock Buffalo Jump

Anatomical Unit	MNI[a]	Percent MAU	Anatomical Unit	MNI[a]	Percent MAU
SKWOT	98.0	88.3	DRUL	58.0	52.3
ATLAS	110.0	99.1	CARP	--	--
AXIS	111.0	100.0	PMTC	83.0	74.8
C3C7	76.0	68.5	DMTC	71.0	64.0
THOR	36.0	32.4	PHAL	72.25	65.1
LUMB	61.4	55.3	PFEM	17.0	15.3
SPEL	69.0	62.2	DFEM	14.0	12.6
CAUD	1.4	1.3	PTIB	20.0	18.0
RIBS	44.9	40.5	DTIB	27.0	24.3
STER	--	--	AST	77.0	69.4
SCAP	68.0	61.3	CALC	81.0	73.0
PHUM	18.0	16.2	PMTT	80.5	72.5
DHUM	29.0	26.1	DMTT	88.0	79.3
PRUL	47.0	42.3			

[a] MNI calculated from bone counts published by Frison (1970:10:Table 2).

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counts, and (2) some units which occur in the body in pairs or groups are only reported by Frison (1970:10) as grouped data. Further clarification of side counts in appendicular units and vertebrae number in the axial skeleton might yield somewhat different MAU and percent MAU values.

Comparison of (S)FUI and (S)MTP Model Applications

In the previous chapter, it was noted that the construction of the gross-weight-based (S)FUI model overestimates the value of the appendicular and atlas-axis units when compared with the construction of the caloric-yield-based (S)MTP model. The overestimation of index values is especially noticeable for the carpal and tarsal units which derive their value as a function of the combined value of these units with a larger, adjacent long bones (the metacarpal or tibia). Figure 9.1 illustrates the relationship between the averaged data total products model, (S)MAVGTP, and the Glenrock Jump lower level percent MAU data, and Figure 9.2 similarly illustrates the relationship with the averaged gross weight model, (S)AVGFUI. Averaged data models are used rather than single class models due to the presence of males and females of adult and immature status in the assemblage, and instead of mixed class models because detailed sex data for the post-cranial bones from this site are not available.

Initial inspection of these figures suggests that the (S)AVGFUI model (Figure 9.2) provides a relatively tight relationship between the model values and the archaeological assemblage composition data with a few exceptions. In Figure 9.2 there are fewer caudal vertebrae (CAUD) units present than would be expected given their relative value compared with the other carcass units of the body. Similarly, several axial units, including the ribs (RIBS), thoracic (THOR), lumbar (LUMB), and cervical vertebrae

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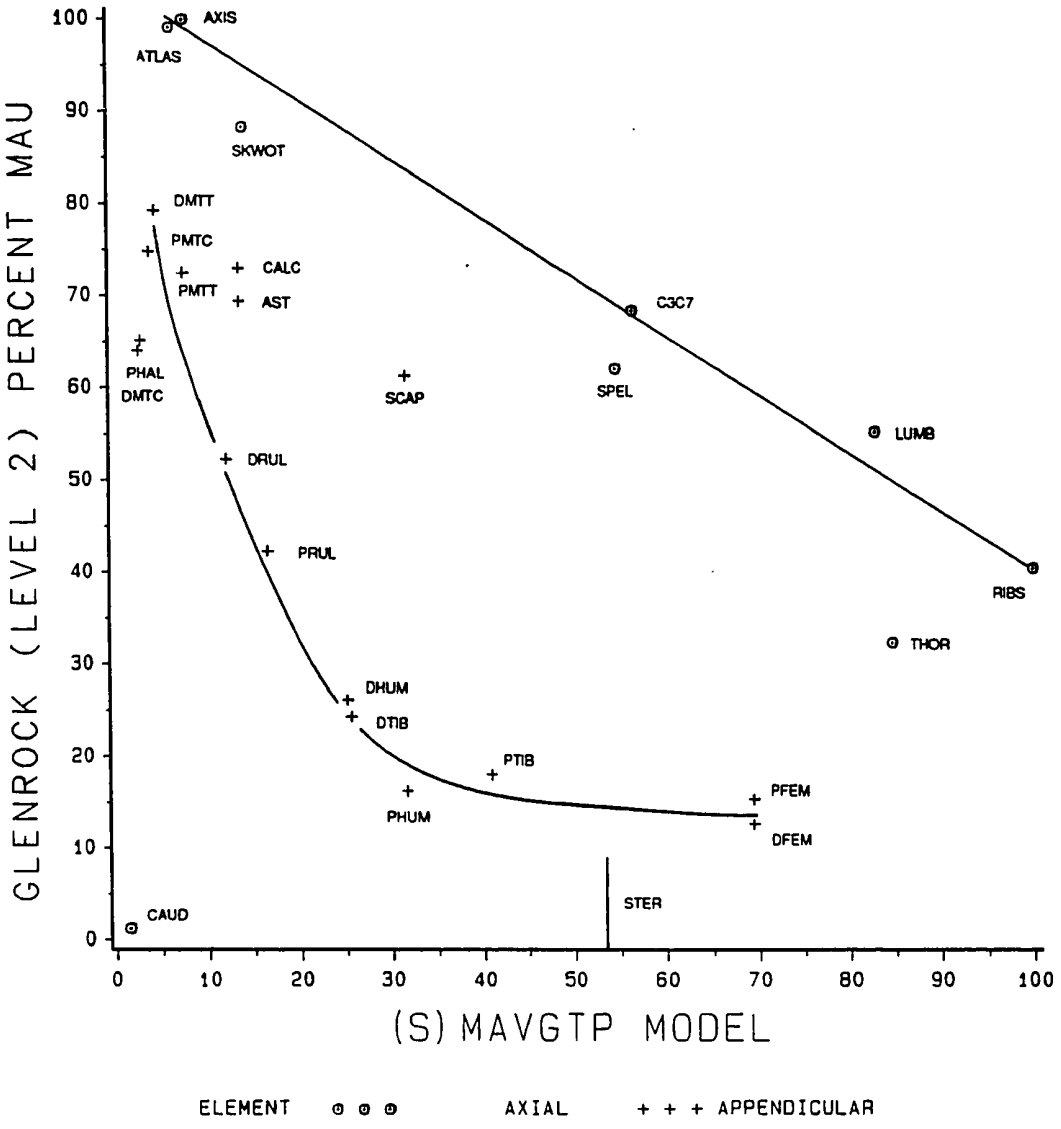

Figure 9.1. Averaged Total Products Model ((S)MAVGTP) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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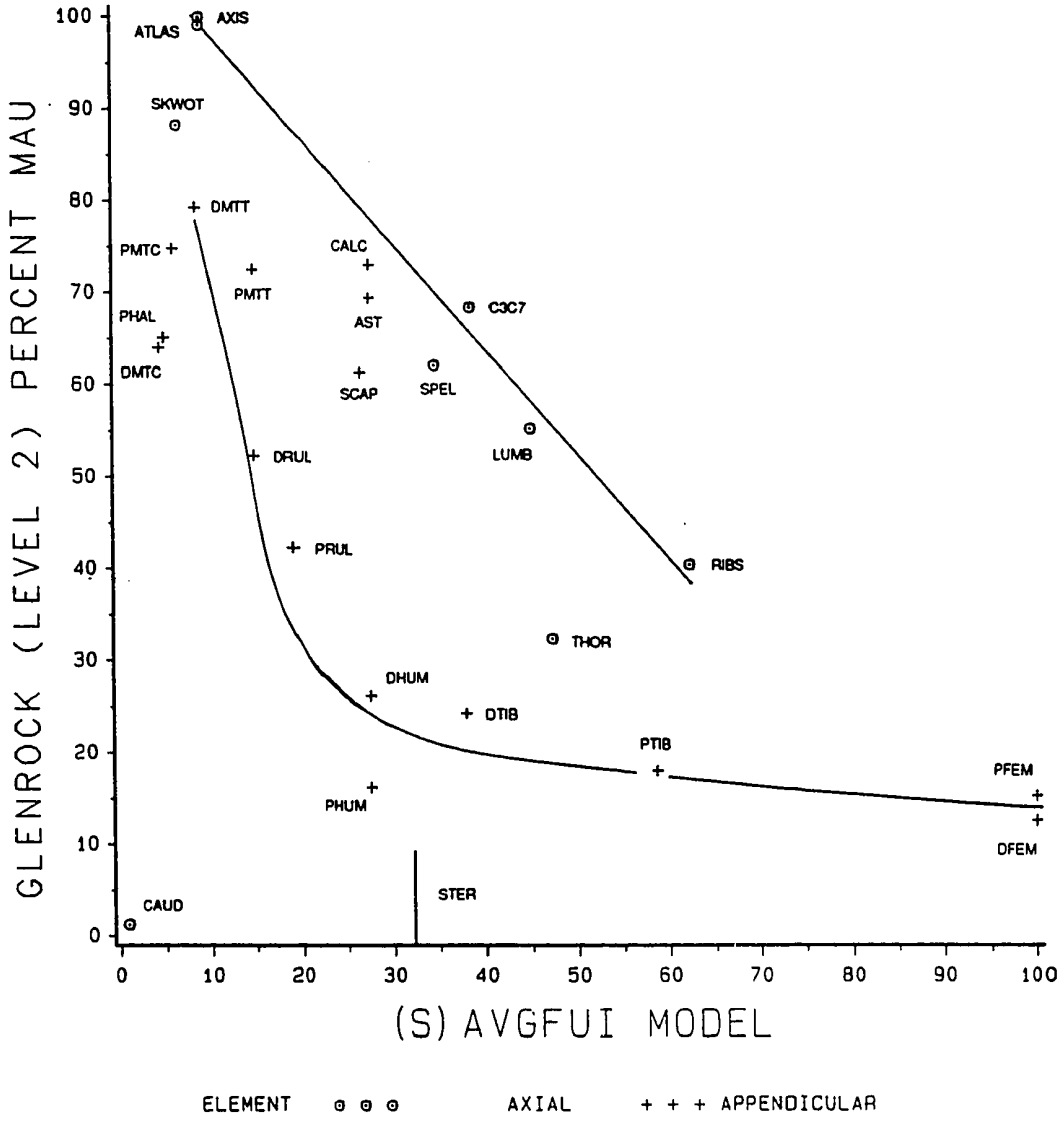

Figure 9.2. Averaged FUI Model ((S)AVGFUI) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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(numbers three through seven, C3C7), as well as several appendicular units, including the scapula (SCAP) and tarsals (TARS), occur in higher proportions than expected, given their index values.

In Figure 9.1, where the assemblage is compared with the caloric yield model for total products, (S)MAVGTP, a similar, but somewhat different pattern emerges. In this figure, the axial units are again overrepresented relative to the appendicular units, as is the scapula (SCAP); the caudal vertebrae (CAUD) are underrepresented. What becomes clear in looking at this scatterplot (Figure 9.1) of the relationship between the (S)MAVGTP model and the archaeological bone assemblage, that is not as clear in Figure 9.2, is that hunter treatment of the the axial and appendicular units differ. The relationship of the model and percent MAU data for the appendicular units in Figure 9.1 shows that these units were recovered according to a bulk strategy (see Figure 8.3). High and moderate valued units were abandoned in low proportions relative to their availability, and low valued units were abandoned in increasingly larger proportions as their index values decrease. This suggests high and moderate valued units were removed in high proportions and low valued units were removed in low proportions as is typical of a bulk recovery strategy.

Many of the axial units (excluding the caudal vertebrae (CAUD), and possibly the sternebrae (STER) whose bone counts were not reported), on the other hand, appear to have been butchered and removed according to what appears to be an unbiased recovery strategy. Although this pattern is evident in the (S)AVGFUI model application in Figure 9.2, the total products model, (S)MAVGTP (Figure 9.1), shows this relationship much better, without the mixing of the tarsal units (AST and CALC) in the axial unit distribution.

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Given the evidence that models based upon caloric yield are not substantially different in their rankings of carcass units from models based upon product weight, and only minimally different from models based on gross weight, the differences in the results of the (S)MAVGTP and (S)AVGFUI applications are attributed primarily to differences in model construction. Apparently the construction of the (S)FUI model, which inflates the value of appendicular units, to some extent obscures the relationship between carcass unit value and bone abandonment between the axial and appendicular units. On the basis of this assessment, the total products model, (S)MAVGTP, is preferred over that of the gross-weight-based (S)AVGFUI model.

Model Applications to the Glenrock Buffalo Jump Assemblage

In the application of the total products model, (S)MAVGTP, to the Glenrock Jump lower level assemblage (Figure 9.1), despite the recognition that the axial and appendicular units were treated differently, it may be noted that several units (e.g., the scapula (SCAP), caudal vertebrae (CAUD), and sternebrae (STER)) appear to be outliers. It is assumed that where the carcass units do not conform to the pattern of recovery expected (i.e., occur as outliers), that several factors might be involved. Failure of the data to describe a relatively smooth linear (given an unbiased recovery strategy) or curvilinear (given a bulk or gourmet recovery strategy) relationship might occur for one of the following reasons: (1) inappropriate application of model type--that is, use of a model constructed using different animal class representatives than are actually present at the site (e.g., use of the averaged total products model on a bull group assemblage); (2) lack of conformity in carcass unit division between model construction and the site butchering pattern; (3) conflict between

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processing and transportation costs that override the expected recovery frequency; (4) insufficient data to refine MAU calculations so that differences between age or sex class treatment may be identified; and (5) inappropriate application of model focus--that is, use of a model that ranks carcass units relative to their yield of a product(s) different from that(those) targeted by the hunters. These problems obviously cannot be resolved based upon the bone assemblage composition and model comparisons alone. References to other analytical data such as the relative proportions of males and females, immature and mature animals, the evidence of butchering patterns on the bones, and gross estimates of relative costs of transport or processing may indicate why some carcass units are not present in proportions expected for their relative index value and the described recovery strategy pattern. These explanations for unit deviation are examined in the model applications below.

Averaged Total Products Model, (S)MAVGTP, Application

Three carcass units, in addition to the caudal vertebrae, appear to differ sharply from their expected placements on the graph of the Glenrock Jump site data plotted against the (S)MAVGTP model (Figure 9.1). The thoracic vertebrae (THOR) and sternebrae (STER) units were removed from the site in higher proportions than expected for the apparent unbiased recovery strategy of the axial units, and scapulae (SCAP) were removed in smaller proportions than expected, given the bulk recovery strategy for the appendicular units. Though less noticeable, the distal metacarpal, phalanges and head (DMTC, PHAL and SKWOT) also appear to be underrepresented at the site, and the cervical and sacrum/pelvis (C3C7 and SPEL) units are reversed in their relative proportions from what would be expected given

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their relative model values. The underrepresentation of the head is probably a function of the underestimation of unit value, rather than variability in its treatment compared to other axial units. Officials at Theodore Roosevelt National Park requested that the skulls be returned to the Park. In order to assure their return in good condition, the brains and bone grease were not collected from the skulls and/or mandibles. Similarly, marrow was collected from the mandibles of only two of the bison, requiring this product to be excluded from the total caloric yield computations as well. It is expected that the actual (S)AVGTP value for the head (SKWOT) unit is higher than the value listed in Table 8.6. This increase in index value might reduce the size of the residual for this unit in Figure 9.1.

Frison (1970:11) suggests that the low proportion of caudal vertebrae (CAUD) at the Glenrock Jump Site may be attributed to its use in the skinning process, where the tail served as a handhold for the removal of the hide from the carcass. A secondary explanation of this unit's unexpectedly low representation at the site (assuming that taphonomic factors are not relevant) is based upon its value as a food producing unit. It was noted in Chapter 6 that tails have a low ratio of protein to fat compared to other carcass units, which might make these more highly valued units than their relative total caloric yield would suggest. At this fall season kill, the importance of the ratio of protein to fat is probably not as critical to hunter nutrition as at spring season sites. The importance of tails, however, may have been overlooked by archaeologists, in part, because their value based on relative caloric or weight yield does not reflect their value that is evident when the relative fatness of the meat is considered. It is not clear, however, how one might distinguish between its use as food and as a hide removal aid based upon kill site data alone. In either case, the

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unit is removed to a processing and/or camp site for further processing. Perhaps examining caudal vertebrae at these other sites for evidence of alteration from cooking would clarify whether tails should be considered a food producing unit.

The higher than expected proportion of scapulae (SCAP) left at the site, Frison (1970:14) attributes to their abandonment without further processing after the associated muscles were stripped from the bone. Assuming that carcass use is largely guided by productivity, this butchering pattern suggests that after removal of the muscle, the scapulae becomes a low valued unit and that processing effort (meat removal) is smaller than the associated transport costs if the bone is left with the meat. To evaluate this, one must look at the relative yield of the skeletal fats. The unmodified, averaged data model, (S)AVGSKF (Appendix C, Table 18), provides this data. The modified data model is not suitable, because the rider averaging routine has been applied in that model and the value of the scapula is raised due to its proximity to the highly valued proximal humerus (PHUM). The average value of the scapula for production of marrow and grease fat, after standardization and prior to modification to account for the effect of riders, is 11.8 (Appendix C, Table 18), which is relatively low. It may be relevant to note that the small amount of grease recovered from processing the scapula was generally hard and flaky which contrasts with that of the other limb bones, suggesting that its grease is more saturated than that in other appendicular units. It appears, therefore, that at the Glenrock Jump, the averaged total products model, (S)MAVGTP, does not predict the treatment of the scapula very well, because its value is largely derived from non-skeletal products which are easily separated from the bone. Apparently the cost of transport with the bone intact, in

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this case, outweighs the cost of processing (see Metcalfe and Jones 1988).

This processing versus transport cost assessment explanation also may account for the underrepresentation of sternebrae (STER), given the generally unbiased recovery strategy suggested by most of the other axial units in their relationship between index value and percent MAU. Frison (1970:10) did not report the number of sternebrae in his bone count table for the bottom level at the Glenrock Jump. In the text, however, he indicates that "this part of the carcass with almost no exceptions was taken from the site" (1970:11). Treatment of the sternebrae unit, therefore, appears to be more like that of the appendicular units at the Glenrock Jump. The index value for the sternebrae unit in the (S)MAVGTP model is 52.9. It is expected, based upon Frison's comment, that this unit would fall somewhere below or in the neighborhood of the line suggested by the relationship between the index values and percent MAU for the appendicular units in Figure 9.1 at the 52.9 index value position. It is not clear why the sternebrae unit should be recovered more in accordance with the appendicular units than with other axial units. Perhaps the processing time that would be required to separate the relatively light, low fat yielding bone (the sternebrae are a major location of hemopoietic tissue) of this unit from the flesh and costal cartilage outweighed the cost of transport with bone and cartilage intact. The sternebrae are relatively light (Table 5.16) and do not add much to transport costs.

The thoracic vertebrae unit (THOR) is similarly underrepresented in the lower level Glenrock Jump assemblage for the axial unit unbiased recovery strategy described in Figure 9.1. Like the sternebrae unit, the thoracic vertebrae produce relatively little skeletal fat (Appendix C, Table 18). It is unlikely that this unit's low proportional representation at the site,

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therefore, is due to these units having been transported elsewhere for recovery of skeletal fat. Nor is is probable that the relationship between processing and transport cost is a factor here. Rather, it appears that differences in carcass unit division between the model and as practiced at the site are responsible for it underrepresentation. According to Frison (1970:20), the dorsal spines of the thoracic and lumbar vertebrae are rare occurrences at the site and he suggests that these were removed with their associated hump meat. Binford (1978) indicates that Nunamiut hunters often dry the thoracic segments as a unit. One would expect the thoracic vertebrae bodies to occur in high, not low proportions of the total possible, as seen here in Figure 9.1. The lower than expected proportional frequency of the thoracic unit appears to be due not to the value of the thoracic unit, but perhaps to the cost of separating the ribs from the thoracic vertebrae. Frison notes:

> There are about equal numbers of ribs that are broken near the distal end as there are complete ones and it is suggested that the ribs from about number 6, 7, 8, or 9 to number 14 constituted a desirable portion of the carcass and that one side was removed by cutting the ribs close to the vertebral column and removing them as a unit. When the carcass was turned over, the ribs on this side were not cut close to the vertebral column but were removed as a unit but still attached to their respective thoracic vertebrae [1970:19].

One might expect, therefore, that the thoracic vertebrae would be removed from the kill site at least in comparable proportion to the ribs. Although the ribs unit is still more abundant than the thoracic unit, this may account for some of the differences in the expected percent MAU. The

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remaining difference in percent MAU between the higher valued ribs and the thoracic units might occur if some ribs were removed at their articulations with the vertebrae, thus increasing the ratio of vertebrae to ribs.

The possibility that use of the averaged model might be responsible for some of the apparent poor fit of the model for the units noted above, must be considered. Specifically, the ratio of the numbers of animals of different sexes is considered for its influence on the resulting unit values in the construction of the total products model.

Model Modification to Reflect Kill Sex Ratios

The averaged model (S)MAVGTP uses the (S)TP data from each of the four bison studied in this project to determine the (S)AVGTP and subsequent (S)MAVGTP index values (Table 8.6). As one of four animals, the male bison, SAM, represents one quarter (25 percent) of the sample population used in these model constructions. At the Glenrock Jump, however, Reher (1970:52) noted that mature males probably constituted from 9 to 14 percent of the bison in the total assemblage. It is possible, therefore, that male differences in variability are overrepresented in the calculations of the averaged model values for application to this particular assemblage.

To determine whether the units in question deviate from their expected proportions due to the differences in the numbers of bulls included in the model construction, an averaged model based upon a 9 percent inclusion of bulls is calculated (Table 9.3) and plotted against the Glenrock Jump data (Figure 9.3). Construction of this model is accomplished by averaging the (S)TP values for FYM, SAF, and FAF, multiplying this average by 91, adding the product of the SAM(S)TP value multiplied by 9, and dividing the sum by 100. The averaging routine that accounts for the effect of riders is then

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Table 9.3. Averaged (S)MTP Model with Nine Percent Bulls--(S)M9PBTP

Carcass Unit	SAM(S)TP	(S)TP Average[a]	(S)9PBTP	(S)M9PBTP	Carcass Unit	SAM(S)TP	(S)TP Average[a]	(S)9PBTP	(S)M9PBTP
SKWOT	13.8	14.3	14.3	14.3	DRUL	6.7	7.8	7.7	12.2
ATLAS	7.1	6.2	6.3	6.3	CARP	0.2	0.5	0.5	6.7
AXIS	8.7	7.5	7.6	7.6	PMTC	0.6	1.0	1.0	4.0
C3C7	63.2	54.4	55.2	55.2	DMTC	0.6	1.2	1.2	2.7
THOR	74.9	87.9	86.8	86.8	APHA	0.4	1.4	1.3	2.0
LUMB	67.0	88.2	86.3	86.3	PFEM	64.5	70.6	70.1	70.5
SPEL	49.4	56.4	55.8	55.8	DFEM	64.2	71.2	70.5	70.5
CAUD	0.8	1.7	1.6	1.6	PTIB	11.2	12.4	12.3	41.4
RIBS	100.0	100.0	100.0	100.0	DTIB	9.1	10.7	10.6	26.0
STER	46.2	55.1	54.3	54.3	TARS	1.0	1.8	1.8	13.9
SCAP	33.1	31.1	31.3	31.3	PMTT	0.7	1.4	1.3	7.8
PHUM	20.5	20.4	20.4	31.3	DMTT	0.8	1.7	1.6	4.7
DHUM	18.0	18.8	18.8	25.1	PPHA	0.6	1.4	1.3	3.0
PRUL	6.6	8.4	8.2	16.6					

[a] Average of (S)TP values for FYM, SAF, and FAF from Table 8.5, Part B.

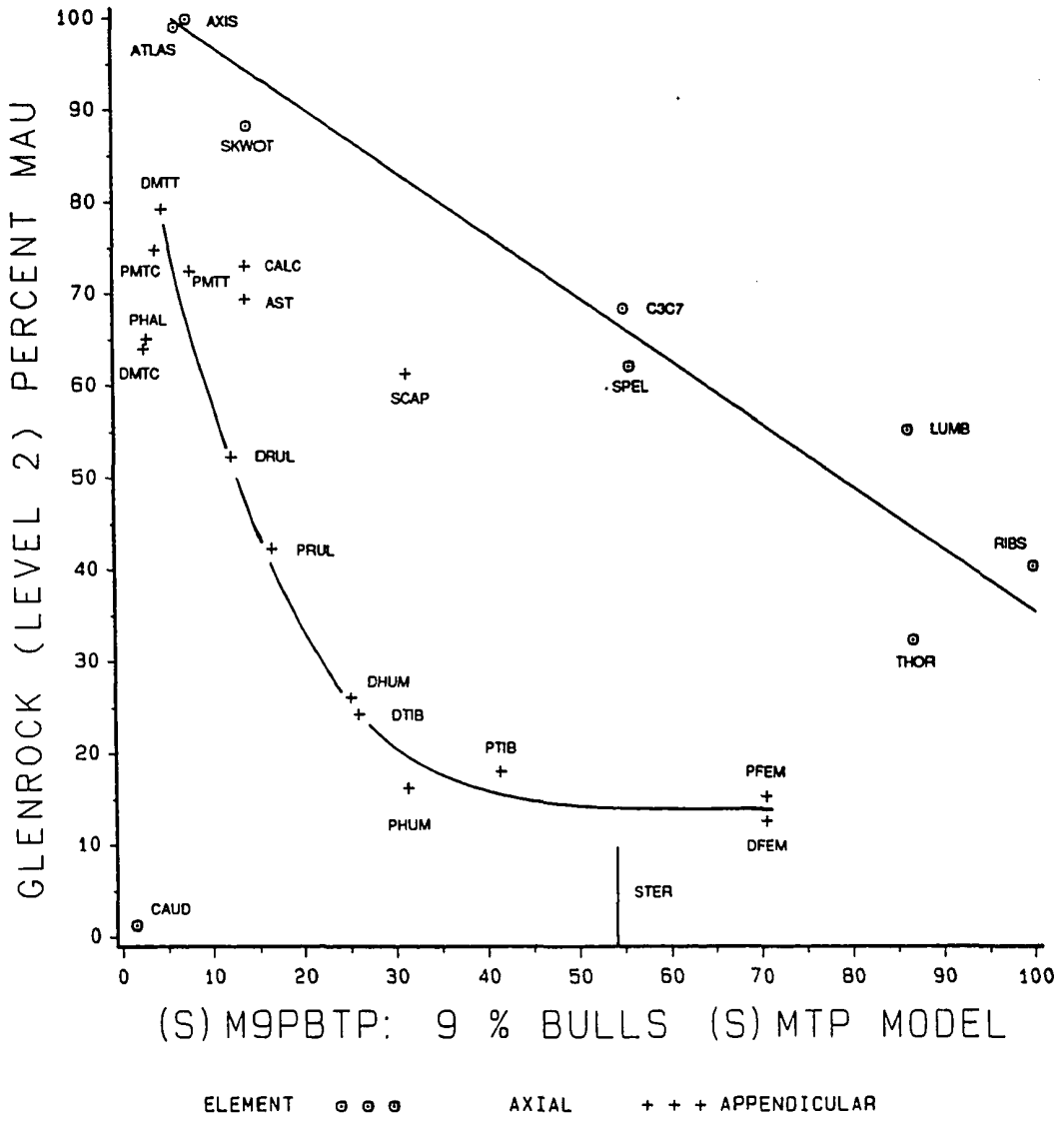

Figure 9.3. Application of the Total Products Model with a Sex Ratio of Nine Percent Bulls (Model (S)M9PBTP) to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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applied to the averaged (S)TP values, yielding model (S)M9PBTP (standardized, modified, nine percent bulls, total products model). A similar model based upon 14 percent representation of adult males could be constructed in a similar manner substituting 14 for 9 and 86 for 91 in the calculations described above. This is not done here, however, because it is clear that the carcass unit values lie intermediate between those listed in Table 8.6 ((S)MAVGTP) and Table 9.3 ((S)M9PBTP).

Comparison of Figures 9.1 and 9.3, and Tables 8.6 and 9.3 shows that very little change occurs in the plots. The units that deviate from their expected values using the (S)MAVGTP model, also deviate with the (S)M9PBTP model. It is perhaps noteworthy that the relationship between the sacrum/pelvis (SPEL) and cervical vertebrae (C3C7) has shifted in the direction that would bring these units more in line with the unbiased strategy relationship. With a smaller proportion of bulls in the model construction, the index value of the SPEL unit increases and that of the C3C7 unit decreases. The neck was quite large in FAF relative to SAF as well, so perhaps the value of this unit has been overrepresented in these models. In general, however, it appears that the use of the (S)M9PBTP model does not substantially improve the fit of the model. At another site where the herd composition includes a substantially larger proportion of males than the 25 percent represented in the (S)MAVGTP model, such modifications might produce significant differences. The limit of those modifications (i.e., 100 percent bulls) are modeled in the single class model based upon data from SAM (SAM(S)MTP).

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Applications of Other Product Models

The difference in recovery strategies used at the Glenrock Jump for most axial and appendicular carcass units (unbiased versus bulk recovery strategies) when percent MAU is plotted against the model of total caloric yield ((S)MAVGTP) is interesting. The difference may be studied in further detail by the application of other averaged models constructed from more limited numbers of products than are used in the total products model (those presented in Appendix C). Applications of these models to the Glenrock Jump data show that different products appear to influence the recovery of the axial and appendicular units at this site.

Graphs of the Glenrock Jump data plotted against the more limited data models for protein ((S)MAVGPRO), total fat ((S)MAVGTF), selected fat ((S)MAVGSF), skeletal fat ((S)MAVGSKF), bone grease ((S)MAVGGRE), white grease fat ((S)MAVGWG), yellow grease fat ((S)AVGYG), and marrow fat ((S)MAVGMAR), all of which are tabulated in Appendix C, show that, excluding the caudal and sternebrae units, the model based upon the caloric yield of all fat depots (skeletal, carcass and intramuscular), (S)MAVGTF, provides the best fit for an unbiased strategy for the axial units (Figure 9.4). Excluding the caudal (CAUD) and sternebrae (STER) units, this model describes a relatively tight linear relationship between the relative value of the units and their proportional representation at the site. The other two units which lie farthest from the line describing this relationship are the head (SKWOT) and the lumbar vertebrae (LUMB) units. The deviation of the SKWOT unit is attributed to the absence of the grease, marrow, and brain data in the calculation of its index value. Their inclusion would increase the unit index value and bring it closer to the line describing the relationship between index value and percent MAU.

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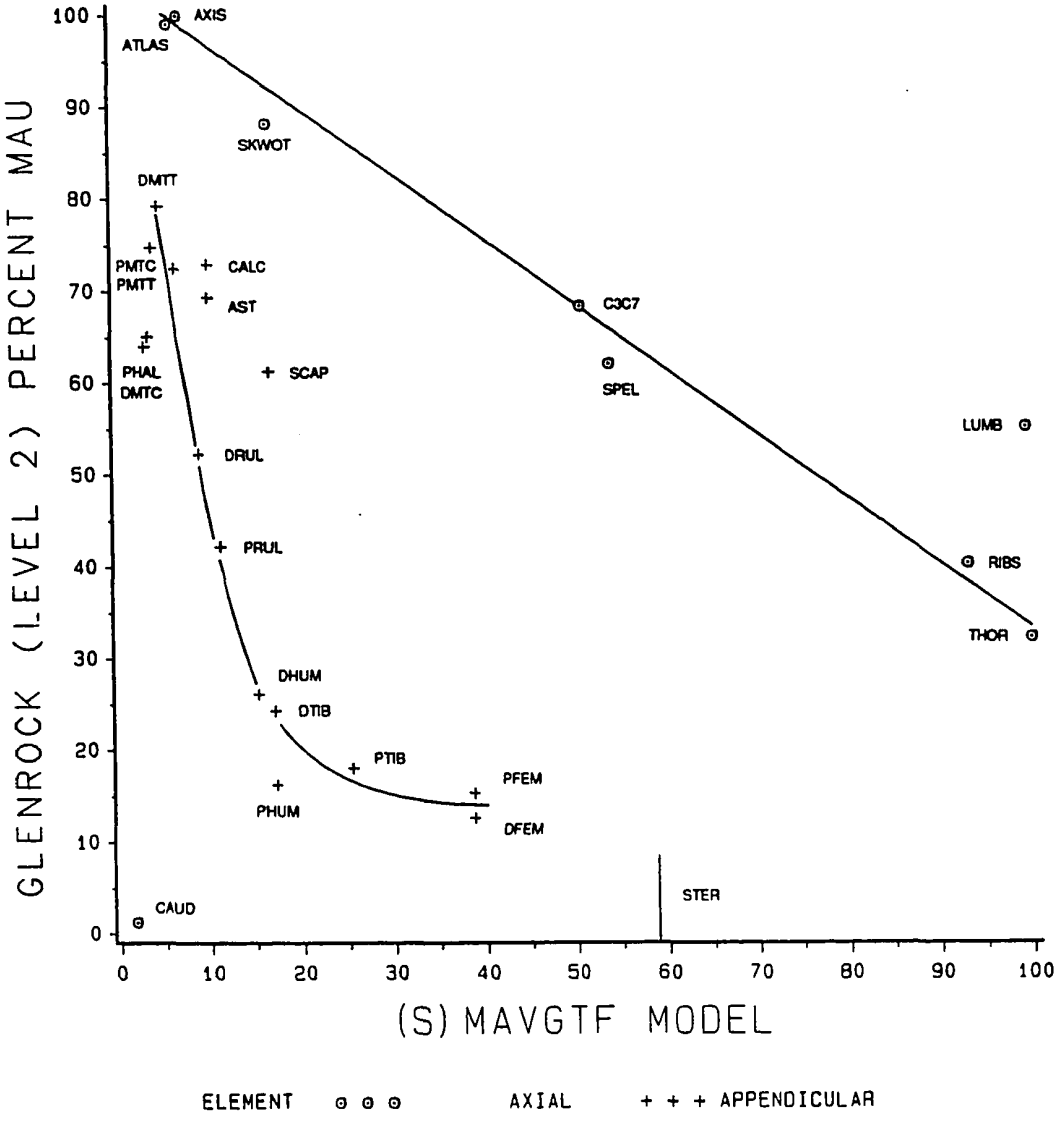

Figure 9.4. Averaged Total Fat Model ((S)MAVGTF) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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The lumbar vertebrae unit (LUMB) is found in higher proportions at the site than would be expected based upon its caloric yield from total fat. Two factors might account for this. First, it is probable that division of the LUMB unit from the rest of the carcass differed between model construction and the site. In this study of bison carcass composition, the LUMB unit included the abdominal muscles and carcass fat found posterior to the fourteenth rib and ventral to the lumbar vertebrae. This abdominal tissue probably should have been evaluated as a separate unit unassociated with bone. If the caloric yield from this part of the abdomen were removed from the calculations for the lumbar (LUMB) unit, it would lower its index value and bring it closer to the line describing the relationship between the index and site data. Alternatively, muscle and fat may have been stripped from the LUMB unit and the bone discarded due to its moderately low skeletal fat yield (comparable to the metacarpal and phalanges).

Despite the deviation of the caudal, sternebrae, and lumbar vertebrae units, the axial units of the bison carcasses at the Glenrock Jump appear to have been butchered and removed from the site in accordance with their value based upon the caloric yield of the total fat. The (S)MAVGTF model (Figure 9.4) provides a better unbiased relationship between index value and site data for the axial units than any other fat model or the protein model. The averaged total fat model, however, does not show an unbiased strategy for the appendicular units (Figure 9.4).

Bulk recovery strategies are indicated for the appendicular units when the Glenrock Jump data are compared with the following models: total fat ((S)MAVGTF), selected fat ((S)MAVGSF), protein ((S)MAVGPRO), and bone grease fat ((S)MAVGGRE). The site data plotted against the marrow fat ((S)MAVGMAR), white grease fat ((S)MAVGWG), and skeletal fat ((S)MAVGSKF)

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models show the appendicular units describing backwards s-shaped curves (e.g., Figure 9.5). The data points lie relatively close around the lines in the plots for (S)MAVGSKF and (S)MAVGWG (Figures 9.5 and 9.6), but are somewhat dispersed in the plot for (S)MAVGMAR (Figure 9.7). Combining the grease and marrow fat caloric yield in (S)MAVGSKF (Figure 9.5) shortens the tail of the curve at the upper end of the index and lengthens the tail at the lower end when compared with the plot for the white grease model ((S)MAVGWG, Figure 9.6). It appears from Figure 9.5, that the combined marrow and grease fat yield was an important factor in the recovery of appendicular carcass units at the Glenrock Jump, otherwise one might expect either the white grease or marrow model to provide a better representation of an unbiased recovery strategy. It should be noted that the suggestion that unit removal was largely influenced by the combined caloric yield of marrow and grease does not suggest that the meat from these appendicular units was wasted. It merely suggests that this model ((S)MAVGSKF) better accounts for the proportions of bones remaining than any of the models that include protein.

In sum, the applications of various caloric-yield-based models to the Glenrock Jump bison bone assemblage data suggest that the axial units were recovered primarily as a reflection of their yield of total fat. The appendicular units, however, appear to have been removed in accordance with their value based upon their yield of skeletal fat, including marrow and bone grease.

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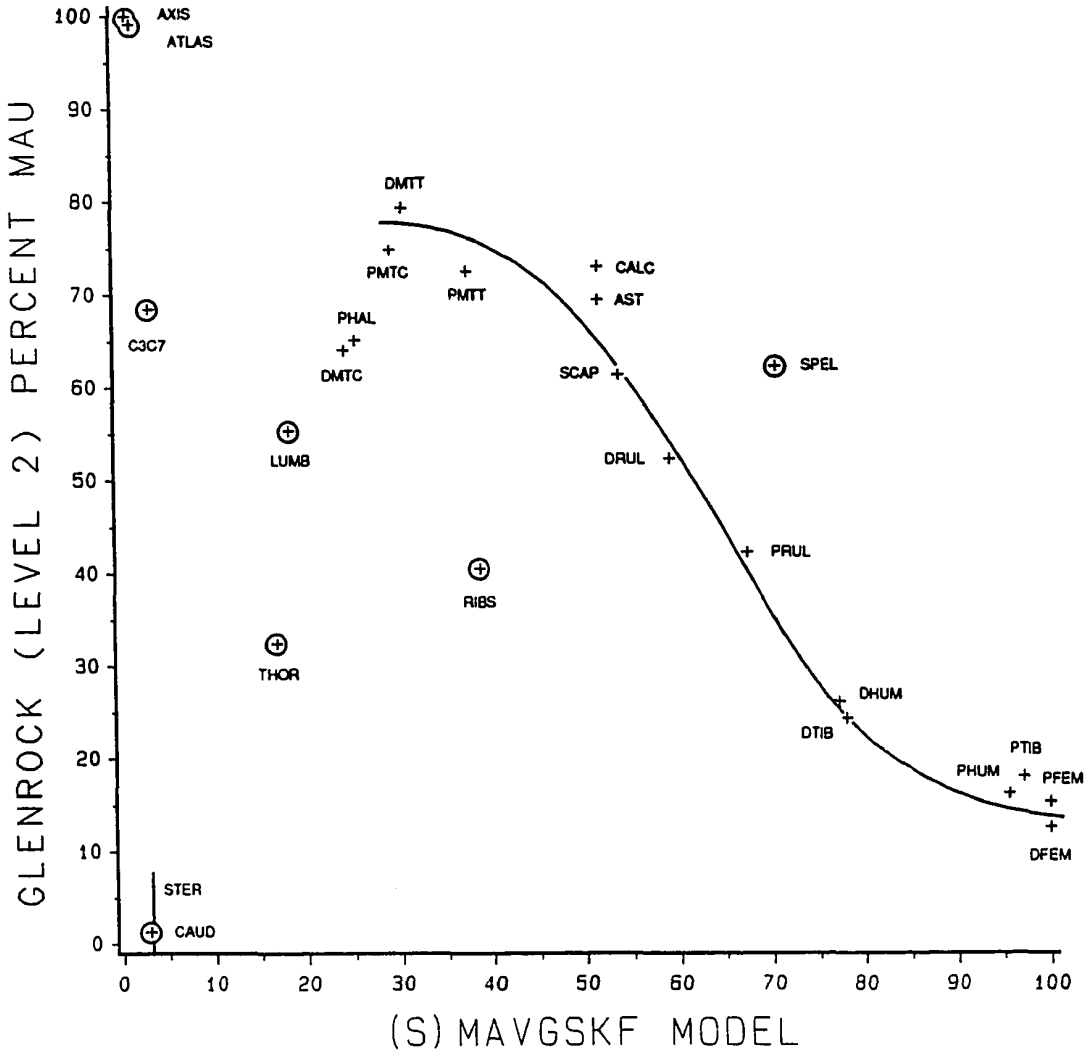

Figure 9.5. Averaged Skeletal Fat Model ((S)MAVGSKF) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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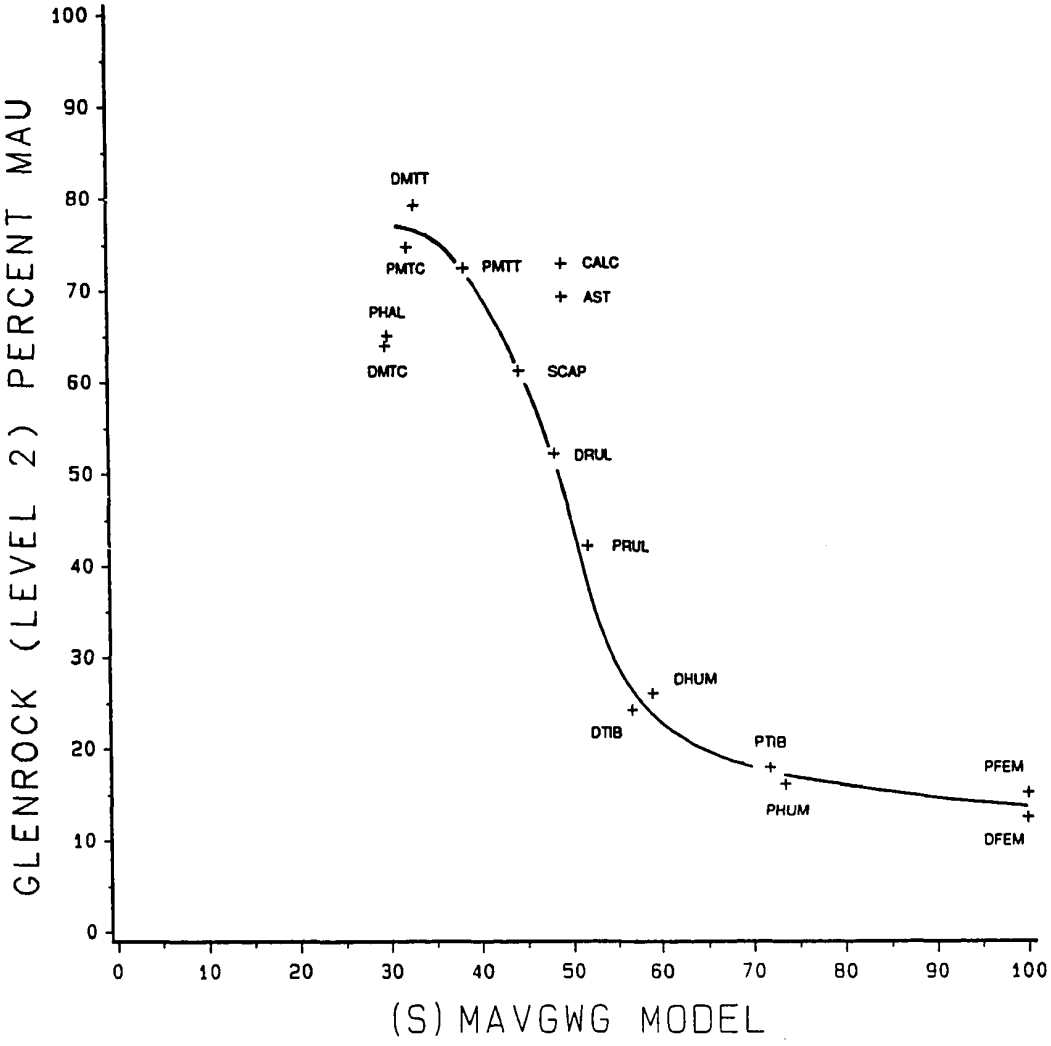

Figure 9.6. Averaged White Grease Fat Model ((S)MAVGWG) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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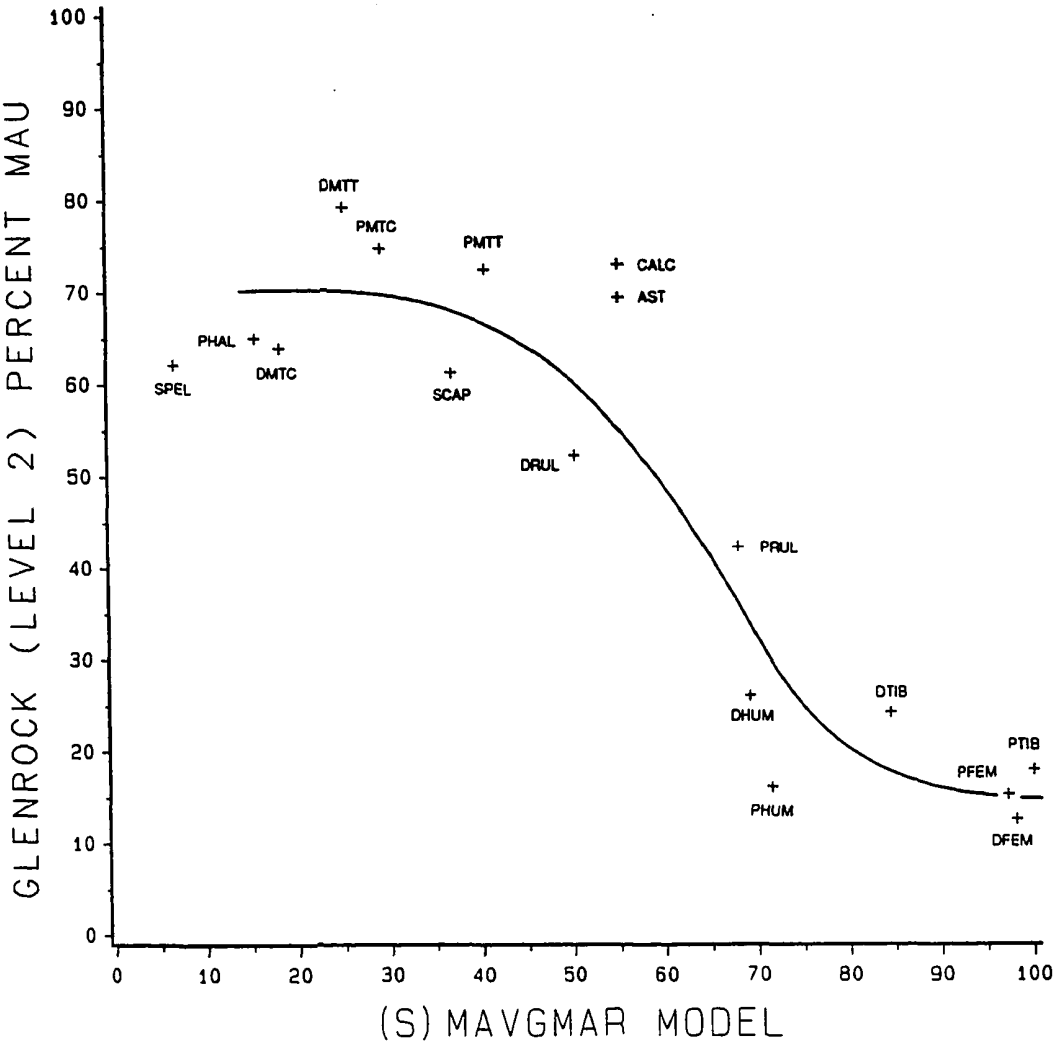

Figure 9.7. Averaged Marrow Fat Model ((S)MAVGMAR) Applied to the Lower Level Assemblage of the Glenrock Buffalo Jump. The Glenrock Jump data are calculated from Frison (1970:10:Table 2).

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Model Applications to the Garnsey Site Assemblage

The Garnsey Site data are examined below using the three carcass unit model types described in the previous chapter--averaged, combined, and single class models. The averaged model application is presented, in part, to show its differences in character from the Glenrock Jump lower level assemblage. The mixed class model which expresses the relative value of carcass units from males and females according to the same scale, shows that males and females were treated differently at this site. The mixed class model application does not produce the intermeshing of male and female assemblages that was expected, and possible reasons for the separation are discussed. Single class models are then applied to the male and female bone assemblages and indicate where selection differed and was similar between these groups.

Application of Averaged Total Products Model, (S)MAVGTP

Figure 9.8 is a graph of the relationship between the averaged total products model, (S)MAVGTP, and the total Garnsey Site bone assemblage data. As in the Glenrock Jump application, the axial elements suggest a possible unbiased recovery strategy, with the exception here of four units, while the appendicular units show only minor variability in their rates of recovery. This pattern of similar bone frequencies for appendicular units is similar to that seen for many Paleoindian period assemblages and has been suggested to be indicative of complete limb removal, rather than by segmented subsets (Todd 1987b:259). As at the Glenrock Jump, the caudal (CAUD) and sternebrae (STER) units are both underrepresented for the axial unit distribution, but unlike that site, the atlas and axis units are underrepresented here as well. The remaining axial units, the head (SKWOT), sacrum/pelvis (SPEL),

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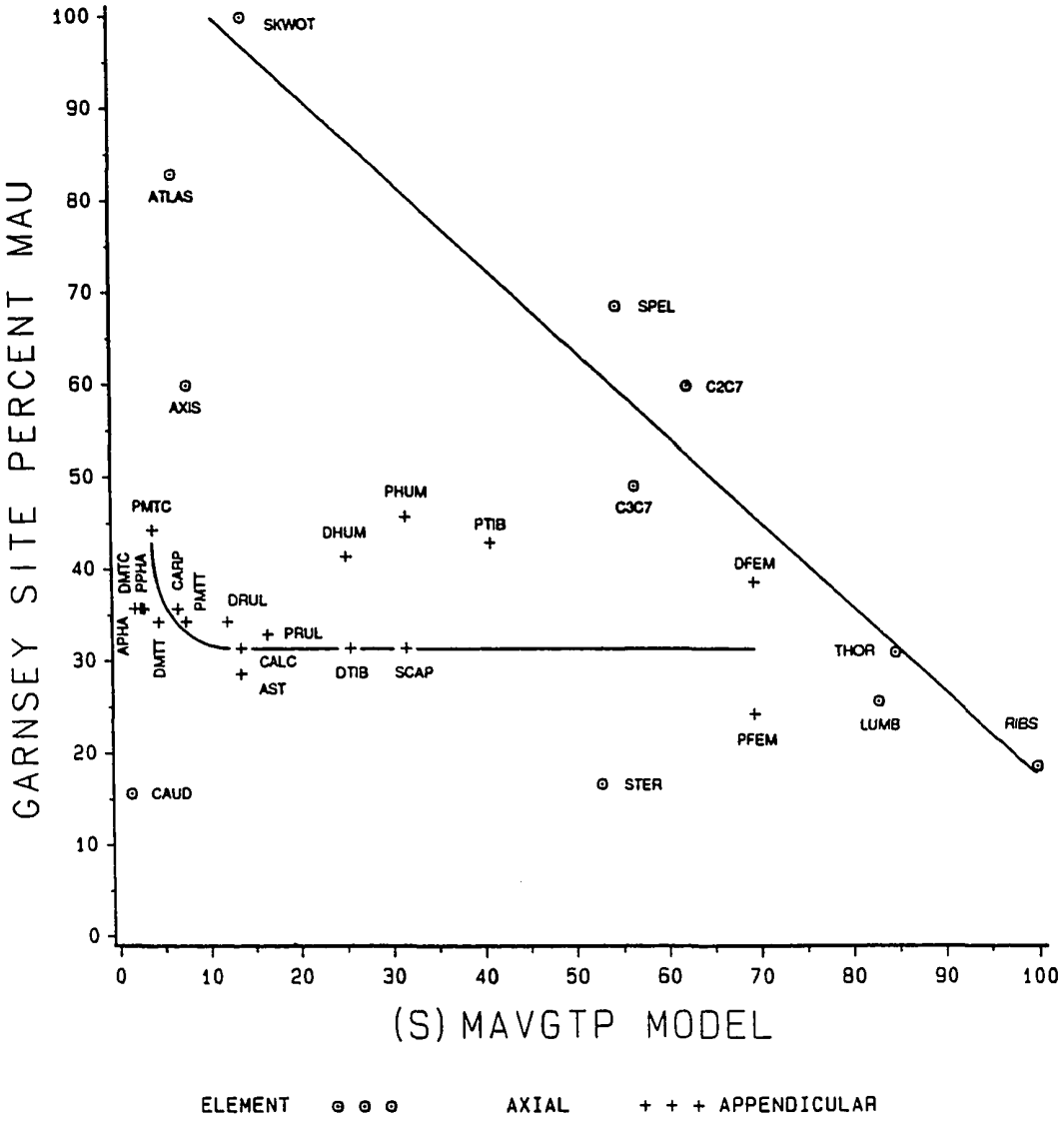

Figure 9.8. Averaged Total Products Model ((S)MAVGTP) Applied to the Total Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:86:Figure 28).

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neck (C3C7), thoracic and lumbar vertebrae (THOR and LUMB), and the ribs, all appear to depict a generally unbiased recovery strategy. The smaller representation of the atlas and axis units alternatively, could indicate that the the neck and sacrum/pelvis are overrepresented, and the axial and appendicular units together indicate a bulk recovery strategy. It also might be an artifact of differences in carcass division between the model and site assemblage.

In commenting upon the sex differences in the numbers of atlases at the Garnsey Site, Speth (1983:110-113) suggested that division of the male and female axial skeleton differed. He notes that male carcasses were divided more frequently than females through the atlas, thus destroying more of than atlases and leading to the discrepency in proportions. The point to be considered here is that the axis and the more posterior cervical unit (C3C7) were probably not divided, but were part of a single unit (C2C7) in males, but not in females. This would increase the value of the major neck unit and the presence of the axis as part of this unit would increase the unit proportional representation at the site. The effect is to remove the axis unit from the lower end of the index and bring the combined unit, C2C7, to a position above the line of the unbiased recovery stragegy. Its position above the line may be attributed to the mixed sex application of a butchering pattern found for only males. The atlas vertebra unit similarly is too low in the unbiased strategy, but this can be attributed to their destruction in the separation of the skulls in male carcasses. Among the female skeletal units, the atlas is the most abundant unit (see Table 9.1). These differences, evident here in the unsexed data, also should be evident in the application of the utility models to the sexed bone assemblage data.

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In general, therefore, it appears that at the Garnsey Site, the axial units were removed according to an unbiased recovery strategy with respect to their caloric yield as represented by the (S)MAVGTP model, except for the caudal (CAUD) and sternebrae (STER) units which were removed in higher percentages than expected. Although this pattern was found at the Glenrock Jump and may be attributable to processing versus transport costs, these are units with high fat to protein ratios in the meat which might make them more desirable cuts.

The averaged total products model, (S)MAVGTP, does not offer much towards the understanding of what was guiding selection of the appendicular units at the Garnsey Site. In Figure 9.8 the appendicular units all fall within 24 and 46 percent MAU, although they appear to follow an extreme bulk oriented recovery strategy. Todd (1987b:259) suggests complete limb removal, rather than removal of smaller carcass parts. It is expected that differences in male and female carcass butchering, as suggested by Speth (1983), are responsible for the somewhat diffused appendicular unit pattern (especially for the proximal long bones) and that division of the data by sex may clarify whether and how butchering patterns differed between the sexes.

Application of the Mixed Class Total Products Model, (S)MMCTP

Speth's (1983) analysis of the sex distribution of the bones from the Garnsey Site provides a data set (see Table 9.1, above) to which the mixed class models may be applied and evaluated. It was expected that the application of the mixed class model, which expresses the value of carcass parts of each animal class (in this case, spring males and poor condition females) relative to the part of highest value regardless of class origin,

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would demonstrate that any differences in male and female treatment would be predicted by the model. If this were true, plotting the carcass parts for each sex using the mixed class total products model should result in the intermeshing of the male and female parts into single curvilinear and linear patterns for the appendicular and axial units at this site. The model application (Figure 9.9), however, does not show the intermeshing of the male and female body part use that Metcalfe and Jones (1988) suggest might occur if yield differences between animal classes were expressed in the model. Two possible causes for the continued separation of male and female curves are suggested. First, this might occur if the differences in the yields of the animals used in the model construction are not representative of the differences present in the archaeological population. That is, if FAF, as the representative of females in poor condition, is in better condition than the Garnsey females, then the female data values for the model may be overestimated and the curves remain separated. Second, separate male and female curves might occur if the composition of the combined site assemblages from separate kill events are not representative of the composition of an assemblage that one would find at a mixed sex, single event kill. These possibilities point to the need for additional studies to increase our knowledge of the range of variability in bison carcass composition, the age and sex distribution of the animals represented by the assemblages, and the timing of the kill event(s).

Figure 9.9 shows the Garnsey Site assemblages of male and female percent MAU's (Table 9.1) plotted against the mixed class model, (S)MMCTP (Table 8.7). As noted above, this model is based upon the data from the male SAM and the female, FAF. This female was in poorer condition than the

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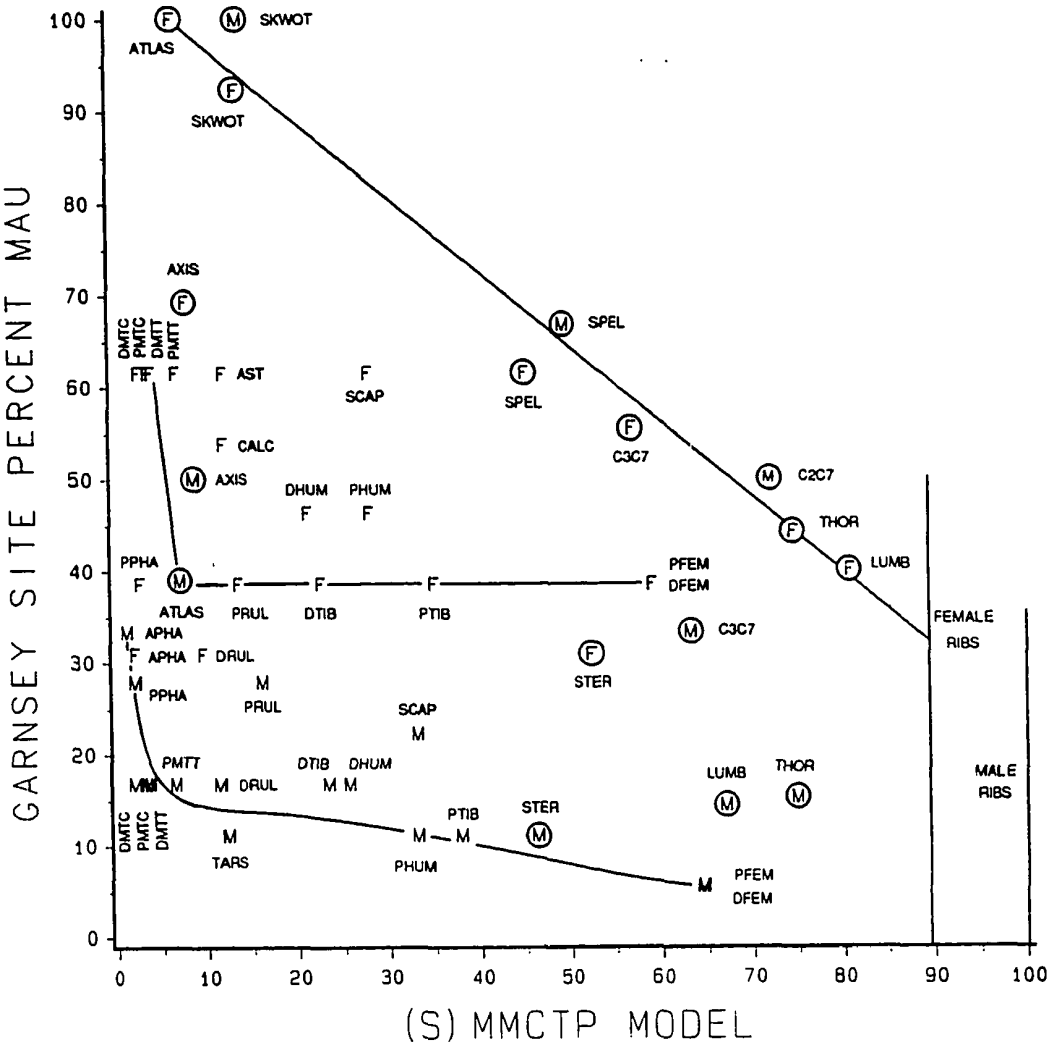

Figure 9.9. Mixed Class Total Products Model ((S)MMCTP) Applied to the Total Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:86:Figure 28).

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female, SAF, and is used in this model to depict the yields of carcass units for poor condition females relative to spring males.

Before discussing the application of the mixed class model in detail, two points need to be clarified. First, the sex distribution of the ribs from the Garnsey Site assemblage was not determined. The location of the ribs along the (S)MMCTP index is illustrated in Figure 9.9 for both males and females, for the purpose of defining the axial units recovery strategies for each sex. It should be noted, that using the combined assemblage (Table 9.1) which disregards animal sex, the ribs have a percent MAU value of 18.7 and a MAU value of 654.5. If all the ribs were from females (Speth (1983) estimated a minimum of 13 females), then the percent MAU for females would be 50.3 and for males would be zero. If all the ribs were from males (Speth (1983) estimated a minimum of eighteen bulls), then the percent MAU would be 36.4 for the males and zero for the females. These are the maximum values for the ranges within which one may expect the percent MAU values for the males and females to fall, had it been possible to separate them on the basis of sexual dimorphism. These ranges are indicated in Figure 9.9 by two vertical lines at (S)MMCTP index values 86.3 and 100 for females and males, respectively. When using these indicators, one should remember that the percent MAU values for these ribs are interdependent upon one another, with the value for the females reducing the maximum range for the males and vice versa.

The second point that needs clarification concerns the additional plotting of the axis plus third through seventh cervical vertebrae unit (designated C2C7) for male data in Figure 9.9. This is done to account for the division of the neck and skull through the atlas, rather than between the skull and one of the cervical vertebrae in the male carcasses.

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Like Speth's (1983:96:Figure 31) depiction of the male and female assemblage composition data plotted against Binford's MGUI, Figure 9.9 shows that the butchering pattern of male and female carcasses at the Garnsey Site differed, with higher proportions of female elements abandoned at the site for all units except the sacrum/pelvis (SPEL), skulls (SKWOT) and anterior phalanges (APHA). It appears that, as seen for the Glenrock Jump, the axial units of the females were abandoned according to an unbiased strategy, while the appendicular units were abandoned according to a bulk strategy. This pattern is also evident for the male data, although the axial units are more mixed in their relationship between their model values and the percent MAU present, and the appendicular units show a greater removal rate than the females in their bulk strategy recovery curve. The position of the male lumbar (LUMB) and thoracic (THOR) units in the graph might also indicate that for the males, a bulk recovery strategy was in effect, and the head (SKWOT), neck (C3C7) and sacrum/pelvis (SPEL) units are overrepresented instead. In either case, there is evidence that these two units and the sternebrae (STER) were treated differently between the carcasses of males and females (with male units abandoned in lower frequencies than female units), whereas, other axial units were similarly treated.

The appendicular assemblage data for males and females in Figure 9.9 differ as well, with female bones present in higher proportions of their potential numbers than their male counterparts. In both cases, bulk recovery strategies are evident. Inspection of the female data curve shows the scapula (SCAP), tarsals (AST and CALC), and the humerus (PHUM and DHUM) units present in higher proportions than expected and the distal radius/ulna (DRUL) and phalanges (APHA and PPHA) units present in lower proportions than expected for this bulk recovery strategy based on the (S)MMCTP model. The

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underrepresentation of the distal radius/ulna (DRUL) and overrepresentation of the humerus (PHUM and DHUM) in the female data may indicate that fat mobility, which proceeds at a more rapid rate in proximal than distal limb elements, had reduced the value of the humerus, but had not yet progressed to the point that the radius was substantially affected. The higher position of the female curve relative to the male curve (Figure 9.9), however, suggests that either the male and female carcasses were evaluated and butchered as separate groups relative to only those members of the same sex, or that many of the females were in appreciably poorer condition than the males, and more importantly, in much poorer condition than the model representative, FAF.

Examination of the male appendicular unit curve (Figure 9.9) shows moderate overrepresentation of the scapula (SCAP) and proximal radius/ulna (PRUL) units, and slight overrepresentation of the distal humerus (DHUM) and proximal tibia (PTIB) units. The higher proportions of the scapula (SCAP) and proximal humerus (PHUM) units are comparable to that seen in the females. The high position of the proximal radius/ulna (PRUL) and the distal tibia (DTIB) units in the male appendicular curve differs from the pattern seen in the female curve and cannot be attributed to fat loss here.

The separation of the male and female appendicular curves in Figure 9.9 was not expected, and its occurrence must be evaluated for its significance relative to the construction and use of mixed class models. In a discussion of utility model construction, Metcalfe and Jones argue:

> the hunter should evaluate the economic utility of a particular body part in relation to all other parts available at the kill site. If weight differences due to the sex and age composition of the Garnsey bison could be monitored, we suspect that much, if not

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> all, of the variation noted by Speth in the selection for male versus female, or adult versus juvenile, body parts would be accounted for simply as a function of their different FUI values [1988:500].

The (S)MMCTP model incorporates the scaled values for males and poor conditioned females, and according to Metcalfe and Jones's assessment, there should be only one curve in Figure 9.9. Does the fact that there are three or four linear relationships between the data and the model indicate the model is poorly designed? I do not think so. It is my opinion that the separation of the male and female data distributions is a product of the analysis of the combined assemblages from separate kill events. As noted above, Speth determined that a series of quasi-contemporary kill events are represented by the combined bone assemblages. It appears, therefore, that the mixed class model does not show a single linear relationship, in part because selection decisions were not made between the body parts of all animals in the assemblage, but on multiple occasions, between the parts of the carcasses present at each kill. The male and female appendicular unit curves are almost completely separated. Even if the females were in poorer condition than the model representative, FAF, one would expect greater overlapping of the curves if selection of female parts was determined with respect to their relative value compared to male parts. The greater rate of abandonment of female than male parts (assuming separate kill events) might be attributable to their poorer condition, or it might reflect a difference in transport capabilities.

Application of mixed class models (using appropriate animal class representatives) to single event, mixed herd kills should show the selection of carcass units on the basis of value as suggested by Metcalfe and Jones.

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At the Garnsey Site for example, such a model (using SAM and SAF this time) applied to the bull group cluster that also included what Speth suspects were non-lactating cows, should show non-separation of male and female units (based upon the assumption that they are in comparable condition). This application is not presented here.

The multiple linear relationships between the mixed class model, (S)MMCTP, and the Garnsey Site data are not entirely due to mixing of the kill assemblages. Obviously, the axial and appendicular units from each sex include units from the carcasses of animals that were killed at the same time. The fact that the axial and appendicular units are not butchered and removed from the site according to the same recovery strategy does not reduce the value of the mixed class model. (It should be noted that plotting the data against the model before the appendicular units have been modified to account for the effect of riders does not change these relationships.) The mixed class model is designed to show how parts are removed from the site with respect to their value based upon total caloric yield and modifications to account for the effects of riders. Apparently, the axial and appendicular units were evaluated and removed according to different criteria.

As the mixed class model applications do not show single linear relationships between the model and the bone assemblages, and because it is expected that this results from the mixing of assemblages, the single class models for males and females are used separately to examine the relationships between bone assemblage composition and the caloric yields of various groups of carcass products.

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Applications of Single Class Models

Due to the spring seasonality of the Garnsey Site, SAM, a spring-killed bison bull, is used to model male carcass unit utility. The female, FAF, is used to model female utility despite her fall kill date, because she was in poor condition and the spring-killed female, SAF, was in better condition than expected. It is assumed that the Garnsey Site female assemblage is dominated by cows in relatively poor condition due to continued high energy demands of late gestation and early lactation following a winter period of low food availability and quality, although some better conditioned females associated with bull groups are also included. The applications of these single class models should indicate where the assemblage compositions best fit the relative value of carcass unit utility for the production of single and multiple carcass resources.

Model Applications to the Male Assemblage

The male data for the Garnsey Site were plotted against the single class models for SAM in order to investigate whether a direct linear relationship could be shown to occur between the percent MAU data and any of the product models. An unbiased strategy was apparent in the data for the axial units, but not for the appendicular units. Figure 9.10 illustrates the relationship between the Garnsey Site data and the total fat model, SAM(S)MTF. This model appears to show the best relationship between the axial unit proportional frequencies and caloric yields. It is somewhat better than that seen for total products or for protein, suggesting that fat quantity is probably a major factor guiding the selection of male axial units at this site. It also suggests that meat fat (intramuscular fat) was an important resource in determining unit recovery, otherwise one would

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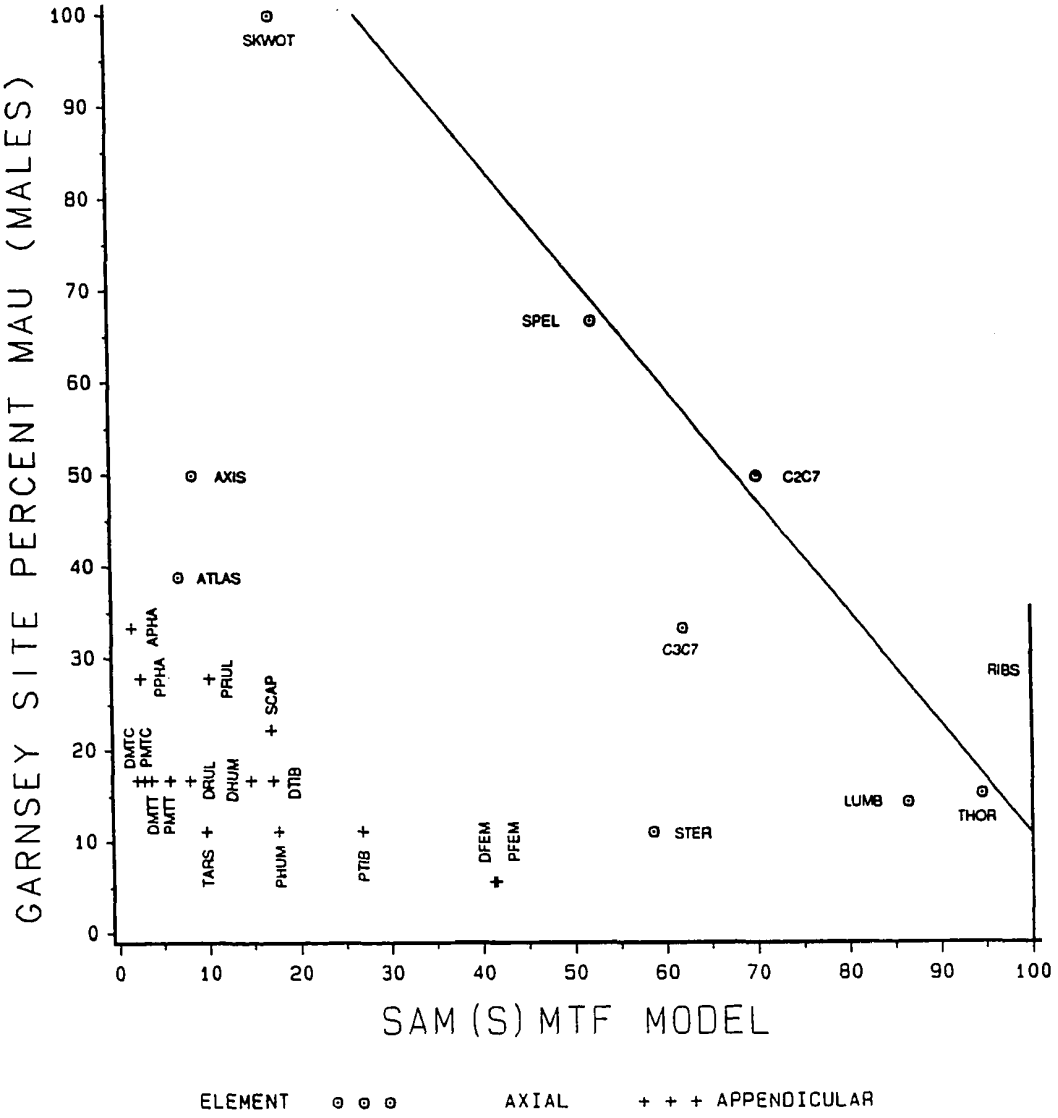

Figure 9.10. Single Class Total Fat Model for Males (SAM(S)MTF) Applied to the Male Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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expect a better relationship with the selected fat model. Given this assessment, if the threat of protein poisoning was a potential problem, then fat recovery from non-intramuscular depots must have been large enough to that axial units were evaluated for their yield of meat as well as fat.

In Figure 9.10, the axial units form a line indicating an unbiased strategy, with the exception of the sternebrae and atlas vertebrae (ATLAS) units. Note that the inclusion of the axis with the more posterior cervical unit brings this neck unit (C2C7) closer to the expected linear relationship. The low proportion of the altas units present is explained by differential destruction in the butchering process, as suggested by Speth (1983). The low proportional frequency of the sternebrae unit suggests that it was more highly valued than would be indicated by caloric yield alone. The low relative protein to fat yield (Table 6.12) may be a factor here, given that it is a spring season kill. Processing and transport costs were discussed as possible factors in its low representation at the Glenrock Jump Site. These factors might be important here as well. The lumbar vertebrae unit (LUMB) remains underrepresented, having been removed from the site in larger proportions than expected, given its index value and the evident unbiased recovery strategy. It is not intuitively obvious why this should be.

None of the utility models plotted against the male Garnsey Site appendicular data produced what could be interpreted as an unbiased recovery strategy relationship. The appendicular units in Figure 9.9 above (the application of the (S)MMCTP model), showed the units removed in a bulk oriented strategy, with the scapula (SCAP), proximal radius/ulna (PRUL), distal tibia (DTIB), and distal humerus (DHUM) somewhat overrepresented. (The male portion of this model is identical to model SAM(S)MTP.) When the

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male Garnsey Site data is plotted against the white grease fat model that has not been modified to account for riders, (S)SAMWG (Figure 9.11), an extreme bulk oriented strategy is evident. Application of the model modified for the effect of riders results in the proximal radius-ulna (PRUL) and scapula (SCAP) being overrepresented. In the unmodified white grease model application (Figure 9.11), these units fall within the upper end of the bulk strategy curve, but the proximal metapodials (PMTC and PMTT) are underrepresented. The better fit of the unmodified model suggests selection was made on the basis of individual unit yield, rather than on the basis of their yield as modified by their position in the limb.

The similar percent MAU's for proximal and distal ends of the metapodials (PMTC, DMTC, PMTT, and DMTT), as well as the femurs (PFEM and DFEM) abandoned at the site, suggests that these bones were being treated as whole bones, rather than as proximal and distal elements. The plot of the marrow model, SAM(S)MMAR (Figure 9.12), is similarly patterned, but with somewhat different horizontal spacing. The implication of both model applications is that even relatively low yielding units were removed from the site in high proportions relative to their availability, suggesting that fat yield was particularly important.

Model Applications to the Female Assemblage

The female data from the Garnsey Site were plotted against the product unit utility models for FAF. Like the male data, the axial and appendicular units were apparently recovered according to different strategies. The female axial units were recovered according to an unbiased strategy based on caloric yield according to many of the models the site data were plotted against. The total products model, FAF(S)MTP, produced the best linear,

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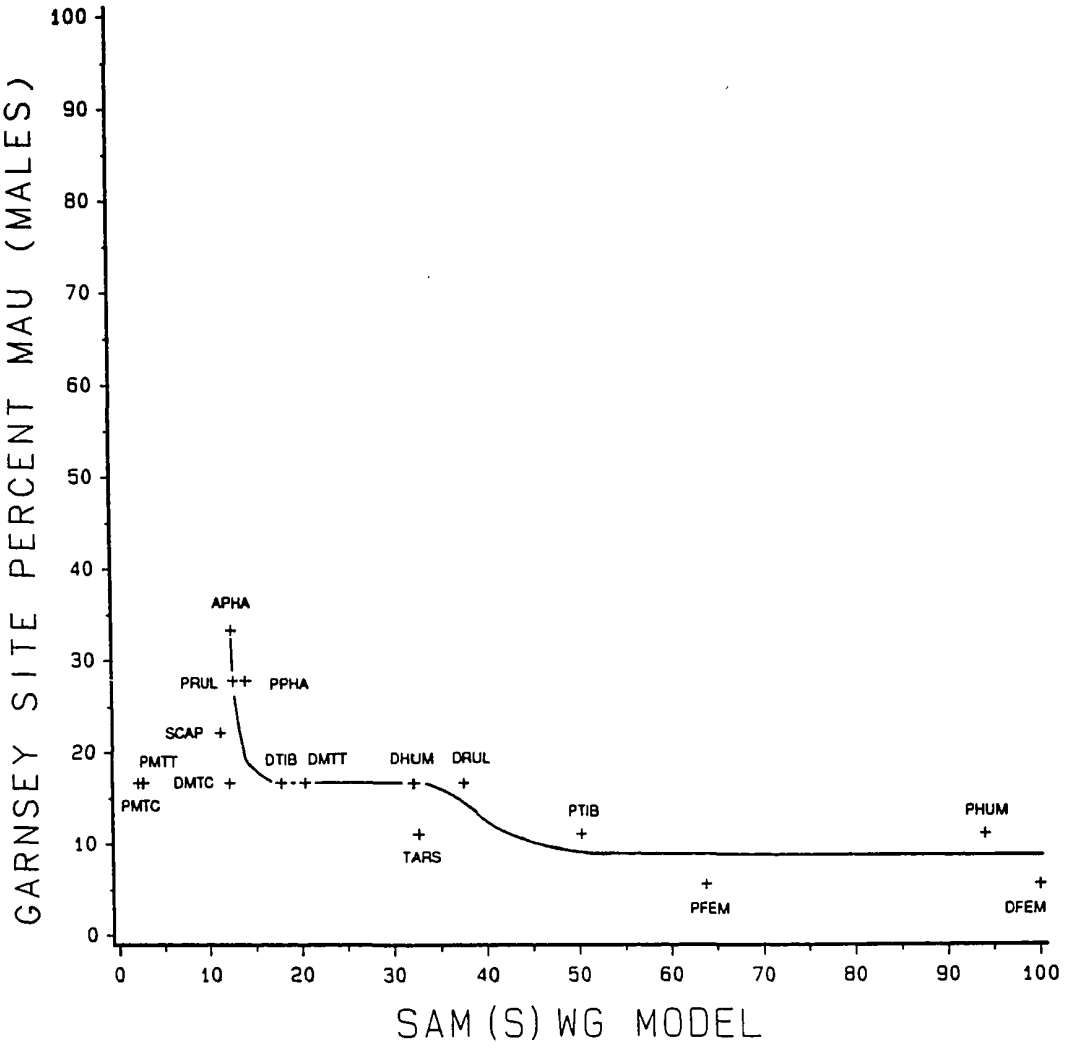

Figure 9.11. Single Class White Grease Fat Model for Males (SAM(S)WG) Applied to the Male Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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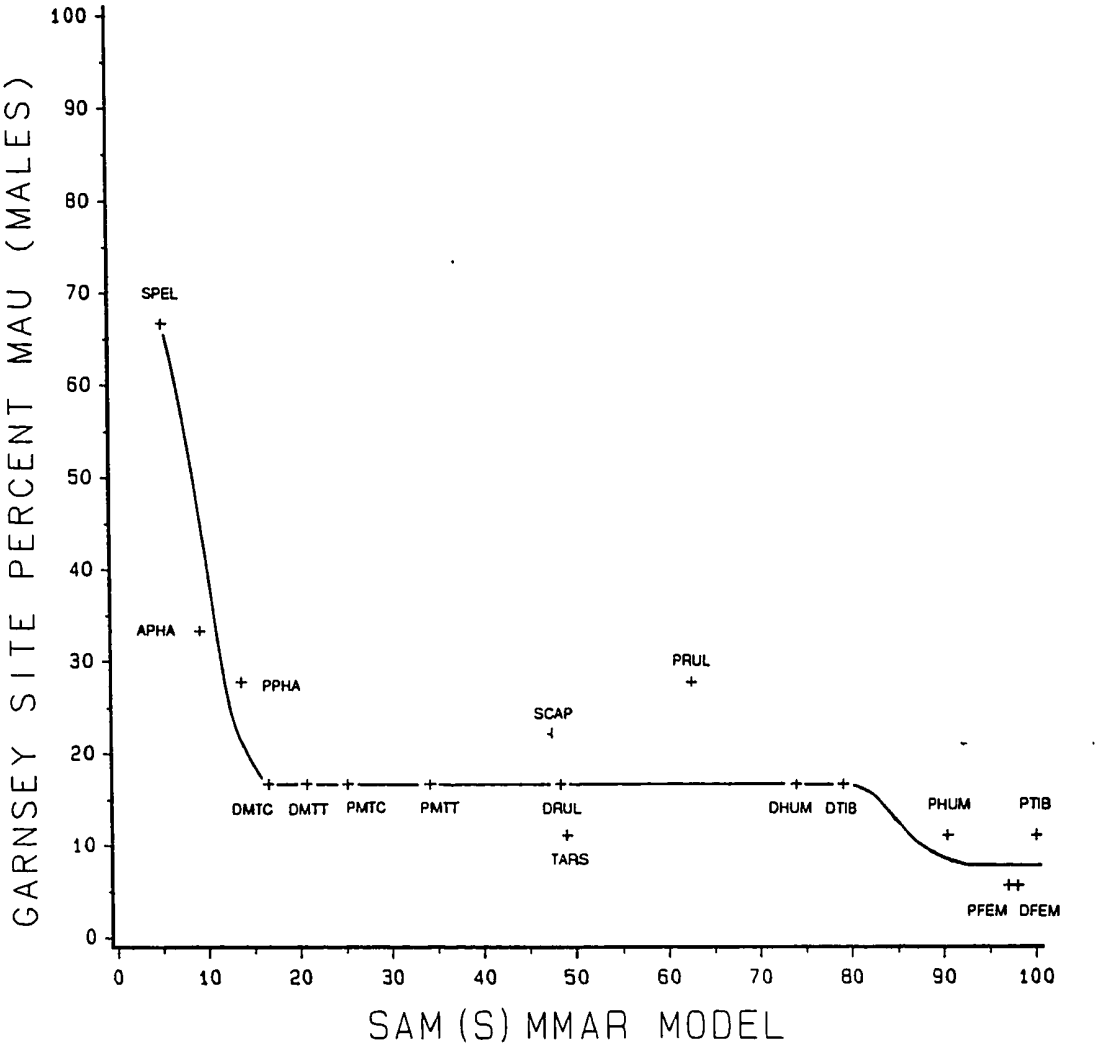

Figure 9.12. Single Class Marrow Fat Model for Males (SAM(S)MMAR) Applied to the Male Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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unbiased relationship for the axial units (Figure 9.13). The axis and sternebrae (STER) units are both underrepresented. The axis is not a large producer of any carcass product, and its low numbers might be due to differential destruction, as was evident for the atlas vertebrae in males. The underrepresentation of the sternebrae unit follows the patterns established for both the Glenrock Jump and the male Garnsey Site data.

The female appendicular data is best described by the unmodified white grease and marrow fat models, FAF(S)WG and FAF(S)MAR (Figures 9.14 and 9.15). Both graphs show a backward "S" relationship with long tails. The white grease fat model application shows the femur (PFEM and DFEM) and humerus (PHUM and DHUM) present in larger numbers than their yield and the general pattern of use would suggest. This pattern is understandable if the females were in poorer condition than the model representative, FAF, and had mobilized greater proportions of the fat from the humerus and femur than noted in FAF. All other units appear to fit the model.

The marrow fat model, FAF(S)MAR (Figure 9.15), is similar to the white grease fat model application, except the phalanges (APHA and PPHA) and distal radius/ulna (DRUL) units are underrepresented and the humerus (PHUM and DHUM) units are overrepresented. The line illustrates the major trend of the relationship between percent MAU and the model. It is extended through the femur units in Figure 9.15 because only the distal radius-ulna (DRUL) unit might pull it lower. There was no indication in the white grease model application that either tibia (PTIB and DTIB) unit had mobilized large quantities of fat. As white grease fat mobilizes at a faster rate than marrow, one would not expect the tibia units to be underrepresented in the marrow application (if the line is drawn lower through the distal radius-ulna (DRUL)), and not also in the white grease model application.

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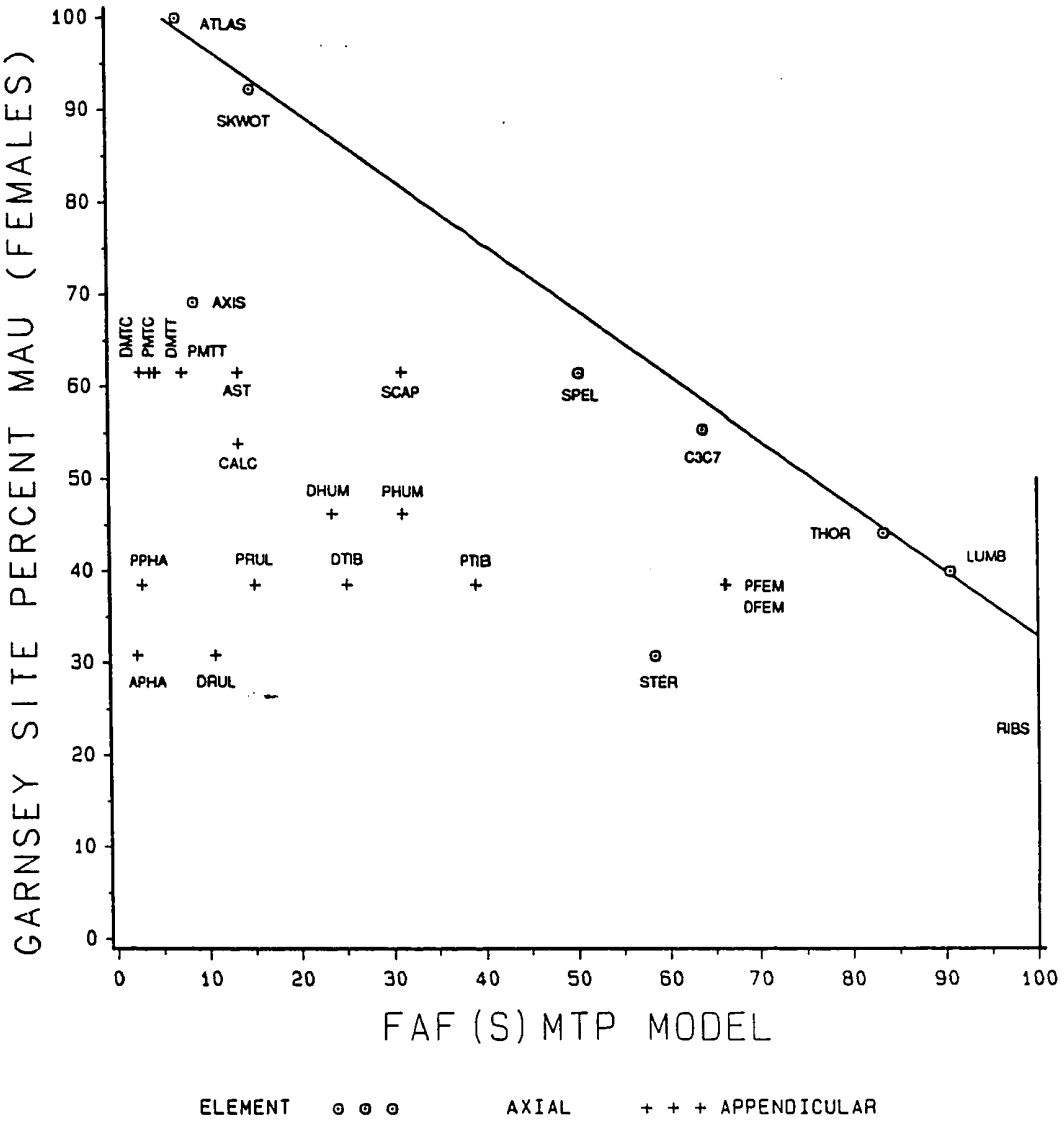

Figure 9.13. Single Class Total Products Model for Poor Condition Females (FAF(S)MTP) Applied to the Female Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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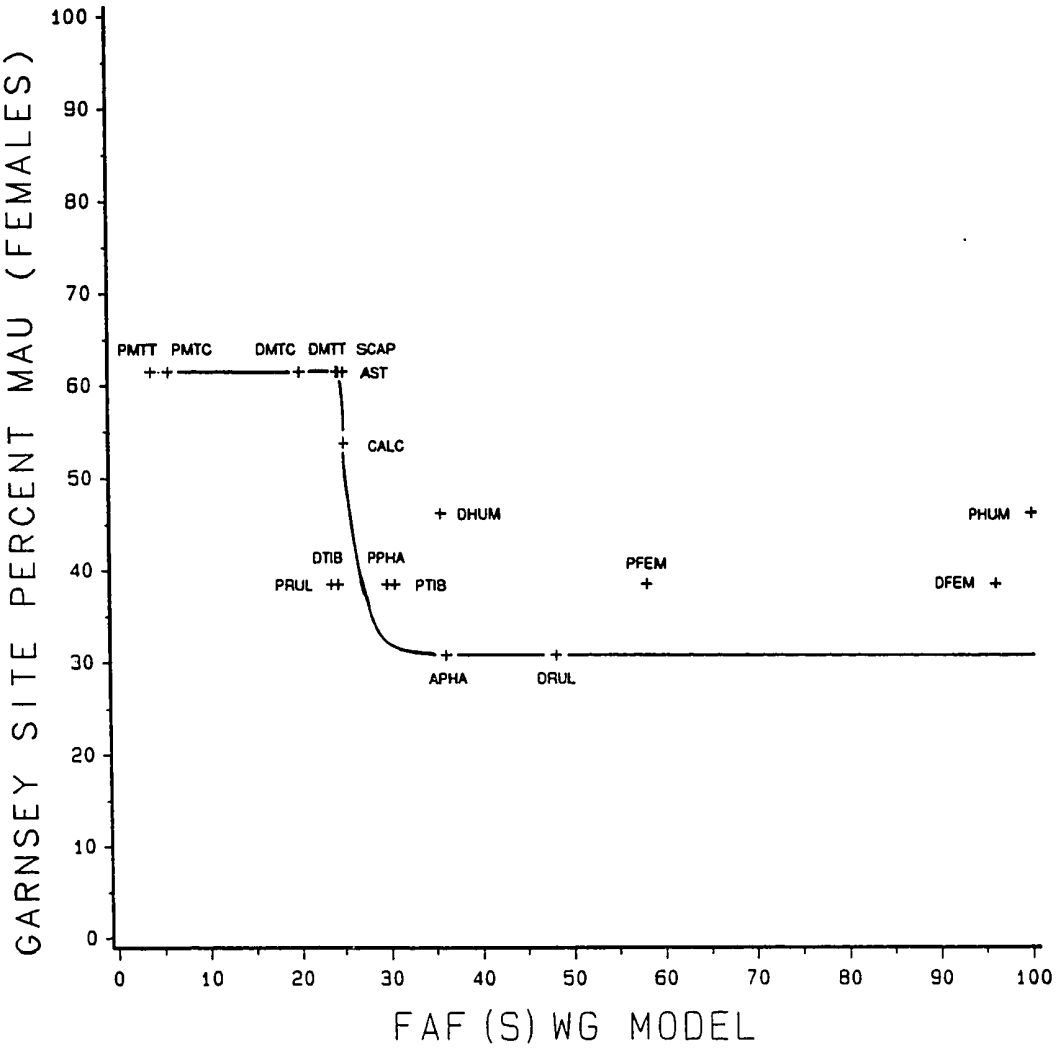

Figure 9.14. Single Class White Grease Fat Model (FAF(S)WG) for Poor Condition Females Applied to the Female Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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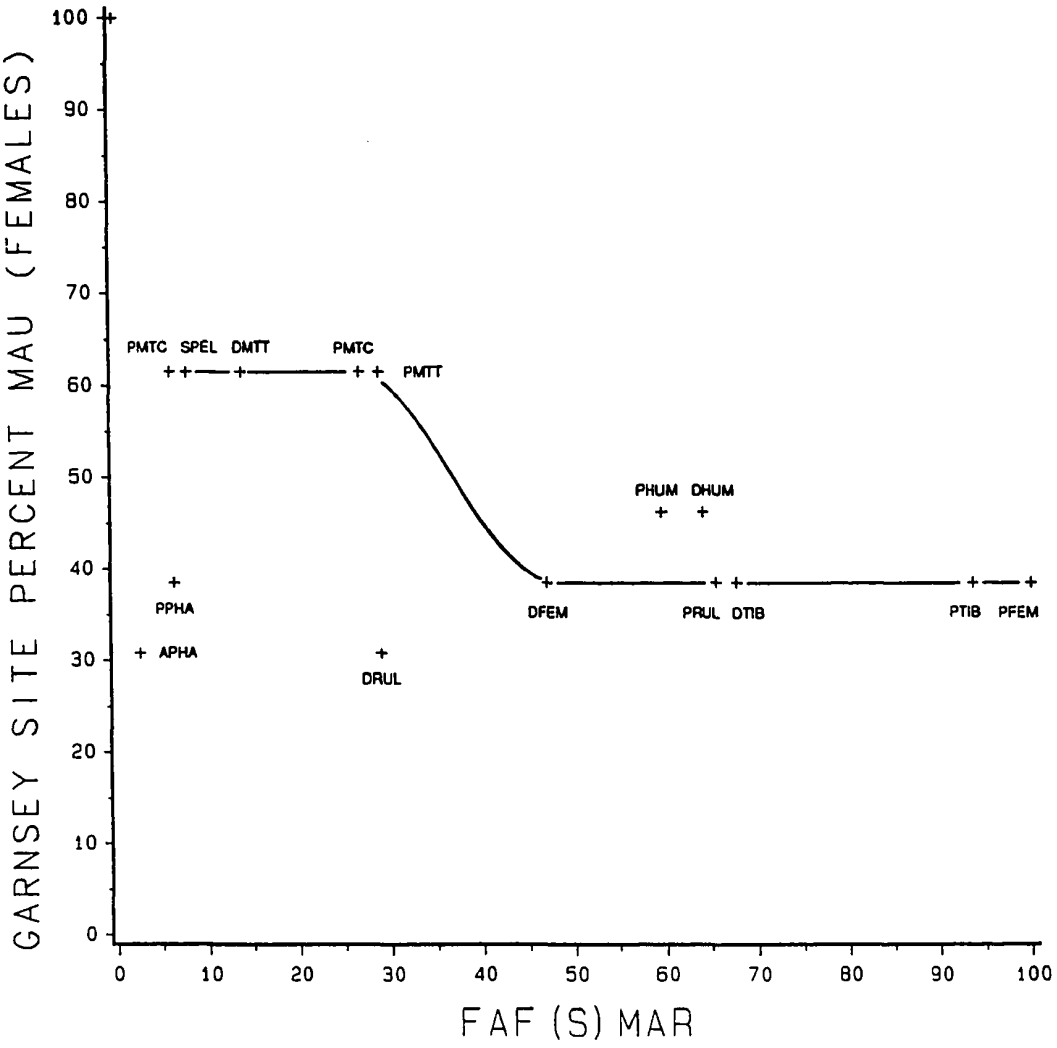

Figure 9.15. Single Class Marrow Fat Model (FAF(S)MAR) for Poor Condition Females Applied to the Female Assemblage of the Garnsey Site. The Garnsey Site data are from Speth (1983:97:Table 13).

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This marrow model application to the female data suggests that fat mobility in the humerus is underrepresented by the FAF based model. It was noted in Chapter 5 that there is a difference in the rate of marrow fat mobility between the limbs, with the hindlimb mobilizing fat at a faster rate than the forelimb. The data from the bison in this study suggest that while fat is lost at a greater rate from the hindlimb than the forelimb as a whole (which Reich (1981) also reports in his study of African impala, but which is contradictory to Ratcliffe's (cited in Speth 1983) study of Roe deer), the humerus, contrary to the limb as a whole, shows greater loss than the femur, and the tibia and more distal bones greater loss than the radius/ulna and more distal bones. These findings are not inconsistent with the results of the model application. The overrepresentation of humerus elements (PHUM and DHUM), however, suggests that perhaps the Garnsey females had lost a larger proportion of the marrow fat from these units than suggested by the model values based upon the FAF composition data.

The greater use of the major long bones relative to the metapodials in both the white grease and marrow fat models, despite the expected greater rate of fat loss in the proximal bones is interesting. Although there are no data available to verify it, it seems probable that despite the greater rate of fat mobility in the more proximal bones, the appreciably larger size of these units preserves their relatively greater fat yield than more distal units until fat mobility has been sustained for some time. If so, this may maintain proximal bones as preferred fat sources. The low number of phalange units present, however, does not fit such expectations. One might suggest that fat loss in the proximal units has not progressed to the point where the yield is less than that of the metapodials.

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Summary and Discussion of Model Applications to Garnsey Site Data

Marrow and white grease fat use at the Garnsey Site appears to largely influence the proportions of male and female appendicular bones remaining at the site. The female units were removed in smaller proportions than male units, and although the shape of the recovery strategies differ somewhat, they appear to differ more as a reflection of sex differences in animal condition. The appendicular use of the male units is an extreme bulk oriented strategy (Figures 9.11 and 9.12). The female appendicular units, however, show bulk recovery for the high and moderate valued units (Figures 9.14 and 9.15), but most of the lower valued units combine to form a flattened tail, rather than continuing to increase in proportion as index value declines. This is similar to some strategy curves Binford (1978:81) illustrates. Tarsals (TARS) were the primary units that poorly fit the model applications to the male data, and the phalanges (APHA and PPHA), distal radius/ulna (DRUL), and humerus (PHUM and DHUM) were the female units showing poor model fit.

Axial units for both males and females were largely recovered according to unbiased strategies. For the male data the total fat model, SAM(S)MTF, showed the best fit with the data, whereas, with the female data the total products model, FAF(S)MTP, was best. Both bison bone assemblages at the Garnsey Site represent spring period kills. Given this seasonality, it is interesting that neither data set showed a better fit with the selected fat model which excludes protein and its associated intramuscular fat. This, and the fact that protein recovery is indicated for the female assemblage through the better fit of the total products model, implies that fat recovery was large enough to offset the threat of protein poisoning at least for recovery of the female axial units. It is interesting to note that it

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is the axial, rather than the appendicular units, which have lower ratios of protein to fat (see Table 6.12).

Having noted the difference between male and female carcass use, it is also interesting to note that the male more than the female data appear to conform with the expectations for spring selection and use. The male axial data indicate an unbiased selection strategy with a total fat model and extreme bulk strategies for use of marrow and white grease fat. This pattern differs from that seen at the fall season Glenrock Jump in the greater use at the Garnsey Site of all male appendicular units suggesting greater skeletal fat use. This might be attributable to greater spring requirements for fat and/or the smaller total number of animals represented at the site which might lead to more intensive use to meet their needs.

It is not clear, however, why the male metapodials at the Garnsey Site would be heavily used, while in the female assemblage these were the most frequently abandoned appendicular units. Two possibilities are suggested. First, the hunters taking the cow/calf groups might have been in better nutritional condition than those taking the bull groups and could be more selective in their exploitation despite the poor condition of the animals. Second, as suggested above, not enough is known concerning the mobility of skeletal fat and the interaction of declining fat content and relative fat weight in the bones as they decrease in yield from proximal to distal locations. Perhaps, despite the more rapid rate of mobilization in the proximal units, depletion below the point of adequate returns for processing investments occurs earliest in the smaller yielding metapodials. The fact that these bones have equal representation for proximal and distal ends suggests further that they were not used due to low yields as a whole. This seems a plausible explanation for the application of the white grease fat

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model to the female data (Figure 9.14), but it fails to explain the high frequency of removal associated with the phalanges (APHA and PPHA) when the marrow model is applied (Figure 9.15). If time or taphonomic factors are not responsible, then perhaps differences in fat quality, ignored in model construction here, are an important factor after all. This is probably the case in the axial and appendicular grease fat. Yellow grease fat, regardless of yield, does not appear to explain selection order of the axial units. This is especially evident for the high yielding sacrum/pelvis (SPEL) unit which is abandoned in much higher proportions than one would expect in applications of the marrow and grease fat (SKF) and total grease fat (GRE) models.

It is my expectation that the questions raised by the applications of these models might be addressed by a better understanding of the range of animal condition for the females at the site and by increased knowledge of the patterns of bone breakage. Presumably, if sample sizes are not reduced too much, separation of the assemblages from different kill events would help the analysis as well. It may be stated unequivocally, that additional data on the range of variability in carcass composition between animals of different age and sex classes, as well as additional data on the effects that condition changes have on production yields as well as on percent fat content, would greatly enhance our understanding of how assemblage compositions reflect modifications of selection affected by differences in relative productivity.

Potential Problems with Utility Model Applications

Three kinds of problems that one might encounter when applying models of carcass utility are considered below. The first concerns differences in

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carcass unit division and identification of carcass unit numbers for archaeological assemblages. The second involves potential weaknesses of the models due to their sole reliance on quantitative data for their construction. The third problem relates to the use of the Theodore Roosevelt National Park (TRNP) animals as model representatives for bison that are potentially larger or smaller in adult stature.

Division of the Bison Carcass

Carcass unit utility models indicate the relative value of body parts based upon differences in either weight or caloric yield. When standardized models are modified to account for the effect of riders, the lower yielding appendicular units are increased in value. Whether modified or unmodifed models are used, their suitability for use in analyzing archaeological bison bone assemblages largely depends upon comparability in the way the bison carcass is divided into units in both model construction and at the site under analysis. If the carcass is divided differently, then the value of one or more body parts may be either over- or underestimated by the model. Therefore, analyses of butchering patterns are vital to appropriate applications of the utility models. For example, in the analysis of the Glenrock Jump data, it was found that thoracic vertebrae (THOR) units were present in smaller proportions than expected based upon their caloric yield. It was noted that Frison (1970) suggested that the vertebrae bodies were often removed with the associated ribs unit after the dorsal spines and their associated meat were removed. If this assessment is correct, the their presence and absence in the assemblage (based on counts of vertebrae bodies) has less to do with the value of the associated meat (which was

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removed primarily with the dorsal spines) than with the cost of separating the vertebrae from the associated ribs.

The problem of error associated with differential butchering between the model carcass units and the archaeological bison remains also involves differences in how easily bone units may be identified by smaller and/or multiple fragments, and how units are divided. Using the ribs as an example, if the heads are removed in the butchering process by chopping through the neck of the ribs and they are abandoned at the site, then despite the fact that all rib meat was removed for processing elsewhere, the presence of the heads which are used to identify their number, count and side, may suggest this carcass unit is overrepresented at the site given its model value. If rib fragments are found that do not include the head, it is difficult, if not impossible to determine a reasonable minimal count due to the absence of diagnostic features for this portion of the bone. In this case, the ribs may be underrepresented in the percent MAU counts when they were actually present in larger numbers. It is important, therefore, to consider the evidence for butchering, in addition to the percent MAU values when applying carcass unit utility models.

Errors in dietary assessments may occur as well, if butchering patterns are not analyzed along with the utility model applications. For example, the Glenrock Jump appendicular units were best described by the white grease and marrow fat models. Nevertheless, Frison's (1970) description of the butchering process includes muscle stripping in conjunction with removal of bone prominances used as handholds. Without consideration of the presence or absence of these bone fragments at the kill site, a factor which is not considered in the determinations of percent MAU values, one might dismiss the importance of the meat component in these appendicular units. Clearly,

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however, the models as constructed, do not adequately model the importance of meat and protein yield when meat recovery is based upon muscle stripping.

Quantitative Emphasis of the Models

The differential use of the axial and appendicular units indicated at the Garnsey Site and Glenrock Jump despite their different seasons of use, may be a reflection of differences in fat quality that is not measured by calorie or weight yield alone. The fat associated with the appendicular units is mostly skeletal fat and is generally more unsaturated and softer than that in the axial units. Carcass fats of the appendicular units are relatively soft as well, which may account for the differences in recovery strategies. Axial units appear to be recovered according to unbiased strategies, whereas appendicular units are frequently recovered according to some variation on a bulk strategy--at least at the two sites discussed.

This difference in recovery and the fact that fat appears to be an important resource at both fall and spring season kill sites, suggests that bison carcass use is probably more complex than reflected by weight or calorie yield alone. Clearly, transport and processing costs as well as perceived differences in quality also work to modify the relationship between carcass unit value and recovery. This is also illustrated by the failure of any of the models to adequately reflect the recovery of the tail and sternebrae units. Perhaps a model based upon the ratio of protein to fat would provide a better model fit.

Animal Representatives Used in Model Construction

The carcass composition data of four modern bison from Theodore Roosevelt National Park (TRNP) were used for the construction of the carcass

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utility models presented in the previous chapter and applied to archaeological bone assemblages in this chapter. In Chapters 2 and 3 the suitability of these specimens as representatives of modern bison was considered. Although some degree of weight loss was suggested for the TRNP bison prior to the collection of the sample specimens, these four bison, possibly with the exception of the female, FAF, appear to be in relatively good, though possibly not prime, condition. Clearly, however, the addition of more specimens to the sample could only enhance the value of the models and carcass composition data presented here. It would be especially beneficial to include an immature female, a fully mature bull, and mature bull and cow in extremely poor condition.

Another point of concern, related to model applications and the animals used as representatives of bison in their construction, involves differences in mature animal size between the modern bison representatives, and historic and prehistoric bison. Is it legitimate to use a model based upon modern animals that are much smaller in mature size than some earlier bison forms? How might composition differ between these representatives and the larger bison? From studies of cattle varieties, it appears that the major effect of the decrease in mature animal size through time should be an earlier onset of the fattening stage in modern bison. Earlier, larger bison might have smaller proportions of carcass fat if measured at the same age as the modern representatives. As larger animals, however, it may also be possible that total production of fat was larger in some young adult animals than in modern fully mature animals. This is suggested by the differences in fat yield of some depots between the larger male, SAM, who was not yet fully mature when killed, and the smaller females. Assuming that the proportional differences in sexual dimorphism have not changed through time, however, it

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does not seem likely that the relative differences in carcass unit value would be significantly different. Growth gradients and fat mobility patterns should remain the same and therefore, the patterns of yield should be similar. Applications of the models presented here to archaeological assemblages of larger or smaller bison forms should not be compromised by these differences in animal size.

Estimations of meat or fat yields, however, are smaller for these modern bison than one would expect for early, larger adult bison. The larger size and greater yield might lead to higher abandonment rates at earlier sites, if fewer carcass units are needed to meet resource requirements or limits in transport capabilities.

Conclusions

In this chapter, carcass unit utility models were applied to two assemblages of archaeological bison bone. This analysis suggests that models constructed in the manner instituted by Binford (1978) and outlined by Metcalfe and Jones (1988) overestimate the relative value of appendicular units relative to axial units with two effects. First, the differences in recovery strategies for axial and appendicular units are partially masked, and second, the value of the tibia, tarsals, metacarpal, carpals, atlas and axis are all exaggerated. I believe that gross-weight-based models, constructed without these modifications would probably be useful, though less informative than models incorporating data on fat yields.

The applications of the averaged data models to the Glenrock Jump Site data suggest that total fat yields (TF) influence axial units recovery while the combined skeletal fat yields (SKF) was important to appendicular unit recovery. This suggests that the value of fat in the diets and selection

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decisions of prehistoric hunters even during the fall season has been underestimated. One should not conclude, however, that meat was an unimportant resource. Frison's (1970) description of the butchering patterns for muscle removal, using bone fragments as handholds for stripping, indicates that the importance of this resource is not always adequately measured by these models.

The new, mixed class models were applied to the Garnsey Site assemblage with limited success. Although male and female unit yields were expressed in relation to one another in these models, they failed as constructed, to account for the differences in the treatment of male and female carcasses at the site. This failure was attributed to two factors: (1) the possible overestimation of female unit values by the use of a female, FAF, that may have been in better condition than the majority of females in the archaeological assemblage, and (2) the lumping of separate kill events into one assemblage. Use of the mixed class models demands animal class division of the assemblage, but also demands identification of discrete kill events to be successfully applied.

The model applications to the spring season Garnsey Site male and female assemblages suggest that there were differences in focus in butchering between these groups for the axial units, but also suggest that skeletal fat yield was still the primary factor influencing abandonment of appendicular bones at the site. Meat use is suggested by the removal of bone fragments for use as handholds in muscle stripping, but it is not known whether there is differential use of this technique between male and female assemblages, or if there is disproportionate recovery or abandonment of these fragments at the kill site. The use of the female axial assemblage and their relationship to the total products (TP) models appears to suggest

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that intramuscular fat and protein were as important as other resources in influencing bone abandonment, while the relative numbers of bones from the male axial assemblage appears to suggest a more restricted value for protein with recovery guided more by total fat (TF) yield (which includes intramuscular fat). The appendicular units of the female assemblage also appear to show some selectivity against metapodials, whereas the male data show relatively high use of these smaller yielding units.

Although it may be overstepping the limits of such analyses, these applications suggest that there may have been greater flexibility in the selection demonstrated by the hunters of the female bison at the Garnsey Site, than by those using the males, despite the fact that the females appear to have been in poorer condition. The use of the female herd(s) despite the poor condition of many of these animals might suggest the hunters were in great need of fat resources, but then one also might expect greater use of the metapodials (assuming they are not fat depleted). These factors, together with the possible selection of axial units based upon total products yield (including protein), rather than upon one of the fat-based models, suggest that fat recovery, though important, may not have been as critical as for the hunters of the bull groups who selected potentially higher fat yielding herds, showed greater use of low fat yielding appendicular units, and showed recovery of axial units that fit the total fat model better than the total products model. Here, the greater than expected removal of higher fat yielding units such as the lumbar and cervical units also suggest fat recovery may have been particularly important.

A final point of consideration that cannot be adequately dealt with here concerns the limits of human perceptions of variability in product

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yield. Clearly, early hunters had a better understanding of the range of variability in fat and meat yields for bison of different age, sex and condition, if for no other reason than from greater exposure to those differences. Some of the variability described above and incorporated into these carcass unit utility models are probably beyond the limits of human perception without the aid of scientific measurement. This is particularly true for low yielding units. Recognition of the point where variation is not incorporated into differences in unit use is difficult given the fact that transportation and processing costs are also inherently involved in which body parts are removed and abandoned at a kill site. Perhaps a pattern will emerge with continued applications of caloric or weight yield based utility models to archaeological bone assemblages. In such applications, furthermore, regression analyses of the relationships between model values and archaeological assemblage compositions or transformations of those relationships can only enhance our ability to determine better model fit. Such analyses undoubtedly would have improved the value of the analyses presented in this chapter.

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CHAPTER 10. DISCUSSION AND CONCLUSIONS

Differences in the production and distribution of meat and fat in the carcasses of bison of different age, sex and condition, as represented by a small sample of four individuals from Theodore Roosevelt National Park (TRNP) were examined in this dissertation. The purpose of this work was to determine how quantitative differences in bison anatomy might influence three phases of selection associated with bison hunting. These phases included determination of which herd type to select for the kill, which carcasses to butcher after the kill, and which carcass units to abandon or remove to other sites for additional processing, storage, or consumption. It is suggested that quantitative differences in yield, as well as other factors such as the nutritional condition of the hunters (Speth 1983), their ability to maneuver the herd to the kill area (Frison 1970), and their labor and transport capabilities (Binford 1978, Metcalfe and Jones 1988) strongly influenced selection decisions. Qualitative differences in meat and fat such as texture, taste, susceptibility to rancidity, etc., probably influenced selection as well, but were not examined in this dissertation.

For purposes of review, this discussion of bison carcass composition and hunter selection may conveniently be divided into four parts. The first part is a review of Chapters 2 and 3, which included analyses to determine whether the bison specimens used in this study were suitable representatives of this species. These included examinations of whether the study specimens were good representatives of bison of their respective age and sex classes, whether animals in the TRNP herd (and thus the study specimens) were

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comparable in size to animals in other modern herds, and whether the TRNP herd was in normal or below normal condition the year the study specimens were killed.

The second part is a review of Chapters 5, 6, and 7, which included analyses of age-, sex-, and condition-related differences in bison carcass composition as determined for specific, individual carcass products. Chapter 5 presented of the data for bone and bone products, Chapter 6 the data for meat, intramuscular fat, and organs, and Chapter 7 the data for the subcutaneous, intermuscular, and cavity fat depots.

The third part is a review of Chapter 8, which focused on selection modeling using quantitative differences in carcass yield. Herd, carcass, and carcass unit selection were discussed, and of a series of body part utility models that indicate the relative value, and presumably the selection priority of different carcass units based upon their caloric yield of one or more carcass products were presented.

The fourth part summarizes the results of analyses of model applications to two archaeological assemblages of bison bone presented in Chapter 9. These applications were conducted in order to evaluate the bison utility models in several respects: (1) to compare model construction procedures and different units of measurement; (2) to compare model types (i.e., single class, averaged, and mixed class models); and (3) to compare model focus (e.g., total products, skeletal fat, or other product combinations). The potential problems that might lead to poor fits between model values and rates of bone abandonment for individual carcass units in some comparisons of index values and assemblage data are also summarized.

To conclude, additional data are identified that might improve our understanding of the range of variability in bison carcass composition and

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its influence on selection as exercised by bison hunters and as expressed in the compositions of archaeological bone assemblages.

TRNP Specimens as Representatives of Bison

Before using the carcass composition data from the four specimens collected from Theodore Roosevelt National Park, their suitability for use as representatives of modern bison of their respective age and sex classes had to be evaluated. These analyses included (1) comparison of the sample bison with other members of the TRNP herd, to assure that they are representative of animals of their respective age and sex classes; (2) comparison of the TRNP herd with other bison herds to determine whether the TRNP herd animals are larger, smaller or about the same size as bison in other modern herds; and (3) consideration of the general condition of the TRNP herd using weather data as a proxy, based upon a study of the relationship between annual records of individual animal liveweights and climatic data at Wind Cave National Park.

Sample Specimens Compared to TRNP Herd Members

After determining their age, sex, and reproductive status, each of the four bison (FYM, an immature, yearling male; SAM, a four-year-old adult, but not fully mature male; SAF, a fully mature, seven-year-old female; and FAF, a 16-1/2 year old, but still reproducing female) was compared (using liveweight data) with other members of the TRNP herd to establish whether they are typical representatives of their age and sex classes in that herd. Although an atypical specimen might provide additional evidence on the range of variability in carcass composition, the assessment of age and sex differences require that the individuals be representative of their classes.

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Although liveweight records for TRNP bison are limited, the bison in this sample appear to be representative of animals in these age and sex classes. Production and distribution differences between the bison specimens, therefore, are assumed to result from the effects of age, sex, or condition differences, and to be typical of those differences, although the sample is obviously too small to have any statistical significance.

Bison Size in the TRNP Herd Compared to Other Modern Herds

Before the first TRNP specimens were killed, their carcass weights were estimated in order to calculate approximate transport costs. These estimates were based on Halloran's (1961) carcass weight data for bison at the Wichita Mountains Wildlife Refuge (WMWR), Cache, Oklahoma, the only data then available on bison weight distributions for animals of different age and sex. Unexpectedly, the carcasses of the TRNP specimens were found to be substantially larger than those of bison of the same age and sex classes in Halloran's (1961) published WMWR data. After demonstrating that the TRNP bison sample specimens appear to be typical for their age and sex classes at that park, their larger size relative to the WMWR bison indicated that mean animal sizes may vary between herds in different geographical regions. To understand differences in carcass production between animals and between regions, it was important to determine how animal size in the TRNP herd compared with that in other modern herds. If the TRNP animals are larger or smaller, then this would be important to understanding differences in production on both a regional basis and in terms of changes in yield associated with the changes in bison size through time. In order to compare the size of the TRNP bison to that in other parks, two kinds of data were examined: liveweights of animals and measurements of bone size. It was

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necessary to examine male and female bison growth patterns first, however, to determine the extent of sexual dimorphism in these animals and determine how liveweight data would be compared between the parks in the analysis of regional bison size.

Growth in Bison

Annually recorded liveweight data for bison of different age classes were used to examine sex differences in bison growth. Previously, Halloran's (1961) data from the WMWR herd have been used (Speth 1983:116) to compare the carcass yields of cows and bulls. Halloran (1961) had only limited data for calves and yearlings, and for old adults of both sexes. Data presented here from Theodore Roosevelt National Park (TRNP), Fort Niobrara National Wildlife Refuge (FNNWR), the National Bison Range (NBR), and Wind Cave National Park (WCNP), in some cases, are more extensive and provide a better picture of the lower portion of the growth curves. The upper portion of the growth curves for males remain less well defined. Since this analysis was done, an article by Berger and Peacock (1988) was found which presents similar data for the NBR, FNNWR and the WMWR.

These liveweight data suggest that the rate of growth in females slows substantially after the second year, although it may take two or three more years of minor weight gain for the mean to reach a mature weight plateau. In males, however, their larger mature size extends the period of substantial yearly increases in liveweight until the fifth or sixth year. Sample sizes for individual age classes of males older than five years were substantially smaller than those for younger ages, and it is not clear from the presently available data at what age bulls generally reach the mature weight plateau. Halloran (1961) suggests bull growth may continue into the

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tenth or twelth year, but this probably represents smaller increments of growth associated with the accumulation of fat, rather than additions of substantial amounts of muscle tissue. Reynolds et al. (1982) suggest bull growth continues into the eighth or ninth year.

Liveweight Evaluations of Regional Differences in Bison Size

Mean data that ignore age- and sex-related differences in liveweight are not appropriate measures to use to evaluate regional differences in bison size, because dimorphism is pronounced in bison (Berger and Peacock 1988). Instead, liveweight means for animals of specific sex and age classes were statistically compared using a series of t-tests. Data from four parks were compared, including Theodore Roosevelt National Park (TRNP), the National Bison Range (NBR), Wind Cave National Park (WCNP), and Fort Niobrara National Wildlife Refuge (FNNWR). The absence of more detailed distribution information in the published data (Halloran 1961) from the Wichita Mountains Wildlife Refuge precluded the possibility of making statistical comparisons with this herd. Peacock and Berger (1988) did a similar analysis comparing data from FNNWR and the NBR to data from the WMWR, and also found animals in the latter herd to be significantly different in size from the animals in the other herds. These authors note, however, that the data were collected over different years and that many factors might be responsible for the size differences.

In the analysis presented in this dissertation, age and sex class liveweight comparisons showed that calves, roughly six-months of age, were significantly different in size between the parks in only one case. In the comparison between FNNWR and the NBR, the NBR calves were significantly smaller. Bison calves apparently differ little in size regionally. Older

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female bison, however, often showed regional differences in size as measured by liveweight. Older male bison could only be shown to consistently differ in size when compared by age classes between animals at WCNP and the NBR and between WCNP and FNNWR. The frequent, significant difference in bison size for females in yearling or older age classes suggests that similar differences might have been found for males had sample sizes been larger. Similarly, the failure to demonstrate differences in the size of males at TRNP compared to those at the other parks and between females and those at some of the other parks may also be due to the small sample sizes for some age and both sex classes in the TRNP herd. Additional future comparisons of bison liveweights for animals in different age and sex classes are suggested. The failure to demonstrate size differences between some herds might also be attributable to their similar genetic makeup. The herd at Theodore Roosevelt National Park, for example, was started with a small herd of animals acquired from the Fort Niobrara National Wildlife Refuge (Sample 1987). This is another aspect of size differences that must be more carefully explored. Berger and Peacock (1988:619) in their analysis of the herd at the Badlands National Park, South Dakota, note that the bison there originated from two sources (Colorado National Monument in western Colorado and the Fort Niobrara National Wildlife Refuge in Nebraska). The smaller animal size of the portion of the herd from Colorado, they (Berger and Peacock 1988:619) suggest might be due to nutritional constraints in that area rather than being the result of the effects of inbreeding.

The occurrence of regional differences in bison size in modern herds, which for a given sex and age class may represent as much as a 25 percent increase in size from the smaller to the larger mean, indicates that care should be used when estimating available meat weights or other yield

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measures for prehistoric kill assemblages. Not only are there major differences in yield associated with animal age and sex, there are also major differences in the size of the animals between regions. If similar differences occurred prehistorically, the meat and fat yields from a kill in one region might differ substantially from those in another. It is important, therefore, to consider potential differences in animal size when using the TRNP data to estimate meat and fat yields. With modern forms of bison the differences in size and meat and fat estimates may be large, but these differences would be exaggerated even more if the TRNP data are used to estimate yields from larger prehistoric bison without giving consideration to the differences in animal size. For younger age classes, both absolute and distribution differences may occur between smaller modern forms and larger, extinct prehistoric forms. The differences between animals from these groups when compared between adult, fully mature age classes are intuitively obvious, in terms of absolute differences in bulk. Differences in meat and fat distribution in the carcasses of fully mature animals of different sizes have not been clarified. It is assumed that they would be similar, but note should be made that the age at which full maturity in liveweight is reached may be quite different.

Significant differences in animal size are important because of the associated differences in the rates of maturation. Studies in the animal sciences have shown that animals of larger adult size generally reach the onset of the fattening phase in the growth process later than animals of smaller adult size. Adult weight is also achieved at a later age in animals of larger adult size. This is clearly evident in the difference in the growth patterns of bison females and males, as noted above. It might also be true within each sex, between parks. Unfortunately, separate

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examinations of the male and female growth curves in which the growth patterns for each park are superimposed on the same figures (Figure 2.7 for females and Figure 2.8 for males) do not clearly indicate whether the animals from parks with larger sized bison show a delay in the decrease in annual growth compared to animals from parks with smaller sized bison. Comparison of the liveweight curves for females from the larger sized FNNWR bison and the smaller WMWR bison suggests that full maturity may occur later in larger bison. This may be examined at a future date through a series of statistical comparisons of weight distributions between sequential age classes.

The magnitude of difference in animal size between males and females of modern bison, and between the animals in herds demonstrating the largest differences in bison size are probably substantially smaller than those between modern forms of bison and larger prehistoric forms such as Bison occidentalis. When differences in the age at which bison achieve full maturity are considered, it is clear that such differences in size might affect relative fat yields. These factors need to be considered by those trying to estimate meat or other carcass product yields for archaeological assemblages of bison bone of larger prehistoric forms.

Metric Differences of Bone Attributes

Bone is the primary carcass product that survives abandonment at bison kill sites. As the primary unit of study for archaeologists interested in bison procurement, some consideration was given to how differences in liveweights translate into differences in bone size. Unfortunately, such data are particularly scarce. It was expected that if the metric attributes of bones of the TRNP bison specimens were larger than, or in the upper range

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of similar measurements determined by Speth (1983) for a collection of animals of mixed regional origin, then larger metric attributes might be indicative of larger animal size, as well.

Comparing the TRNP sample distal humeri (fused in each animal except FYM) to Speth's (1983) measurements of a sample of bison humeri of known sex, but from variable geographic locations, the TRNP sample females were often separted from the other females when the measurements for two attributes were plotted against one another. The TRNP female distal humeri are larger than those of Speth's sample for many measurements and of comparable size for others. The TRNP male, SAM, generally falls closer to the middle of the range of the male specimens in Speth's sample.

In essence, this analysis of bone size was inconclusive for several reasons. First, the number of specimens is quite small. Second, the regional distribution of the sample providing the comparative measurement data presented by Speth (1983) is quite large (including northern Alberta, Oregon, Montana, Wyoming, South Dakota, Nebraska, Kansas, and Colorado). Third, it is clear that appositional bone growth continues after epiphyseal fusion, but it is not clear at what rate this growth continues and how this is reflected in measurements of metric attributes. Differences in the measurements of the proximal radii of FYM and SAM (a bone of early epiphyseal fusion) suggest that these differences may be quite large even after fusion. The intermediate size of SAM in the comparison of his distal humerus to those in the Speth sample, therefore, might be indicative of his lack of full maturity in growth. Additional modern samples of animals of known age and sex are needed to determine whether and how appositional growth after fusion of the epiphyseal plates in bone affects sexual distributions of metric bone measurements. Analyses suggest that some

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metric attributes are early to demonstrate sexual dimorphism (even prior to epiphyseal fusion) while others develop later. At present, it appears that archaeological assemblages offer the largest samples of bone that might be compared through metric attributes to determine whether differences in animal size can be demonstrated in contemporary, regionally derived populations in much the same way that liveweight data were compared.

TRNP Animal Size

From analyses of age- and sex-grouped liveweight data, it appears that statistically significant differences in bison size may occur on a regional basis. For example, cows eight years of age and older at TRNP are 153.6 lb (69.7 kg) heavier on average than cows from Wind Cave National Park. This represents almost a 16 percent increase in liveweight from the smaller animals at WCNP. Theodore Roosevelt National Park cows tend to be larger than those from the Wichita Mountains Wildlife Refuge (based upon inspection of Figure 2.7), from WCNP and from the NBR (based upon statistical comparisons). TRNP males could not be shown to be statistically different in size from these other populations, but it is thought that the wider range of weight distributions and small sample sizes are probably responsible, and that males, as well as females, differ in size regionally. Graphed liveweight data (Figure 2.8), though lacking in statistical significance, show TRNP bulls to be generally larger than those from WMWR, WCNP, and possibly, the NBR. The size comparability between animals from TRNP and FNNWR may also be attributable to the recent (1956) establishment of the TRNP herd from animals originating from the FNNWR herd (Sample 1987).

A comparison of bone size through the measurement and comparison of bone attributes of distal humeri in the study specimens and a sample of

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bison studied by Speth (1983) gave inconclusive results concerning the relative size of the TRNP animals. The female specimens appeared to be generally larger. The male, SAM, was not larger, but lack of full maturity was thought to be a factor in the failure to show a difference. It seems probable that bone measurements should reflect regional differences in bison size.

TRNP bison appear to be relatively large compared to other modern bison, and regional differences in size are large enough to represent substantial differences in liveweight and presumably in product yields between this and some other parks. These differences are important in respect to how these composition data are applied to archaeological remains of bison kill assemblages (e.g., in determinations of usable meat weights, etc.), and in respect to the possible implications of regional differences in carcass yield due to regional differences in animal size, growth rate, and fattening. These size differences need to be defined more clearly and the implications of their existence studied for their potential effects upon prehistoric patterns of bison hunting.

Herd Condition at Theodore Roosevelt National Park

In order to assure that the TRNP bison herd was not in a condition so different from the norm (either poor or good) the year the sample specimens were collected, as to limit their usefulness in studying carcass composition in bison, an analysis of the general condition of the herd was attempted. In order to determine condition, one might compare changes in annual, individual liveweight records for these bison. Unfortunately, no annually recorded, individual animal liveweight data were available for any of the bison at TRNP. In order to assess the condition of the TRNP herd,

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therefore, a proxy measure (annual and seasonal changes in precipitation and temperature) was found which can not directly indicate the specific condition of the TRNP herds or their individual members, but which may suggest the trend. The rationale for using weather data as the proxy measure was based upon their availability in many areas of the country and more importantly, their effect on range productivity. As the food source for bison, changes in grassland productivity can logically be tied to changes in animal liveweight. It should be noted that the bison in the herds studied are not given supplemental feed so changes in liveweight should be a reflection of changes in their food source (or in some individuals, a reflection of injury or disease).

The suitability of using weather data was evaluated first by comparing annual records of individual animal liveweight changes at Wind Cave National Park with annual and seasonal changes in temperature and precipitation at the nearby weather station at Hot Springs, South Dakota. Having established that mean changes in individual animal liveweights corresponded to changes in the temperature and precipitation data in South Dakota, similar weather data were examined for Medora, North Dakota for the years just prior to and including the period when the TRNP bison specimens were collected. The trends in the weather data suggest that the TRNP bison might be in poorer condition than normal for the years 1983 through 1985, with a particularly low period in 1984. This indicates that the study specimens used in this dissertation might be in poorer condition than normal, although the magnitude of this suggested decline cannot be assessed from this kind of analysis. It is also recognized that microclimates exist in most landscapes and these areas may provide adequate forage growth to permit normal patterns of growth or liveweight maintenance in some herds or animals. These

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analyses indicate that additional sources of data would have to be examined to determine more precisely, the specific conditions of the TRNP bison specimens, but suggested that these animals might not be in peak condition. Subsequent analyses of marrow fat content in Chapter 5 indicated that the TRNP bison specimens were in reasonably good, although not prime condition, and the older female, FAF, appeared to be in suboptimum condition.

Variability in Bison Carcass Composition

In a discussion of how the body parts of carcasses of animals of different age and sex are used by Nunamiut hunters, Binford (1978:474) suggested that use is related to differences in body size. He argues that size differences between animals, rather than differences in the relative meat and fat production of their parts determines age- and sex-related carcass use differences. In essence, Binford recognized the existence of bulk weight production differences between animals, but dismissed the importance of differences in the distribution of products in the carcasses of animals of different age, sex or condition. Growth and sexual dimorphism clearly play roles in determining differences in the absolute yield or production of meat and fat in bison. These differences in yield were examined through analyses of production differences in carcass yield, as well as differences in smaller subdivisions of the bison carcass. Measures of the distribution of a carcass component, on the other hand, are designed to eliminate the effects of size differences, by dividing the weight or volume yield for each carcass unit by the total in the carcass. Thus, Thus, production values show that bulls have more meat than cows, but distribution figures indicate how meat and fat weights are distributed in the carcasses of animals of different age, sex, and condition, independent of size differences.

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Extensive literative on livestock growth and development, as well as the data presented in Chapters 5, 6, and 7 clearly demonstrate that despite size-related differences in production, bison bulls are not just larger versions of cows, and cows larger versions of immature males and females. Rather, significant differences in the production and distribution of carcass resources exist that may be related to differences in animal age, sex, and condition. Furthermore, these differences are large enough that they may affect carcass selection and the calculations of utility model carcass unit values. The major focus of Chapters 5, 6, and 7, therefore, was on the identification and description of production (yield) and distribution differences in individual carcass products in the carcasses of the four study specimens, and consideration of whether the magnitude of differences attributable to age, sex, and condition are large enough that such differences in bison might have affected hunter selection for recovery of these single products. It was expected that to understand differences in carcass production and distribution when all products available are considered, it is first necessary to understand differences in the production and distribution of the component products.

Production Differences

Analyses of meat and fat in the carcasses of the four TRNP study specimens indicate that age and sex are important factors influencing the quantity of each product that may be recovered from the carcasses of bison. Generally speaking, young animals produce smaller amounts of meat and fat, as indicated by the yearling representative, FYM. Sex-related size differences leading to greater production in the male were also evident in

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the not quite fully mature specimen, SAM, but only for two carcass products. The male, SAM, produced more protein and marrow fat than either female (Table 10.1). The females, however, produced more fat in the form of bone grease and all other carcass fat depots. It is expected, however, that bison males of comparable maturity to the females used in this study would produce greater quantities of fat due to their larger size. At four years of age, the male bison, SAM, was close to the mature females in the quantity of fat produced (i.e., at least 80 percent of female production) in the intramuscular and cavity depots (Table 10.1). This male produced only 35.3 percent of the quantity of subcutaneous fat produced by SAF, however, and approximately 60 and 65 percent of the bone grease and intermuscular fat produced by SAF and FAF, respectively (Table 10.1). These data suggest that males older than four years of age (and thus closer to full maturity) may be almost as productive, or more productive than females when evaluated in terms of the absolute yield of individual carcass products, rather than in terms of yields expressed relative to carcass size. Comparable yields of subcutaneous, bone grease and intermuscular fat depots in males compared to females apparently do not occur until sometime after the fourth year.

Production differences related to animal condition were also discussed in Chapters 5, 6, and 7. Although specific losses in fat or protein weight cannot be addressed without large sample sizes or longitudinal studies of composition, the two females in this study were compared for their relative yields of meat and fat. Comparisons of production between these two animals appear to show that FAF was in suboptimum condition while the female, SAF, was in reasonably good condition, which echoes the marrow fat content analysis findings. The data in Table 10.1 can be used to estimate the relative difference in fat production between these two females. As

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Table 10.1. Relative Production of Carcass Products in Male and Female Bison

Product	Product Yield (gm)				Male Product Weight as a Percent of Largest Female Weight			FAF:SAF Percent
	FYM	SAM	SAF	FAF	FYM	SAM	Female	
Protein[a]	13,177.9	28,401.4	20,332.2	21,595.9	61.0	131.5	FAF	106.2
Marrow Fat	385.5	618.1	514.1	451.8	75.0	120.2	SAF	87.9
Bone Grease Fat	312.6	596.9	988.7	778.6	31.6	60.4	SAF	78.7
Subcutaneous Fat	306.4	966.9	2,742.8	1,766.6	11.2	35.3	SAF	64.4
Intermuscular Fat	2,227.2	3,405.9	4,047.2	5,187.7	42.9	65.7	FAF	128.2
Intramuscular Fat	644.8	3,508.0	4,053.0	3,668.4	15.9	86.6	SAF	90.5
Cavity Fat	735.8	1,141.4	1,401.9	1,276.8	52.5	81.4	SAF	91.1

[a] Data from Table 8.1, Part B. All other product calculations derived from data in Table 7.1.

expected, the subcutaneous fat depot shows the greatest difference in production. Subcutaneous fat is late to develop and has a high rate of mobility during submaintenance nutrition. As a depot with high proportions of unsaturated fat, this loss might be expected to influence hunting decisions.

Distribution Differences

Product distributions in the bison carcass are also subject to age, sex, and condition differences. Rather than discussing specific carcass products, it is perhaps more helpful to note that the bison in this study appear to conform to Hammond's (c.f., Berg and Butterfield 1976:40-43) reported pattern of mammalian growth. At birth, the head and limbs represent larger proportions of total weight than later in life. Growth rates vary for different parts of the body, but are more rapid in the limbs than in the trunk in young, immature animals. Eventually, however, the rate of growth in the more proximal limb units and in the segments of the axial skeleton increase. The effect of these growth patterns is that young animals appear to be mostly legs and head until growth rates in other portions of the body increase and bring the animals to adult proportions. The principle behind these differences in development is that portions of the body that are most essential to survival are the fastest to develop and also the slowest to degenerate under submaintenance nutrition. This rule is useful in trying to understand age- and condition-related differences in product distributions in the bison carcass.

In the previous section, it was noted that the greatest difference in fat depot production between the two females was in the subcutaneous depot. This fat depot is the latest to develop and shows the greatest rate of

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mobility in studies of submaintenance nutrition. This is to be expected, given the general rule of early growth and the protection of carcass components necessary for survival. This rule applies to major components of the carcass, as well as to the development and distribution of particular fats and protein in the carcass. As such, fat has a higher rate of loss than muscle, and muscle a higher rate than bone when food intake is below maintenance levels.

Sex-related differences in product distributions appear to exist for meat weights and for some fat weights. Mature males tend to carry larger proportions of their meat weight in the forequarter than cows who carry greater proportions of their weight in the hindquarter. No differences in distributions between major divisions of the carcasses of the sexes were identified for the various fat depots. Distribution differences in smaller divisions of the carcass were discussed, but are not itemized here.

Although the size of the bison sample is small, and thus precludes statistical measurement of distribution differences, if one assumes the differences are representative of age, sex or condition differences, statistical significance is not necessarily important archaeologically. As shown in Chapters 5, 6, and 7, many products appear to differ in their distributions (as measured by differences in rank order) under the influence of age, sex, or condition differences. However, sometimes these differences (1) were not large enough to change the order of the carcass unit when ranked by yield; (2) changed the rank order, but to such a small degree and in conjunction with such small differences in the yields of adjacently ranked units that they might not affect selection; and (3) changed the rank order of units, but only in units of such low product yield that it is doubtful that it would have had a major effect on selection. Figures

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showing the change in rank orders of each carcass product when compared between individual bison were presented and summarized. In most cases, age differences (i.e., maturity effects) were responsible for the greatest number of differences in product distributions, but some sex and condition differences were also evident. The marrow fat depot was particularly noteworthy for the small number of rank order differences due to either age, sex or condition. Other products, however, showed a substantial number of rank order differences, although they were not always very large in magnitude.

Modeling Selection

Meat and fat products that were analyzed individually for their relative production and distribution in animals of different age, sex, and condition in Chapters 5, 6, and 7, were evaluated in combination in Chapter 8. This was done in recognition of the fact that bison hunters probably did not pursue this prey in order to recover single resources such as meat or bone marrow, but chose herd types, carcasses and carcass units on the basis of their yield of multiple products. In this chapter, the caloric yields of the carcass products of the four TRNP bison were compared and related to earlier discussions of growth and development in livestock animals and other wildlife species. Complete carcasses and smaller subdivisions were compared using different combinations of carcass products. Three series of utility models which are based upon quantitative differences in yield and that express the value of each carcass unit relative to the unit with the largest yield, but which include different combinations of the study animals, were presented. These analyses were presented in a framework that focused upon the fact that choices or selections are made at each stage of a bison hunt.

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The three phases of selection considered include determinations of (1) which herd type provides the greatest yield of meat and fat at different seasons of the year; (2) which of the available carcasses--those of males, females, or immature animals--provide the greatest returns for effort expended in butchering; and (3) which parts of these carcasses, given their relative yields, would be adandoned at the kill site or transported to other sites for processing, storage, or consumption. Differences between animals were evaluated on the basis of caloric yield, rather than product weight, in recognition of the higher energy value of fat over protein. Herd type and carcass selection are largely influenced by differences in herd organization and differences in the caloric yields associated with the whole carcasses of animals of different age, sex, and condition. The third phase of selection, determination of which parts to abandon and which parts to transport from the kill site, is governed more by relative differences in the yields of the carcass parts. It is assumed that these determinations are not made with respect to the yield of the parts of single carcasses, but with respect to all of those available.

It was noted that archaeological examination of the three phases of selection requires different kinds of information. Determination of the herd type requires information on the age and sex structure of the kill assemblage. Determinations of carcass and carcass unit selection patterns both require sexing of the bone elements in the assemblage, in order to fully explore the possibility of differential use of carcasses due to age, sex, or condition differences. This is not yet a common analytical practice, however, in part due to the fact that such analyses are time consuming, but also because they are often not possible due to the poor condition of the skeletal remains.

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Herd Selection

Based upon (1) carcass composition data and the calculations of the caloric yields of bison of different age, sex, and condition, and (2) estimations (from livestock and wildlife studies) of relative yields of animals of ages not specifically represented in this study, it was suggested that post-rut, fall kills that focused upon cow/calf herds and early spring kills that focused upon bull groups with fully mature members were evidence of strategies that were aimed at recovery of carcasses with high fat yields, rather than carcasses with high total energy yields. This is based upon the fact that during the fall, cows are in better condition than fully mature bulls who are recovering after major energy expenditures associated with the rut and that bull bison, as young as four years old, have higher total caloric yields than fully mature cows. Immature bison, although in good condition in the fall, do not have large amounts of fat in their carcasses. Cows in this study produced 37.9 and 40.5 percent of their total caloric yield in fat (Table 8.1, Part B), whereas the immature and not fully mature males produced 26.1 and 26.6 percent of their yield in fat. If total energy value (including protein and fat), rather than the yield of fat, were the controlling factor influencing herd type selection in the fall, then one would expect to see greater use of bull groups in the archaeological record. The fact that cow/calf groups dominate archaeological bone assemblages in the fall, despite the fact that bulls appear to have larger total energy yields (even taking breeding season losses in males into consideration) is interesting. It suggests that, if differences in the maneuverability of bull and cow/calf groups or in herd size were not responsible for this difference, then it was the relative yields of fat that was the primary influence in fall, herd type selection.

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In the early spring, following a winter period of reduced food quantity and quality, fully mature male bison may provide greater amounts of fat and meat in their carcasses than pregnant or lactating cows. This is expected due to both the larger body size of bulls and the greater energy demands on reproductive females at this time of year. Non-pregnant cows may have a higher fat content than bulls at this time of year, but it is not known whether they are more productive, given the differences in animal size. The carcasses of immature animals are generally lean at this time of year. Immature animals have smaller amounts of fat in their carcasses because a greater percentage of their energy intake is directed toward growth processes. Growth may be slowed during winter months when energy intake is reduced. Winter use of available fat reserves to provide energy for metabolism during periods of submaintenance nutrition further reduces the fat productivity of the immature bison carcass. In the early spring, therefore, fully mature bulls provide a reasonable target when human nutritional needs may make fat recovery critical. It is interesting to note that the bull, SAM, at four years of age had substantially higher marrow fat yields than either of the females studied. Marrow fat is mobilized at lower rates than many other fat depots, a fact which together with the higher male yield (due to size) may further promote the selection of bull groups during periods of critical need.

Sex differences in the adult size of bison, together with the differences in the age at which they reach maturity, suggest that bison cows would become the focus of bison hunter pursuits earlier in their development than bulls. The earlier age at which cows mature would enhance the value of cow/calf groups and the late maturity of bulls might reduce the value of some bull groups containing larger proportions of young animals.

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Carcass Selection

The carcass composition data also suggest that once the herd type has been selected and the animals killed, determination of which carcasses to butcher should also be influenced largely by quantitative differences in carcass yield. Those carcasses and carcass parts that provide the largest amounts of the desired products should be butchered before those with smaller amounts, and greater percentages of their body parts should be removed to other sites for processing or consumption. Low priority use might be reflected in greater rates of bone abandonment for elements of less productive animals as was seen at the Garnsey Site (Speth 1983) for female and immature carcasses.

At fall and spring kill sites, the carcasses of adult bison should be used prior to those of immature animals if fat or total caloric yield are important factors influencing selection. The carcasses of immature bison should be given priority in selection only when lean meat with relatively little connective tissue is sought. Although it could not be demonstrated with the sample in this study, it is suggested that larger amounts of fat are produced by cows in the fall, and by bulls in the spring. Despite the fact that cows may be fatter than bulls (have a higher fat content), the differences in yield due to differences in animal size must be considered when one is trying to understand hunter selection. If total caloric energy return were more important than fat yield, the archaeological record should show greater use of male carcasses than is evident.

Carcass Unit Selection

In Chapter 8, carcass unit utility models based upon Binford's (1978) pioneering example of the relationship between body part value and use, and

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Metcalfe and Jones's (1988) arguements for the simplifications of model construction were presented. In contrast to the work of Binford, and Metcalfe and Jones, three types of models (single class, averaged and mixed class models) were identified here, each of which is needed to cover different analytical circumstances.

The single class models presented in this dissertation are based upon the anatomical data from each of the four TRNP bison. Single class models are constructed to represent particular animal classes such as immature males, adult males, adult females, and adult females in poor condition. These models are constructed with the recognition that differences in the relative yield or value of a particular body part may differ between animals of different age, sex, and condition in much the same manner as single products were shown to differ in their production and distribution between the members of the bison sample. These models are referred to here as single class models, despite the fact that they represent data from individual animals, in the hopes that further studies of bison anatomy may increase the sample size of each class.

Single class models are most useful in the analysis of bison bone assemblages dominated by a single class of animals or in applications to meaningful subgroups of assemblages representing multiple event kills. Bull group kill assemblages for example, might be better understood using the single class models based upon the male, SAM, than averaged models. Similarly, aged or sexed portions of assemblages might also be studied using single class models if the subgroups represent single event or similarly treated assemblages from a multiple event kill site, as was done in Chapter 9.

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Averaged models are appropriate for analytical use when bone assembalges include a mix of animal classes (e.g., animals of different maturity and sex), but for which there are no specific bone counts for animals of different age or sex with which to study differential use of animal carcasses. Comparisons of carcass unit values derived for averaged and single class models showed that averaged models may over- or underestimate carcass unit value and thus, expected bone counts when applied to an assemblage dominated by a single animal class. Other analyses showed that these units were often the ones that demonstrated age, sex, or condition differences in the production or distribution of single carcass products as discussed in Chapters 5, 6 and 7. These differences in unit value estimation were shown to be unimportant in some situations, however. In model applications to archaeological assemblages, depending upon the kind of recovery strategy in evidence at the site (i.e., an unbiased, bulk or gourmet strategy), the differences in unit value estimations between an averaged and single class model might or might not be expected to show up as a carcass unit whose associated bone is over- or underrepresented at the site. These studies indicate that the extent to which the discrepencies in the expected and observed frequencies of bone at a kill site are due to misrepresentation of the actual unit values (e.g., through use of an averaged model when a single class model might have been more appropriate) might be identifiable.

The third model type discussed, the mixed class model, represents a new development in modeling body part utility. Mixed class models are based upon the expectation that more than one animal class is present in the assemblage and that choices of selection are made with respect to the relative differences in all the parts available. In the examples presented,

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male and female caloric yield data were scaled to the part of highest value, regardless of animal origin, before the normal standardizing and rider modification routines were applied. By expressing the value of the parts to the same scale, one may then determine how a particular unit from one class of animals might be used compared to the same unit in another class when value is expressed in terms of their relative yields. Applications of such models, however, require that the archaeological assemblage has been analyzed to indicate the number of bones remaining of the potential total for each animal class represented in the model. For use of the models presented, for example, male and female bones must be identified and counted in the assemblage.

Carcass unit utility models, whether of the single class, averaged, or mixed class type, may focus upon any combination of products present in the bison carcass. A variety of single class, averaged, and mixed class models were presented in Chapter 8 and Appendix C which included all carcass products (TP, total products) and which included various combinations of the component products included in TP (e.g., skeletal fat, SKF). The models with more limited products included were developed in recognition of the fact that selection decisions might not always be based upon the yield of all available resources, and might not be the same in every procurement situation.

Construction of these models all differed from the complex model calculations of Binford (1978) and the simplifications of Metcalfe and Jones (1988) in two respects. First, the bison utility models presented in this disseration are not based upon weight differences, but upon calorie data that recognize the differnce in the energy yield of protein and fat.

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Second, unlike Binford's (1978) and Metcalfe and Jones's (1988) constructions, no amplifications of the values of the appendicular units (other than to account for riders) were made, thus preserving the relative differences in yield between axial and appendicular units. The importance of these construction differences, together with the usefulness of models of different type and focus were briefly evaluated in Chapter 9 and are reviewed below.

Applications of Carcass Unit Utility Models

Carcass unit utility models were applied to two archaeological assemblages of bison bone in Chapter 9, for three reasons: first, to evaluate the relative merits of two methods of model construction (gross-weight- and caloric-yield-based models); second, to evaluate the potential usefulness of the different model types (single class, averaged, and mixed class models); and third, to evaluate the usefulness of models of variable focus (e.g., based upon total products (TP) or some other combination of products) in their applications to two archaeological sites of different seasonality. Utility model application involves graphing the model values of carcass units against their relative abundance at the sites. The Glenrock Jump (Frison 1970) was used as a representative of a fall season kill site, and the Garnsey Site (Speth 1983) was used as the representative of the spring season kill. Both sites represent pre-horse bison procurement activities of the late prehistoric period.

Model Construction

Model construction methods were evaluated by applications of averaged models, including all carcass products, to the Glenrock Jump assemblage.

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The application of the average model, (S)AVGFUI, was compared to the application of the model (S)MAVGTP. The averaged model, (S)AVGFUI, is based upon the construction procedure outlined by Metcalfe and Jones (1988). Carcass unit values in this model are based upon yields of carcass products as measured by the gross weight of the unit minus the weight of the associated dry bone. In the averaged model, (S)MAVGTP, on the other hand, carcass unit value is based upon differences in caloric yield. Although both model constructions incorporate an averaging routine to account for the effect of riders (Binford's term for the tendency of low value appendicular units to be removed in higher frequencies than their yield alone would suggest, due to their location next to, or between parts of higher value) which inflates the value of some appendicular units, the gross-weight-based model as described by Binford (1978) and Metcalfe and Jones (1988) overestimates the value of appendicular units in another respect.

Comparisons of the two graphs (Figures 9.1 and 9.2) of model values plotted against the Glenrock Jump bone assemblage data suggested that the gross-weight-based (S)AVGFUI model overestimates the value of some appendicular units (specifically the tarsals) relative to other appendicular units, and overestimates the value of all appendicular units relative to the axial units. This inflation of the appendicular unit values tends to mask the difference in the relationship between the uses of the axial and appendicular units with respect to their combined product yields. The rationale for making this modification was never adequately justified by Binford (1978), and given its adverse effect in relating unit value to use, the (S)FUI model and its derivatives were not used in further analyses in this dissertation.

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It also was necessary to determine whether model constructions based on gross weight and caloric yield data might have been similar, had the appendicular and atlas-axis unit values not been inflated prior to standardization and application of the rider averaging routine in the construction of the (S)FUI models. This analysis compared the units of measure used to construct the models. An analysis in Chapter 8 of the differences in carcass unit values based upon a measure of gross weight (GWT) as compared with a measure of caloric yield suggests that in low-fat yielding species, models based upon gross weight analyses, though somewhat different in their ranking of carcass units (particularly in the head and tail), provide reasonable estimates of relative yield. The easier task of determining gross-weight-based yields might suggest that detailed analyses of product weights are not necessary, but the additional analyses presented in Chapter 9 suggests that the added effort of determining relative yields of meat and fat provide additional insights that cannot be obtained based upon analyses of gross weight and total products models alone. Additionally, it is not clear that in other species with higher fat contents, that gross weight and caloric yield rankings of carcass units would be as much alike as in these bison. Whenever possible, therefore, detailed data recovery including separate meat and fat weights and ultimately, caloric yields are preferred.

Model Types

Applications of averaged models to the Glenrock Jump assemblage and mixed class and single class models to the Garnsey Site demonstrated that each model type has value as an analytical tool in the study of bison bone assemblages. In general, all of the models produced results that

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demonstrate that bison carcass units were removed from these two kill sites according to a measure that is related to their quantitative yields. In each case, where utility models were plotted against bone assemblage data, the points (representing individual carcass units) were not randomly distributed across the plots, but were distributed in linear and/or curvilinear patterns. If there were no relationship between use and unit value based upon yield, such linear patterns would not be expected.

The application of single class models was suggested above to be appropriate when the bone assemblage is dominated by animals of one particular class, or when the assemblage is a mixture of kill events and the individual events may be separated and are dominated by single animal classes. Such applications reduce the risk of over- or underestimating the value of a carcass unit. Averaged models are applied when a mixed class assemblage is represented, but there are no individual bone counts for each class. These models offer an analytical tool when detailed analyses of differences in the treatment of the members of different classes are not possible, either due to limitations on the time and money available for analysis, or due to the poor condition of the bones which may prevent such analyses. If the animal classes were treated quite differently at the kill, then an averaged model application may show more widely distributed points than if the classes are similarly treated. Although it cannot be unquestionably demonstrated with the data available from the Glenrock Jump, it is possible that the tighter relationship between the model (S)MAVGTP and that assemblage (Figure 9.1) than between this model and the complete Garnsey Site assemblage (Figure 9.8) is attributable to this factor. It must also be apparent that models that more accurately reflect the

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composition of the kill should be less likely to under- or overestimate the value of a carcass unit.

Mixed class model applications to the Garnsey Site male and female bone assemblage data (Speth 1983) were expected to show bone elements abandoned in proportion to the values of units expressed according to the same scale. By basing model construction upon a spring-killed male, SAM, and a female in poor condition, FAF, it was expected that the two separate distributions for male and female elements resulting when the same values are used for each element of both sexes would change to a single distribution. This did not happen, however, and it was suggested that two possible reasons might account for this. First, the female, FAF, might not be in as poor condition as the females represented in the Garnsey Site assemblage. The higher frequencies of humerus units present than expected in the female assemblage suggests that this indeed might be partially responsible. Second, the male and female assemblages might represent separate kill events of bull groups and cow/calf groups in which the hunters evaluated each carcass unit, not with respect to those of both sexes as assumed by the model, but as separate selection decisions in which each male unit was evaluated against the other male units and each female unit was evaluated against the other female units from their respective kills. To support this explanation, it was noted that Speth (1983) suggested that the bison assemblage represents the aggregation of a number of bone clusters which he interpreted to be separate, but quasi-contemporary kill events. By violating one of the assumptions of the model application (assessment of unit value in relation to all available units in the kill) and combining the assemblages, the maintenance of the separate male and female assemblage distributions is not surprising. In this

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respect, this has not been an adequate test of the usefulness of the mixed class model type. It does illustrate, however, that these models might be useful in identifying multiple kill events when differences in transport strategies were in effect.

Model Focus

Applications of models with varied inclusions of carcass products have been useful in demonstrating (1) that axial and appendicular carcass units may be abandoned at the same kill site in numbers that suggest the use of different selection criteria for major divisions of the bison carcass, and (2) that between sites, different product combinations may be more important at one site than another in explaining the frequencies of bones abandoned. Applications of the total products and some fat based models, regardless of whether single class, averaged, or mixed class models were used, showed the axial and appendicular units in the bone assemblages at the Glenrock Jump and the Garnsey Site were treated differently with respect to the relationship between model value and rate of bone abandonment. In these applications, the axial units were abandoned according to unbiased strategies and the appendicular units according to bulk strategies. This difference is not attributable to the application of the rider averaging routine, but represents a clear difference in the treatment of major portions of the bison carcass with respect to quantitative measurements of yield. It is possible that failure to incorporate qualitative measurements of relative carcass unit value might be a factor in the separation of the axial and appendicular distribution. Qualitative data, however, were not available for use in this study.

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It was also noted that different assemblages and the different distributions of axial and appendicular units sometimes showed tighter alignments for different combinations of carcass resources, suggesting that portions of the kill and portions of carcasses might have been used and abandoned according to different selection criteria. In the Glenrock Jump assemblage, for example, the axial units showed an unbiased recovery strategy in the numbers of bones abandoned with respect to the total fat model (TF), whereas the appendicular units appeared to relate more closely to their relative values as measured by their yield of skeletal fat. Applications of the appropriate single class models of different product combinations to the male and female Garnsey Site assemblages, suggest that female axial units were abandoned with respect to their total products (TP) yield, while the corresponding male units fit the total fat (TF) model. Appendicular unit bone abandonment at the site in both the male and female assemblages appears to relate to their yield of skeletal fats.

At both of these sites, the axial and appendicular bone frequencies appeared to be responses to different selection criteria. It also appears, however, that while relative yields of one or both sources of skeletal fat influenced appendicular bone abandonment at both sites, the axial bone abandonment frequencies suggest that different strategies were in effect between the female and male Garnsey Site assemblages, and between the female Garnsey Site assemblage and the Glenrock Jump assemblage. Total fat (TF) appeared to be important to axial unit usage at both the Glenrock Jump and in the male bone assemblage at the Garnsey Site, while total products (TP) appeared to be more important to the Garnsey Site female axial unit usage.

The importance of total fat to axial unit bone abandonment at the Glenrock Jump, together with the apparent selection of cow/calf herds over

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bull groups, if not a product of herd size or maneuverability differences, may be indicative of the greater importance that fat has in guiding selection decisions in the fall season than was previously recognized. Apparently, adequate amounts of meat are recovered when selection is based upon fat productivity rather than combined meat and fat recovery.

The apparent better fit between the female axial assemblage and the total products model (TP) than the total fat (TF) model was somewhat surprising given the spring seasonality of the site. It was suggested that the better fit of the total products model to the female axial data, the use of poor conditioned females, and the nature of the male carcass use with more intensive use of the appendicular units and some axial units, were indicative of the possibility that the hunters who took the females were not as poorly nourished as were those who took the male herds. This is a difficult arguement to support, however, and it may be overstepping the bounds of the conclusions one should make. It could not be shown, however, that the alternative explanation, that poor animal representation for the TF model was involved, because those units whose frequencies at the site were not correctly predicted by the model were those units that showed the greatest drop in total fat yield from SAF to FAF. If poor model representation were a factor, these units should have been overrepresented at the site, rather than underrepresented for this site to model relationship. Perhaps at this point, it is adequate to note that differences in use appear to exist and leave the conclusions as to why these exist until a more thorough study of the distributions and their implications can be made.

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Utility Model Application Problems

A discussion of the potential problems involved in using utility models based upon quantitative measures of product yield was also presented in Chapter 9. It was suggested that differences in the butchering patterns used in the construction of the models and at the archaeological site could easily lead to model values over- or underrepresenting the actual value of the carcass units. It was also suggested that the failure to include measures of relative value that are based upon qualitative, as well as quantitative differences in carcass unit value, may account for the differences in axial and appendicular unit use. The third problem discussed was differences in the size and potential productivity of bison from modern herds compared with prehistoric forms. It was suggested that the larger size of the earlier forms might have been associated with longer delays in the attainment of maturity, a factor that might affect the relative unit values of single class models, but which should not dramatically affect models based upon averaged data or data from fully mature adults. It is not clear how prolonged periods of immaturity would affect herd organization. If extended immaturity in males was not also associated with extended association with the cow/calf group, then selection of bull groups might result in more encounters with animals with low fat yielding carcasses. Under such circumstances, and given the smaller herd size of bull groups, it is unclear how herd type selection would have been influenced. The potential for differences in selection related to differences in animal size in earlier prehistoric forms needs more consideration.

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Conclusion

Differences in the production and distribution of carcass products in bison that might be attributable to differences in animal age, sex and condition, and their potential effects upon the selection decisions of pre-horse bison hunters were considered in this dissertation. This study demonstrates that differences in meat and fat production and distribution (at least in the four bison studied) are not attributable to animal size differences alone, but represent differences in body composition and product distributions that are related to changes associated with growth and the attainment of full maturity, as well as to changes associated with uneven rates of fat mobility between depots during periods of submaintenance nutrition. Bison carcass productivity changes with age, sex, and animal condition in ways that reflect more than a simple differences in body size.

Although the data presented here provide the most detailed decriptions of bison anatomy currently available, they also suggest that the addition of similar data for animals belonging to other age, sex, and condition classes, as well as a larger sample of animals similar to those studied here, would greatly enhance our understanding of the basis of hunter selection decisions. This study, had time permitted, could also have been improved by the inclusion of measures of qualitative differences in fats. Perhaps the axial and appendicular unit differences noted in the relationship between carcass unit abandonment and carcass unit value (as measured by quantitative yields in caloric energy) in the applications of utility models to site assemblage data are attributable to differences in quality between these major divisions of the bison carcass. Although a variety of models were presented for applications to two archaeological assemblages, other models suitable for applications to cow/calf or other herd types might also have

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been constructed. The data necessary to do so has been presented here (Appendix D).

The primary focus of this work has been to study differences in carcass composition attributable to differences in age, sex, and condition, and to present models of utility that might be used to study archaeological assemblages. A more detailed and extensive (more sites) consideration of how utility model applications might be useful as an analytical tool would have been ideal, but could not be included here. Obviously, much remains to be learned about how differences in animal carcass production might or might not be reflected in selection models and in archaeological assemblages. Clearly, more data are needed concerning how changes in animal age, sex, and especially condition affect product yields and their distributions in the bison carcass. It also is apparent from the applications of utility models to the archaeological assemblages that if butchering processes include separation of bone prominences to strip muscle, then this information needs to be incorporated into model constructions, or the effect on the protein yields of total product models needs to be appropriately adjusted. Clearly, utility model applications to archaeological assemblages should not be done without careful consideration of the assumptions implied by their use and the problems that might lead to errors in interpretation. It should be clear, as well, that this dissertation provides an abundance of information that may be of value to those who study human patterns of bison procurement and use. Speth's (1983) work and the results of these carcass composition analyses and model applications also suggest that more detailed analyses of bone assemblages than is the current practice may offer greater insights into studies of bison procurement.

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APPENDIX A

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SELECTED SKELETAL ATTRIBUTES OF THE TRNP BISON

Table 1 presents the measurements of selected skeletal attributes for the four Theodore Roosevelt National Park bison. These attributes are described in one or more of four sources, which may be consulted for descriptions of how the measurements are taken. Measurements reported to 0.00 mm were taken using sliding dial calipers; measurements reported to 0.0 mm were taken using an osteometric board.

Although these data include measurements from only four animals, they suggest that sexual dimorphism in bone measurements may be expressed as early as 1-1/2 years of age in male bison, often before epiphyseal fusion in is complete. Clearly, the bones from four animals do not constitute a representative sample of the range of variability in attribute measurements, but the data do suggest that some attributes may be more helpful than others in distinguishing between the sexes. Given the fact that bison size may vary on a regional basis, these attribute measurements should not be used as references to determine age or sex for bones from other populations. These data are presented as a indication of where differences might be most pronounced. As throughout the dissertation, acronyms are used here to distinguish between the individual bison: FYM (Fall Yearling Male), SAM (Spring Adult (four year old) Male), SAF (Spring Adult (seven year old) Female), FAF (Fall Adult (16-1/2 year old) Female).

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Appendix A. Table 1. Metric Attributes of Theodore Roosevelt Bison Bones

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm)			
			FYM	SAM	SAF	FAF
Atlas	GL	1	97.5	123.5	111.5	112.5
	GLF	1	96.0	102.5	93.0	95.5
Mandible	M3	4	69.55	71.35	70.00	70.50
Pelvis	LA	1	82.15	92.15	82.60	79.50
	SH	1	38.80	48.15	45.20	48.50
Scapula	SLC	1	51.55	72.50	64.50	64.40
	LG	1	69.50	75.65	67.20	63.50
	BG	1	51.20	62.50	53.20	53.15
	GLP	1	79.55	93.80	76.10	77.70
Humerus	2	3	45.50	59.90	53.10	54.50
	3	3	34.60	46.25	40.00	44.70
	BP	1	84.0	113.5	94.0	95.0
	A	2	---	104.65	93.20	93.95
	B	2	---	74.40	70.10	67.50
	C	2	115.0	134.0	117.0	118.0
	E	2	66.05	91.20	81.00	78.35
	F	2	---	131.5	111.0	113.5
	G	2	---	98.15	77.90	81.10
	H	2	91.05	124.30	106.30	103.65
	BD	1	95.0	107.0	93.0	94.5
	BT, I	1, 2	84.75	95.60	83.40	83.10
	J	2	51.90	62.50	54.50	53.00
	K	2	86.70	96.10	82.60	80.30

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Appendix A. Table 1. (continued)

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm) FYM	SAM	SAF	FAF
Humerus (cont.)	L	2	43.95	57.50	49.45	50.40
	M	2	77.15	88.10	75.90	73.30
	N	2	37.40	42.05	35.70	34.80
	O	2	47.40	49.20	44.05	42.85
Radius	BP, A	1, 2	89.20	103.80	88.25	89.90
	B	2	48.35	61.20	50.05	50.90
	C	2	28.85	31.70	25.75	27.15
	D	2	49.90	58.10	50.90	49.65
	E	2	38.40	41.35	36.25	36.30
	F	2	53.60	71.60	62.90	60.40
	BD, G	1, 2	82.20	95.60	81.50	81.20
	BFD	1	68.00	74.10	66.65	65.05
	H	2	---	53.90	46.60	44.60
	I	2	45.30	52.35	45.90	46.50
	J	2	13.35	15.60	14.30	14.95
	K	2	29.60	34.10	30.80	32.90
	2	3	25.00	30.90	29.40	28.20
	3	3	40.15	54.15	48.50	48.40
Ulna	LO	1	102.05	137.40	108.30	106.60
	DPA	1	74.60	98.10	78.40	79.20
	SDO	1	56.05	65.20	58.90	63.10
	BPC	1	52.55	59.55	52.60	52.15

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Appendix A. Table 1. (continued)

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm) FYM	SAM	SAF	FAF
Metacarpal	BP, A	1, 2	69.50	74.20	66.75	65.05
	B	2	37.00	45.20	39.65	39.35
	C	2	42.80	43.05	40.05	38.40
	BD	1	69.80	79.05	69.40	71.60
	D	2	68.75	75.80	69.40	69.55
	E	2	33.15	39.10	32.50	36.15
	F	2	31.40	36.40	30.45	32.40
	G	2	30.70	33.25	29.40	28.00
	H	2	27.15	29.75	25.80	24.90
	I	2	40.55	43.10	37.95	36.50
	J	2	39.00	41.70	37.10	35.15
	2	3	25.50	30.70	26.05	24.50
	3	3	34.60	48.20	39.35	39.50
Anterior First Phalanges (lateral)	BP	1	32.30	38.50	34.55	35.40
	BD	1	32.95	39.80	34.60	36.50
(medial)	BP	1	32.75	40.15	35.80	36.10
	BD	1	32.90	39.40	34.35	36.20
Femur	BP	1	124.0	153.5	136.5	135.5
	A	2	124.70	147.40	129.50	129.20
	B	2	55.10	77.05	66.05	63.50
	C	2	55.05	63.50	55.60	56.35
	D	2	56.65	78.75	69.70	74.80

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Appendix A. Table 1. (continued)

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm) FYM	SAM	SAF	FAF
Femur (cont.)	E	2	28.10	28.20	27.50	25.50
	F	2	55.80	62.50	56.20	57.05
	G	2	54.90	63.30	50.75	55.40
	H	2	48.90	59.30	51.45	50.55
	BD, I	1, 2	100.5	119.5	107.5	107.0
	J	2	63.60	69.35	60.45	61.15
	K	2	132.0	143.5	130.5	127.5
	L	2	51.25	65.70	49.50	48.60
	M	2	41.50	58.80	45.65	54.10
	N	2	57.90	71.45	60.10	55.70
	O	2	89.20	105.20	91.30	87.90
	2	3	39.40	46.75	43.20	46.50
	3	3	37.05	47.80	42.15	42.50
Tibia	BP, A	1, 2	105.0	119.5	111.0	108.5
	B	2	97.8	121.10	107.70	103.90
	C	2	77.45	92.25	83.95	77.70
	D	2	101.75	115.40	107.20	103.45
	E	2	48.50	55.65	50.50	45.70
	F	2	50.80	59.00	54.45	52.35
	G	2	80.45	89.30	82.25	78.50
	BD, H	1, 2	71.75	73.95	71.00	67.75
	I	2	51.10	55.90	52.50	52.45
	J	2	53.40	53.70	52.80	49.30

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Appendix A. Table 1. (continued)

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm)			
			FYM	SAM	SAF	FAF
	K	2	---	45.50	41.90	44.55
	L	2	---	56.30	50.15	48.65
	2	3	30.95	35.75	34.30	33.50
	3	3	39.70	49.80	45.80	44.40
Lateral Malleolus	GD	1	38.50	41.90	37.85	37.55
Patella	GL	1	69.90	77.75	76.30	70.60
	GB	1	54.70	73.30	60.55	64.15
Astragalus	GLM	1	77.95	76.40	75.65	68.85
	GLL	1	84.75	80.80	77.85	72.35
	BP	1	55.00	58.45	54.90	51.70
	BD	1	51.80	54.80	50.25	50.75
Calcaneus	GL	1	154.5	172.0	164.0	155.5
	GB	1	49.5	57.5	52.0	50.5
Naviculo Cuboid	GB	1	64.0	68.0	61.5	61.5
Metatarsal	BP, A	1, 2	51.80	56.75	50.90	52.25
	B	2	52.70	56.50	52.20	52.35
	C	2	30.60	28.40	27.15	26.50
	BD	1	65.80	72.55	63.70	65.50
	D	2	65.80	71.55	63.70	63.05
	E	2	30.60	34.60	29.15	34.15
	F	2	28.60	32.75	27.60	28.00
	G	2	29.85	32.30	28.75	27.50

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Appendix A. Table 1. (continued)

Skeletal Element	Attribute	Source[a]	Attribute Measurement (mm) FYM	SAM	SAF	FAF
Metatarsal (continued)	H	2	27.05	28.80	25.95	24.10
	I	2	39.80	42.95	38.50	36.55
	J	2	38.15	41.70	37.00	34.65
	2	3	30.05	32.80	31.30	28.90
	3	3	28.70	36.70	31.30	31.75
Posterior First Phalanges (lateral)	BP	1	30.05	35.10	31.50	31.15
	BD	1	30.75	35.10	31.30	32.40
(medial)	BP	1	32.00	36.70	32.55	35.55
	BD	1	31.00	36.10	32.60	32.30

[a] Sources describing skeletal attribute measurements: (1) von den Driesch (1976); (2) Speth (1983); (3) McDonald (1981); (4) Reher (1973).

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APPENDIX B

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INDIVIDUAL MUSCLES WEIGHTS IN THE TRNP BISON

The carcasses of the two spring collected animals, SAM and SAF, were split and the right halves dissected, separating muscle from fat (excluding intramuscular fat) and bone. In some cases the split along the midline was not exact, but this is not a factor in the weights recorded below. Corrections for these differences were made in the laboratory. Where muscles from the right side did not belong with the unit or were absent, they were removed, or were added from the left side to make the side complete. Divisions between bone units were made as described in Chapter 4. At the point where the muscle fibers ended along tendon, the tendon was cut and not included in the weights recorded below.

Muscle weights were originally recorded in pounds and ounces, and in some cases when the muscles were quite small, they were weighed on a dial-o-gram balance. All weights in Appendix B are reported in grams. Conversions were made from ounces to grams using 28.35 grams per ounce.

Muscle terminology in the following tables is that used in Pasquini's (1982) Atlas of Bovine Anatomy.

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Appendix B. Table 1. Weights of Appendicular Muscles in the Right Side Carcasses of SAM and SAF

			SAM			SAF		
Limb Part	Muscle	Carcass Unit	Muscle Weight (gm)	Muscle Distribution Between Units	Percent of Total Limb Muscle Weight	Muscle Weight (gm)	Muscle Distribution Between Units	Percent of Total Limb Muscle Weight
proximal pelvic limb	adductor femoris	sacrum-pelvis	14.2	0.7	---	4.6	0.3	---
		femur	2154.6	99.3	---	1637.2	99.7	---
		total	2168.8	---	5.6	1641.8	---	5.5
	biceps femoris	sacrum-pelvis	28.4	0.4	---	14.2	0.2	---
		femur	7413.5	97.8	---	6194.5	99.1	---
		tibia	141.8	1.9	---	42.5	0.7	---
		total	7583.8	---	19.7	6251.2	---	20.9
	gastrocnemius	femur	1375.0	61.8	---	1226.1	76.9	---
		tibia	850.5	38.2	---	368.6	23.1	---
		total	2225.5	---	5.8	1594.7	---	5.3
	gemelli	sacrum-pelvis	56.7	66.6	---	63.8	94.8	---
		femur	28.4	33.4	---	3.5	5.2	---
		total	85.1	---	0.2	67.3	---	0.2

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
proximal pelvic limb	accessory gluteal	sacrum-pelvis	340.2	100.0	---	333.1	88.7	---
		femur	0.0	0.0	---	42.5	11.3	---
		total	340.2	---	0.9	375.6	---	1.3
	deep gluteal	sacrum-pelvis	396.9	87.5	---	170.1	66.7	---
		femur	56.7	12.5	---	85.1	33.3	---
		total	453.6	---	1.2	255.2	---	0.9
	middle gluteal	lumbar	113.4	3.1	---	70.9	2.5	---
		sacrum-pelvis	3494.1	94.1	---	2764.1	97.0	---
		femur	106.3	2.9	---	14.2	0.5	---
		total	3713.8	---	9.7	2849.2	---	9.5
	gracilis	sacrum-pelvis	28.4	2.0	---	0.0	0.0	---
		femur	1360.8	98.0	---	1041.9	100.0	---
		total	1389.2	---	3.6	1041.9	---	3.5

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
proximal pelvic limb	external and internal obturator	sacrum-pelvis	375.6	55.8	---	163.0	42.6	---
		femur	297.7	44.2	---	219.7	57.4	---
		total	673.3	---	1.8	382.7	---	1.3
	quadratus femoris	sacrum-pelvis	0.0	0.0	---	4.8	8.8	---
		femur	70.9	100.0	---	49.6	91.2	---
		total	70.9	---	0.2	54.4	---	0.2
	rectus femoris	sacrum-pelvis	113.4	5.3	---	28.4	1.7	---
		femur	2041.2	94.7	---	1651.4	98.3	---
		total	2154.6	---	5.6	1679.8	---	5.6
	sartorius	femur	318.9	100.0	0.8	212.6	100.0	0.7
	semimembranosus	sacrum-pelvis	28.4	0.6	---	5.6	0.1	---
		femur	4961.3	99.4	---	4373.0	99.9	---
		total	4989.7	---	13.0	4378.6	---	14.6

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
proximal pelvic limb	semitendinosus	sacrum-pelvis	28.4	0.9	---	38.0	1.8	---
		femur	2962.6	98.1	---	2076.6	95.6	---
		tibia	28.4	0.9	---	56.7	2.6	---
		total	3019.4	---	7.9	2171.3	---	7.3
	tensor fasciae latae	sacrum	1474.2	100.0	3.8	1268.7	100.0	4.2
	vastus intermedius	femur	375.6	100.0	1.0	446.5	100.0	1.5
	vastus lateralis	femur	2494.8	100.0	6.5	2112.1	100.0	7.1
	vastus medialis	femur	1247.4	100.0	3.2	567.0	100.0	1.9
	pectinus	sacrum-pelvis	14.2	1.8	---	2.9	0.6	---
		femur	793.8	98.2	---	467.8	99.4	---
		total	808.0	---	2.1	470.7	---	1.6
distal pelvic limb	lateral digital extensor	tibia	241.0	100.0	0.6	177.2	100.0	0.6

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
distal pelvic limb	long digital extensor	tibia	134.7	100.0	0.4	99.2	100.0	0.3
	middle digital extensor	tibia	134.7	100.0	0.4	99.2	100.0	0.3
	short digital extensor	metatarsal	14.2	100.0	0.0	12.0	100.0	0.0
	deep digital flexor	tibia	1034.8	100.0	2.7	652.1	100.0	2.2
	superficial digital flexor	femur	99.2	22.6	---	177.2	53.2	---
		tibia	340.2	77.4	---	155.9	46.8	---
		total	439.4	---	1.1	333.1	---	1.1
	peroneus longus	tibia	99.2	100.0	0.3	70.9	100.0	0.2
	peroneus tertius	tibia	304.7	100.0	0.8	233.9	100.0	0.8

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
distal pelvic limb	popliteus	femur	7.1	2.2	---	56.7	20.5	---
		tibia	311.9	97.8	---	219.7	79.5	---
		total	319.0	---	0.8	276.4	---	0.9
	soleus	tibia	7.1	100.0	0.0	7.1	100.0	0.0
	cranial tibial	tibia	127.6	100.0	0.3	99.2	100.0	0.3
proximal thoracic limb	anconeus	humerus	127.6	97.0	---	113.4	99.6	---
		radius-ulna	4.0	3.0	---	0.5	0.4	---
		total	131.6	---	0.7	113.9	---	4.4
	biceps brachii	humerus	808.0	100.0	4.4	510.3	100.0	4.4
	brachialis	humerus	581.2	94.3	---	425.3	97.5	---
		radius-ulna	35.4	5.7	---	10.7	2.5	---
		total	616.6	---	3.4	436.0	---	3.8
	coracobrachialis	humerus	141.8	100.0	0.8	99.2	100.0	0.9

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
proximal thoracic limb	infraspinatus	scapula	2976.8	98.7	---	1757.7	100.0	---
		humerus	38.6	1.3	---	0.0	0.0	---
		total	3015.4	---	16.5	1757.7	---	15.2
	subscapularis	scapula	1360.8	99.7	---	793.8	100.0	---
		humerus	4.3	0.3	---	0.0	0.0	---
		total	1365.1	---	7.5	793.8	---	6.8
	supraspinatus	scapula	1899.5	100.0	---	1502.6	99.4	---
		humerus	0.0	0.0	---	8.4	0.6	---
		total	1899.5	---	10.4	1511.0	---	13.0
	tensor fasciae antibrachii	humerus	70.9	100.0	0.4	70.9	100.0	0.6
	muscle group: deltoideus, teres major, teres minor, and triceps brachii	scapula	1963.3	26.9	---	467.9	10.2	---
		humerus	5273.1	72.3	---	4094.4	89.3	---
		radius-ulna	58.0	0.8	---	20.5	0.4	---
		total	7294.4	---	39.9	4582.8	---	39.5

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
distal thoracic limb	abductor pollicis longus	radius-ulna	35.4	100.0	0.2	18.0	100.0	0.2
	common and medial digital extensor	humerus	37.0	14.0	---	15.5	12.7	---
		radius-ulna	226.8	86.0	---	106.3	87.3	---
		total	263.8	---	1.4	121.8	100.0	1.1
	lateral digital extensor	radius-ulna	141.8	100.0	0.8	85.1	100.0	0.7
	extensor carpi radialis	humerus	354.4	47.2	---	226.8	57.1	---
		radius-ulna	396.9	52.8	---	170.1	42.9	---
		total	751.3	---	4.1	396.9	---	3.4
	ulnaris lateralis	humerus	0.3	0.1	---	trace	0.0	---
		radius-ulna	333.1	99.9	---	241.0	100.0	---
		total	333.4	---	1.8	241.0	---	2.1

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Appendix B. Table 1. (continued)

Limb Part	Muscle	Carcass Unit	SAM Muscle Weight (gm)	SAM Muscle Distribution Between Units	SAM Percent of Total Limb Muscle Weight	SAF Muscle Weight (gm)	SAF Muscle Distribution Between Units	SAF Percent of Total Limb Muscle Weight
distal thoracic limb	deep digital flexor	humerus	4.5	0.6	---	0.0	0.0	---
		radius-ulna	788.3	99.4	---	417.5	100.0	---
		total	792.8	---	4.3	417.5	---	3.6
	flexor carpi radialis	humerus	9.5	13.0	---	2.3	4.4	---
		radius-ulna	63.8	87.0	---	49.6	95.6	---
		total	73.3	---	0.4	51.9	---	0.4
	superficial digital flexor	humerus	3.3	0.9	---	2.5	1.0	---
		radius-ulna	354.4	99.1	---	255.2	99.0	---
		total	357.7	---	2.0	257.7	---	2.2
	flexor carpi ulnaris	humerus	1.8	1.0	---	1.0	0.8	---
		radius-ulna	177.2	99.0	---	120.5	99.2	---
		total	179.0	---	1.0	121.5	---	1.0
	pronator teres	radius-ulna	3.7	100.0	0.0	1.7	100.0	0.0

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Appendix B. Table 2. Weights of Axial Muscles in the Half Carcasses of SAM and SAF

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
rectus abdominis	back ribs and vertebrae	24.8	2.7		0.0	0.0	
	lumbar vertebrae	907.2	97.3		822.2	100.0	
	total	**932.0**	**1.5**	**average**	**822.2**	**1.9**	**average**
transverse abdominis	back ribs and vertebrae	7.1	0.7		21.3	2.4	
	lumbar vertebrae	156.0	15.4		177.2	19.8	
	sternebrae	850.5	83.9		694.6	77.8	
	total	**1013.6**	**1.6**	**average**	**893.1**	**2.1**	**right side**
external abdominal oblique	front ribs and vertebrae	99.2	3.2		78.0	3.7	
	back ribs and vertebrae	1148.2	37.0		864.7	41.1	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
external abdominal oblique (continued)	lumbar vertebrae	496.1	16.0		404.0	19.2	
	sacrum-pelvis	99.2	3.2		28.4	1.3	
	sternebrae	1261.6	40.6		730.0	34.7	
	total	**3104.3**	**4.9**	**left side**	**2105.1**	**4.9**	**right side**
internal abdominal oblique	back ribs and vertebrae	28.4	1.6		21.3	1.6	
	lumbar vertebrae	1757.7	97.1		1282.8	98.4	
	sacrum-pelvis	24.5	1.4		0.0	0.0	
	total	**1810.6**	**2.9**	**left side**	**1304.1**	**3.0**	**right side**
brachio-cephalicus	cervical vertebrae	722.9	59.3		581.2	56.9	
	humerus	496.1	40.7		439.4	43.1	
	total	**1219.0**	**1.9**	**right side**	**1020.6**	**2.4**	**right side**

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
coccygeus	sacrum-pelvis	**57.4**	**0.1**	**complete**	**87.4**	**0.2**	**complete**
cutaneus trunci	front ribs and vertebrae	194.9	12.5		131.1	12.4	
	back ribs and vertebrae	443.0	28.4		258.7	24.4	
	lumbar vertebrae	510.3	32.7		494.8	46.8	
	sternebrae	411.1	26.4		173.7	16.4	
	total	**1559.3**	**2.5**	**average**	**1058.3**	**2.5**	**average**
diaphragm	back ribs and vertebrae	676.9	46.8		492.6	45.9	
	lumbar vertebrae	311.9	21.6		379.2	35.3	
	sternebrae	457.2	31.6		202.0	18.8	
	total	**1446.0**	**2.3**	**average**	**1073.8**	**2.5**	**average**

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
iliocostalis	cervical vertebrae	0.0	0.0		24.8	4.2	
	front ribs and vertebrae	655.6	55.1		283.5	48.1	
	back ribs and vertebrae	485.5	40.8		248.1	42.1	
	lumbar vertebrae	49.6	4.2		32.5	5.5	
	total	**1190.7**	**1.9**	**average**	**588.9**	**1.4**	**average**
latissimus dorsi	front ribs and vertebrae	1038.4	46.1		949.7	44.8	
	back ribs and vertebrae	1208.4	53.6		1105.7	52.1	
	scapula	7.1	0.3		56.7	2.7	
	humerus	0.0	0.0		8.3	0.4	
	total	**2253.9**	**3.6**	**average**	**2120.4**	**4.9**	**left side**

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
levator ani	sacrum-pelvis	**24.0**	**0.1**	**left side**	**28.6**	**0.1**	**right side**
longissimus	cervical vertebrae	1169.5	14.6		800.9	15.0	
	front ribs and vertebrae	1367.9	17.1		992.3	18.6	
	back ribs and vertebrae	2764.1	34.6		1764.8	33.1	
	lumbar vertebrae	2572.8	32.2		1708.1	32.0	
	sacrum-pelvis	120.5	1.5		70.9	1.3	
	total	**7994.8**	**12.7**	**left side**	**5337.0**	**12.4**	**right side**
multifidus	cervical vertebrae	382.7	19.7		241.0	17.2	
	front ribs and vertebrae	588.3	30.3		411.0	29.3	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
multifidus (continued)	back ribs and vertebrae	439.4	22.6		248.1	17.7	
	lumbar vertebrae[a]	460.7	23.7		418.2	29.8	
	sacrum-pelvis	70.9	3.7		85.1	6.1	
	total	**1942.0**	**3.1**	**left side**	**1403.4**	**3.3**	**right side**
omohyoideus	cervical vertebrae	**81.6**	**0.1**	**average**	**35.4**	**0.1**	**left side**
omotransversarius	cervical vertebrae	**453.6**	**0.7**	**left side**	**241.0**	**0.6**	**average**
ascending (deep) pectoral	front ribs and vertebrae	1428.1	42.9		121.9	38.4	
	sternebrae	1779.0	53.4		1378.6	43.4	
	scapula	42.6	1.3		78.0	2.5	
	humerus	34.1	1.0		418.2	13.2	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
ascending (deep)	radius-ulna	46.1	1.4		81.5	2.6	
	total	**3329.9**	**5.3**	**average**	**3175.4**	**7.4**	**average**
descending (superficial) pectoral	front ribs and vertebrae	209.1	13.9		0.0	0.0	
	sternebrae	1286.5	85.6		751.3	82.8	
	humerus	7.4	0.5		156.0	17.2	
	total	**1503.0**	**2.4**	**average**	**907.3**	**2.1**	**average**
rhomboideus and splenius	cervical vertebrae	2640.2	63.8		666.3	39.7	
	front ribs and vertebrae	1492.0	36.0		999.4	59.5	
	scapula	7.1	0.2		14.2	0.8	
	total	**4139.3**	**6.6**	**average**	**1679.9**	**3.9**	**average**
sacrococcygeus	sacrum-pelvis	**42.5**	**0.1**	**complete**	**35.1**	**0.1**	**complete**

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
dorsal and medial scalenus	cervical vertebrae	521.0	76.2		400.4	77.9	
	front ribs and vertebrae	163.0	23.8		113.4	22.1	
	total	**684.0**	**1.1**	**average**	**513.8**	**1.2**	**average**
semispinalis capitis	cervical vertebrae	1492.0	81.4		854.1	83.1	
	front ribs and vertebrae	340.2	18.6		173.7	16.9	
	total	**1832.2**	**2.9**	**average**	**1027.8**	**2.4**	**average**
serratus dorsalis caudalis	back ribs and vertebrae	**35.5**	**0.1**	**average**	**35.5**	**0.1**	**average**
serratus dorsalis cranialis	front ribs and vertebrae	60.3	80.9		39.0	52.3	
	back ribs and vertebrae	14.2	19.1		35.0	47.0	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
serratus dorsalis cranialis (cont.)	**total**	**74.5**	**0.1**	**average**	**74.5**	**0.2**	**average**
serratus ventralis cervicalis and serratus ventralis thoracis	cervical vertebrae	988.7	13.6		170.1	3.7	
	front ribs and vertebrae	5875.6	80.8		3976.1	87.3	
	back ribs and vertebrae	354.4	4.9		290.6	6.4	
	sternebrae	24.8	0.3		88.6	1.9	
	scapula	24.8	0.3		28.4	0.6	
	total	**7268.3**	**11.6**	**average**	**4553.8**	**10.5**	**average**
spinalis et semispinalis and semispinalis cervicis	cervical vertebrae	301.2	11.4		379.2	15.2	
	front ribs and vertebrae	2069.5	78.1		1690.5	67.6	
	back ribs	280.0	10.6		432.3	17.3	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
spinalis et semi-spinalis and semispinalis cervicis (cont.)	lumbar vertebrae[b]	0.0	0.0		0.0	0.0	
	total	**2650.7**	**4.2**	**average**	**2502.0**	**5.8**	**average**
sterno-cephalicus	cervical vertebrae	**847.0**	**1.3**	**average**	**538.7**	**1.2**	**left side**
sternothyro-hyoideus	cervical vertebrae	**120.5**	**0.2**	**average**	**113.4**	**0.3**	**left side**
subclavius	cervical vertebrae	**74.4**	**0.1**	**average**	**28.4**	**0.1**	**left side**
other tail muscles	sacrum-pelvis	56.7	17.8		16.0	6.1	
	tail	262.2	82.2		248.1	93.9	
	total	**318.9**	**0.5**	**complete**	**264.1**	**0.6**	**complete**
transverse thoracic	sternebrae	**262.3**	**0.4**	**average**	**152.4**	**0.4**	**average**
rectus thoracis	front ribs and vertebrae	95.7	77.1		67.4	65.6	
	sternebrae	28.4	22.9		35.4	34.4	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
rectus thoracis (cont.)	**total**	**124.1**	**0.2**	**average**	**102.8**	**0.2**	**average**
trapezius	cervical vertebrae	92.1	8.3		85.1	9.6	
	front ribs and vertebrae	885.9	79.6		666.2	75.2	
	back ribs and vertebrae	134.7	12.1		134.7	15.2	
	total	**1112.7**	**1.8**	**left side**	**886.0**	**2.1**	**left side**
muscle group 1[d]	cervical vertebrae	4022.2	88.9		2076.7	87.2	
	front ribs and vertebrae	503.2	11.1		304.8	12.8	
	total	**4525.4**	**3.8**	**left side**	**2381.5**	**2.8**	**average**
muscle group 2[e]	front ribs and vertebrae	1644.3	31.5		1010.0	30.4	

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Appendix B. Table 2. (continued)

Muscle or Muscle Group	Carcass Unit	SAM Muscle Weight (grams)	SAM Percent of Carcass Unit Total or Percent of Axial Unit Total	SAM Carcass Unit Computation	SAF Muscle Weight (grams)	SAF Percent of Carcass Unit Total or Percent of Axial Unit Total	SAF Carcass Unit Computation
muscle group 2	back ribs and vertebrae	2927.2	56.1		1881.8	56.7	
	sternebrae	645.0	12.4		428.8	12.9	
	total	**5216.5**	**4.4**	**left side**	**3320.6**	**3.9**	**average**
muscle group 3[f]	back ribs and vertebrae	67.3	1.8		14.2	0.5	
	lumbar vertebrae	2027.1	55.5		1531.0	55.5	
	sacrum-pelvis	1428.2	39.1		1173.0	42.5	
	femur	127.6	3.5		39.0	1.4	
	total	**3650.2**	**5.8**	**average**	**2757.2**	**6.4**	**average**
axial total		62894.7			43169.5		

[a] Weight of multifidus also includes weight of spinalis et semispinalis for this unit.

[b] These muscles were collected with the multifidus for the lumbar vertebrae units.

Appendix B. Table 2. (continued)

[c] Muscles of this group in the lumbar vertebrae unit were collected with the psoas muscles in muscle group 2.

[d] Muscle group 1 includes: intertransversari cervicis, longus colli, obliquus capitis caudalis, rectus capitis, longus capitis.

[e] Muscle group 2 includes: *intertransversari thoracis, external* and internal intercostals, levator costarum.

[f] Muscle group 3 includes: psoas major, psoas minor, intertransversari lumborum, quadratus lumborum and iliacus.

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APPENDIX C

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ADDITIONAL MODEL EVALUATION AND PRESENTATION

The tables in Appendix C are all concerned with modeling carcass unit utility. Tables 1 through 9 present the single class models for assorted carcass products, including some individual products such as protein (Table 2) and some combined carcass resources such as total fat (Table 6). These single class model tables include calorie yields (Part A), standardized model values (Part B) and the modified, standardized model values (Part C). Tables 10 through 18 present the averaged utility models for the same products and combinations of products as in Tables 1 through 9. These each represent standardization and modification for riders of averages of standardized model values presented in Part B of Tables 1 through 9. Tables 19 through 26 present the mixed class models (in these cases, based upon sex) in which the carcass unit value of SAM and FAF are each standardized with respect to the unit from either animal that has the maximum value. The calorie yield data for each bison with which these models are constructed are presented in Appendix D.

Tables 27 through 30 represent continuations of the evaluations of the relationships between averaged and single class models, the relationship of these differences to age, sex, and condition differences in product distributions, and the importance of recovery strategy type to determining whether poor model fit to archaeological assemblage composition is a factor in individual deviations of carcass units from their expected proportional frequencies at the site analyzed, as presented for the total products (TP) models in Chapter 8.

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Appendix C. Table 1. Single Class, Gross Weight Models (MJ-MUI and FUI)

Part A. Model MJ-MUI (gm weight production)

Anatomical Unit	Gross Weight Minus Dry Bone Weight			
	FYM	SAM	SAF	FAF
SKWOT	8279.4	17988.5	12104.2	12870.4
ATLAS-AXIS[a]	2394.2	7456.8	3863.9	5278.6
C3C7[a]	10448.9	31303.5	16306.5	22273.7
THOR	14299.8	32218.8	24330.4	25569.4
LUMB	12704.2	27552.7	25701.7	25662.3
SPEL	10444.6	23393.1	19330.1	17458.6
CAUD	274.8	484.1	558.2	544.5
RIBS	17338.7	43462.9	31307.3	35803.9
STER	10871.0	20549.8	14927.3	18799.8
SCAP	7948.2	19809.6	11320.5	13235.5
HUM	8577.1	19259.8	14696.5	13300.7
RUL	3908.6	7511.7	4942.0	5140.4
CARP + MTC	1192.1	2104.3	1243.5	1342.0
APHA	583.5	1170.0	707.0	745.2
FEM	33160.6	64750.6	51765.4	51641.6
TIB + TARS	6723.1	11010.7	7153.0	8954.1
MTT	937.4	1380.2	866.8	1027.5
PPHA	602.1	1003.5	601.0	631.8

[a] The values for these units are estimated subdivisions of the larger cervical unit, based upon the following proportions: ATLAS + AXIS = 20 % CERV and C3C7 = 80 % CERV.

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Appendix C. Table 1. (continued)

Anatomical Unit	Part B. (S)MJ-MUI				Part C. (S)FUI			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	25.0	27.8	23.4	24.9	5.0	7.4	7.6	6.4
ATLAS	7.2	11.5	7.5	10.2	7.2	11.5	7.5	10.2
AXIS	7.2	11.5	7.5	10.2	7.2	11.5	7.5	10.2
C3C7	31.5	48.3	31.5	43.1	31.5	48.3	31.5	43.1
THOR	43.1	49.8	47.0	49.5	43.1	49.8	47.0	49.5
LUMB	38.3	42.6	49.7	49.7	38.3	42.6	49.7	49.7
SPEL	31.5	36.1	37.3	33.8	31.5	36.1	37.3	33.8
CAUD	0.8	0.7	1.1	1.1	0.8	0.7	1.1	1.1
RIBS	52.3	67.1	60.5	69.3	52.3	67.1	60.5	69.3
STER	32.8	31.7	28.8	36.4	32.8	31.7	28.8	36.4
SCAP	24.0	30.6	21.9	25.6	25.0	30.6	25.2	25.7
PHUM	25.9	29.7	28.4	25.8	25.9	30.6	28.4	25.8
DHUM	25.9	29.7	28.4	25.8	25.9	30.2	28.4	25.8
PRUL	11.8	11.6	9.5	10.0	18.9	20.9	19.0	17.9
DRUL	11.8	11.6	9.5	10.0	15.4	16.3	14.3	14.0
CARP	3.6	3.2	2.4	2.6	9.5	9.8	8.4	8.3
PMTC	3.6	3.2	2.4	2.6	6.6	6.5	5.4	5.5
DMTC	3.6	3.2	2.4	2.6	5.1	4.9	3.9	4.1
APHA	1.8	1.8	1.4	1.4	3.5	3.4	2.7	2.8
PFEM	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
DFEM	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
PTIB	20.3	17.0	13.8	17.3	60.2	58.5	56.9	58.7

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Appendix C. Table 1. (continued)

Anatomical Unit	Part B. (S)MJ-MUI				Part C. (S)FUI			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	20.3	17.0	13.8	17.3	40.3	37.8	35.4	38.0
TARS	20.3	17.0	13.8	17.3	30.3	27.4	24.6	27.7
PMTT	2.8	2.1	1.7	2.0	16.6	14.8	13.2	14.9
DMTT	2.8	2.1	1.7	2.0	9.7	8.5	7.5	8.5
PPHA	1.8	1.5	1.2	1.2	5.8	5.0	4.4	4.9

Note: (S)MUI values calculated from data in Appendix C, Table 1, Part A, except for the head (SKWOT). Binford (1978) reduced the value of the skull by half in order to account for the large amount of nonedible material included in the weight. Here I used the proportional value based upon caloric yield.

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Appendix C. Table 2. Single Class, Protein (PRO) Model

Part A. Model PRO (kcal production)

Anatomical Unit	Protein + Ash (PRO)			
	FYM	SAM	SAF	FAF
SKWOT	671.2	1,858.8	1,453.6[a]	1,202.4
ATLAS[b]	408.4	1,208.8	597.2	982.8
AXIS[b]	499.2	1,477.2	729.6	1,201.2
C3C7[b]	3,629.6	10,744.4	5,306.8	8,737.2
THOR	4,648.8	10,134.4	7,152.0	7,336.4
LUMB	4,318.8	8,824.4	7,188.0	7,419.6
SPEL	3,823.6	7,922.0	6,541.6	5,422.4
CAUD	72.4	120.4	114.8	115.2
RIBS	6,639.2	16,749.2	11,260.4	12,580.8
STER	3,554.8	6,208.8	4,166.4	5,406.0
SCAP	3,395.2	7,622.8	4,301.6	5,113.6
PHUM	1,524.8	3,775.8	2,849.0	2,429.4
DHUM	1,524.8	3,775.8	2,849.0	2,429.4
PRUL	699.4	1,247.6	848.8	860.0
DRUL	699.4	1,247.6	848.8	860.0
CARP	0.0	0.0	0.0	0.0
PMTC	0.0	0.0	0.0	0.0
DMTC	0.0	0.0	0.0	0.0
APHA	0.0	0.0	0.0	0.0
PFEM	7,451.2	13,598.2	11,405.0	10,585.6
DFEM	7,451.2	13,598.2	11,405.0	10,585.6

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Appendix C. Table 2. (continued)

Part A. Model PRO (kcal production)

Anatomical Unit	Protein + Ash (PRO)			
	FYM	SAM	SAF	FAF
PTIB	844.2	1,732.6	1,150.0	1,551.4
DTIB	844.2	1,732.6	1,150.0	1,551.4
TARS	0.0	0.0	0.0	0.0
PMTT	5.2	6.2	5.2	6.0
DMTT	5.2	6.2	5.2	6.0
PPHA	0.0	0.0	0.0	0.0

[a] calorie yield estimate

[b] The values for these units are estimated subdivisions of the larger cervical unit, based upon the following proportions: ATLAS = 9 % CERV, AXIS = 11 % CERV, and C3C7 = 80 % CERV.

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Appendix C. Table 2. (continued)

Anatomical Unit	Part B. (S)PRO				Part C. (S)MPRO			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	9.0	11.1	12.7	9.6	9.0	11.1	12.7	9.6
ATLAS	5.5	7.2	5.2	7.8	5.5	7.2	5.2	7.8
AXIS	6.7	8.8	6.4	9.5	6.7	8.8	6.4	9.5
C3C7	48.7	64.1	46.5	69.4	48.7	64.1	46.5	69.4
THOR	62.4	60.5	62.7	58.3	62.4	60.5	62.7	58.3
LUMB	58.0	52.7	63.0	59.0	58.0	52.7	63.0	59.0
SPEL	51.3	47.3	57.4	43.1	51.3	47.3	57.4	43.1
CAUD	1.0	0.7	1.0	0.9	1.0	0.7	1.0	0.9
RIBS	89.1	100.0	98.7	100.0	89.1	100.0	98.7	100.0
STER	47.7	37.1	36.5	43.0	47.7	37.1	36.5	43.0
SCAP	45.6	45.5	37.7	40.6	45.6	45.5	37.7	40.6
PHUM	20.5	22.5	25.0	19.3	45.6	45.5	37.7	40.6
DHUM	20.5	22.5	25.0	19.3	33.1	34.0	31.4	30.0
PRUL	9.4	7.4	7.4	6.8	21.2	20.7	19.4	18.4
DRUL	9.4	7.4	7.4	6.8	15.3	14.1	13.4	12.6
CARP	0.0	0.0	0.0	0.0	7.7	7.0	6.7	6.3
PMTC	0.0	0.0	0.0	0.0	3.8	3.5	3.3	3.1
DMTC	0.0	0.0	0.0	0.0	1.9	1.8	1.8	1.6
APHA	0.0	0.0	0.0	0.0	1.0	0.9	0.8	0.8
PFEM	100.0	81.2	100.0	84.1	100.0	81.2	100.0	84.1
DFEM	100.0	81.2	100.0	84.1	100.0	81.2	100.0	84.1
PTIB	11.3	10.3	10.1	12.3	55.7	45.8	55.1	48.2

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Appendix C. Table 2. (continued)

Anatomical Unit	Part B. (S)PRO				Part C. (S)MPRO			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	11.3	10.3	10.1	12.3	33.5	28.0	32.6	30.3
TARS	0.0	0.0	0.0	0.0	16.8	14.0	16.3	15.1
PMTT	0.1	0.0	0.0	0.0	8.4	7.0	8.1	7.6
DMTT	0.1	0.0	0.0	0.0	4.3	3.5	4.1	3.8
PPHA	0.0	0.0	0.0	0.0	2.1	1.8	2.0	1.9

Note: (S)PRO values calculated from data in Appendix C, Table 2, Part A.

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Appendix C. Table 3. Single Class, Marrow Fat (MAR) Model

Part A. Model MAR (kcal production)

Anatomical Unit	Marrow Fat (MAR)			
	FYM	SAM	SAF	FAF
SKWOT	----	----	----	----
ATLAS	0.0	0.0	0.0	0.0
AXIS	0.0	0.0	0.0	0.0
C3C7	0.0	0.0	0.0	0.0
THOR	0.0	0.0	0.0	0.0
LUMB	0.0	0.0	0.0	0.0
SPEL	51.3	46.8	30.6	51.3
CAUD	0.0	0.0	0.0	0.0
RIBS	0.0	0.0	0.0	0.0
STER	0.0	0.0	0.0	0.0
SCAP	3.6	40.5	25.2	0.0
PHUM	416.7	818.1	403.2	391.5
DHUM	295.2	519.3	534.6	421.2
PRUL	377.1	464.4	574.2	431.1
DRUL	210.6	309.6	199.8	190.8
CARP	0.0	0.0	0.0	0.0
PMTC	112.5	157.5	164.7	175.5
DMTC	48.6	72.9	37.8	39.6
APHA	18.0	16.2	10.8	17.1
PFEM	414.9	869.4	782.1	657.0
DFEM	297.9	519.3	358.2	308.7

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Appendix C. Table 3. (continued)

Part A. Model MAR (kcal production)

Anatomical Unit	Marrow Fat (MAR)			
	FYM	SAM	SAF	FAF
PTIB	596.7	905.4	671.4	615.6
DTIB	405.0	523.8	534.6	445.5
TARS	0.0	0.0	0.0	0.0
PMTT	143.1	174.6	206.1	189.0
DMTT	50.4	66.6	59.4	90.0
PPHA	28.8	59.4	36.0	42.3

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Appendix C. Table 3. (continued)

Anatomical Unit	Part B. (S)MAR				Part C. (S)MMAR			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---	---	---	---	---
ATLAS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AXIS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C3C7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
THOR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LUMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SPEL	8.6	5.2	3.9	7.8	8.6	5.2	3.9	7.8
CAUD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
RIBS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
STER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCAP	0.6	4.5	3.2	0.0	35.2	47.5	32.2	31.1
PHUM	69.8	90.4	51.6	59.6	69.8	90.4	61.3	62.2
DHUM	49.5	57.4	68.4	64.1	66.5	73.9	70.9	64.9
PRUL	63.2	51.3	73.4	65.6	64.9	62.6	73.4	65.6
DRUL	35.3	34.2	25.5	29.0	50.1	48.4	49.5	47.3
CARP	0.0	0.0	0.0	0.0	34.5	32.9	35.3	37.0
PMTC	18.9	17.4	21.1	26.7	26.7	25.2	28.2	31.9
DMTC	8.1	8.1	4.8	6.0	17.4	16.6	16.5	18.9
APHA	3.0	1.8	1.4	2.6	10.2	9.2	8.9	10.8
PFEM	69.5	96.0	100.0	100.0	77.1	97.0	100.0	100.0
DFEM	49.9	57.4	45.8	47.0	84.8	98.0	92.9	96.9
PTIB	100.0	100.0	85.8	93.7	100.0	100.0	89.4	95.3

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Appendix C. Table 3. (continued)

Anatomical Unit	Part B. (S)MAR				Part C. (S)MMAR			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	67.9	57.9	68.4	67.8	84.0	79.0	78.9	81.5
TARS	0.0	0.0	0.0	0.0	54.0	49.1	52.6	55.2
PMTT	24.0	19.3	26.4	28.8	39.0	34.2	39.5	42.0
DMTT	8.4	7.4	7.6	13.7	23.7	20.8	23.6	27.8
PPHA	4.8	6.6	4.6	6.4	14.2	13.7	14.1	17.1

Note: (S)MAR values calculated from data in Appendix C, Table 3, Part A.

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Appendix C. Table 4. Single Class, White Grease Fat Model (WG)

Part A. Model WG (kcal production)

Anatomical Unit	White Bone Grease Fat (WG)			
	FYM	SAM	SAF	FAF
SCAP	36.9	79.2	182.7	190.8
PHUM	138.6	662.4	747.0	778.5
DHUM	79.2	226.8	306.9	278.1
PRUL	105.3	89.1	301.5	183.6
DRUL	178.2	264.6	517.5	375.3
CARP	133.2	48.6	96.3	30.6
PMTC	17.1	15.3	45.0	45.0
DMTC	152.1	86.4	190.8	162.0
APHA	131.4	88.2	255.6	281.7
PFEM	133.2	449.1	596.7	452.7
DFEM	343.8	703.8	1316.7	747.9
PTIB	135.9	353.7	691.2	238.5
DTIB	119.7	126.0	175.5	189.9
TARS	279.0	230.4	332.1	195.3
PMTT	11.7	19.8	48.6	30.6
DMTT	158.4	144.0	244.8	189.0
PPHA	168.3	99.0	165.6	232.2

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Appendix C. Table 4. (continued)

Anatomical Unit	Part B. (S)WG				Part C. (S)MWG			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SCAP	10.7	11.3	13.9	24.5	26.2	52.7	35.3	62.3
PHUM	40.3	94.1	56.7	100.0	41.7	94.1	56.7	100.0
DHUM	23.0	32.2	23.3	35.7	43.2	65.9	48.0	74.1
PRUL	30.6	12.7	22.9	23.6	46.1	51.7	43.7	61.2
DRUL	51.8	37.6	39.3	48.2	51.8	44.7	41.5	54.7
CARP	38.7	6.9	7.3	3.9	48.0	28.6	30.4	45.4
PMTC	5.0	2.2	3.4	5.8	46.1	20.5	24.9	40.8
DMTC	44.2	12.3	14.5	20.1	45.2	16.5	22.2	38.5
APHA	38.2	12.5	19.4	36.2	41.7	14.5	20.8	37.4
PFEM	38.7	63.8	45.3	58.2	100.0	100.0	100.0	96.1
DFEM	100.0	100.0	100.0	96.1	100.0	100.0	100.0	96.1
PTIB	39.5	50.3	52.5	30.6	90.6	75.2	76.3	63.4
DTIB	34.8	17.9	13.3	24.4	85.9	53.9	50.7	46.6
TARS	81.2	32.7	25.2	25.1	83.6	43.3	38.0	38.2
PMTT	3.4	2.8	3.7	3.9	66.3	31.9	28.3	34.0
DMTT	46.1	20.5	18.6	24.3	57.6	26.2	23.4	31.9
PPHA	49.0	14.1	12.6	29.8	53.3	20.2	18.0	30.8

Note: (S)WG values calculated from data in Appendix C, Table 4, Part A.

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Appendix C. Table 5. Single Class, Yellow Grease Fat (YG) Model

Part A. Model YG (kcal production)

Anatomical Unit	Yellow Bone Grease Fat (YG)			
	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---
ATLAS	12.6	3.6	18.0	27.0
AXIS	5.4	6.3	27.0	12.6
C3C7	8.1	3.6	35.1	98.1
THOR	34.2	135.9	334.8	311.4
LUMB	150.3	205.2	219.6	216.9
SPEL	208.8	954.9	1291.5	795.6
CAUD	19.8	5.4	61.2	42.3
RIBS	50.4	326.7	689.4	812.7
STER	1.8	44.1	7.2	89.1

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Appendix C. Table 5. (continued)

Part B. Standardized Model

Anatomical Unit	Model (S)YG			
	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---
ATLAS	6.0	0.4	1.4	3.3
AXIS	2.6	0.7	2.1	1.6
C3C7	3.9	0.4	2.7	12.1
THOR	16.4	14.2	25.9	38.3
LUMB	72.0	21.5	17.0	26.7
SPEL	100.0	100.0	100.0	97.9
CAUD	9.5	0.6	4.7	5.2
RIBS	24.1	34.2	53.4	100.0
STER	0.9	4.6	0.6	11.0

Note: (S)YG values calculated from data in Appendix C, Table 5, Part A.

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Appendix C. Table 6. Single Class, Total Fat (TF) Model

Part A. Model TF (kcal production)

Anatomical Unit	Total Fat (TF)			
	FYM	SAM	SAF	FAF
SKWOT	850.1	2147.9	2384.8	2697.5
ATLAS[a]	270.0	852.8	813.2	886.5
AXIS[a]	320.6	1044.2	999.5	1063.4
C3C7[a]	2300.4	7554.2	7108.7	7742.3
THOR	5396.0	11544.5	17222.9	14212.4
LUMB	5437.8	10560.4	16192.8	15976.4
SPEL	2907.0	6376.3	9237.6	7594.2
CAUD	50.0	102.6	404.3	423.7
RIBS	4118.2	12190.1	16824.8	13204.1
STER	2826.9	7159.1	9123.3	9714.8
SCAP	947.7	1954.4	1793.7	2940.3
PHUM	937.8	2163.2	2879.0	2165.9
DHUM	756.9	1428.8	2570.3	1695.2
PRUL	592.3	675.0	989.5	845.5
DRUL	498.7	695.7	831.1	796.9
CARP	133.2	48.6	96.3	30.6
PMTC	137.1	172.8	210.1	264.7
DMTC	208.2	159.3	229.0	245.8
APHA	166.3	122.6	306.2	429.8
PFEM	1569.5	5063.5	5920.2	6500.7
DFEM	1663.1	4968.1	6216.3	6447.6

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Appendix C. Table 6. (continued)

Part A. Model TF (kcal production)

Anatomical Unit	Total Fat (TF)			
	FYM	SAM	SAF	FAF
PTIB	795.1	1516.1	1611.5	1577.7
DTIB	587.2	907.4	959.0	1359.0
TARS	300.6	297.9	367.2	354.6
PMTT	211.3	198.4	257.3	322.9
DMTT	265.3	214.6	306.8	382.3
PPHA	209.9	169.2	219.2	366.3

[a] The values for these units are estimated subdivisions of the larger cervical unit, based upon the following proportions: ATLAS = 9 % CERV, AXIS = 11 % CERV, and C3C7 = 80 % CERV.

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Appendix C. Table 6. (continued)

Anatomical Unit	Part B. (S)TF				Part C. (S)MTF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	15.6	17.6	13.8	16.9	15.6	17.6	13.8	16.9
ATLAS	5.0	7.0	4.7	5.5	5.0	7.0	4.7	5.5
AXIS	5.9	8.6	5.8	6.7	5.9	8.6	5.8	6.7
C3C7	42.3	62.0	41.3	48.5	42.3	62.0	41.3	48.5
THOR	99.2	94.7	100.0	89.0	99.2	94.7	100.0	89.0
LUMB	100.0	86.6	94.0	100.0	100.0	86.6	94.0	100.0
SPEL	53.5	52.3	53.6	47.5	53.5	52.3	53.6	47.5
CAUD	0.9	0.8	2.3	2.7	0.9	0.8	2.3	2.7
RIBS	75.7	100.0	97.7	82.6	75.7	100.0	97.7	82.6
STER	52.0	58.7	53.0	60.8	52.0	58.7	53.0	60.8
SCAP	17.4	16.0	10.4	18.4	17.4	16.9	13.6	18.4
PHUM	17.2	17.7	16.7	13.6	17.4	17.7	16.7	18.4
DHUM	13.9	11.7	14.9	10.6	15.7	14.7	15.8	14.5
PRUL	10.9	5.5	5.7	5.3	13.3	10.2	10.8	9.9
DRUL	9.2	5.7	4.8	5.0	11.2	8.0	7.8	7.5
CARP	2.5	0.4	0.6	0.2	7.5	4.7	4.8	5.1
PMTC	2.5	1.4	1.2	1.7	5.7	3.0	3.3	3.9
DMTC	3.8	1.3	1.3	1.5	4.7	2.2	2.5	3.3
APHA	3.1	1.0	1.8	2.7	3.9	1.6	2.2	3.0
PFEM	28.9	41.5	34.4	40.7	30.6	41.5	36.1	40.7
DFEM	30.6	40.8	36.1	40.4	30.6	41.2	36.1	40.6
PTIB	14.6	12.4	9.4	9.9	22.6	26.8	22.8	25.2

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Appendix C. Table 6. (continued)

Anatomical Unit	Part B. (S)TF				Part C. (S)MTF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	10.8	7.4	5.6	8.5	16.7	17.1	14.2	16.9
TARS	5.5	2.4	2.1	2.2	11.1	9.7	8.1	9.6
PMTT	3.9	1.6	1.5	2.0	8.0	5.8	5.0	6.0
DMTT	4.9	1.8	1.8	2.4	6.5	3.8	3.4	4.2
PPHA	3.9	1.4	1.3	2.3	5.2	2.6	2.3	3.3

Note: (S)TF values calculated from data in Appendix C, Table 6, Part A.

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Appendix C. Table 7. Single Class, Selected Fat (SF) Model

Part A. Model SF (kcal production)

Anatomical Unit	Selected Fat (SF)			
	FYM	SAM	SAF	FAF
SKWOT	549.5	1589.0	1609.9	2105.3
ATLAS[a]	201.6	393.8	491.9	483.3
AXIS[a]	236.9	483.5	606.2	570.2
C3C7[a]	1690.2	3474.5	4248.5	4154.9
THOR	4390.7	7082.3	10045.4	8966.3
LUMB	5315.4	8173.6	12996.0	12252.2
SPEL	2560.5	4415.2	6924.6	5723.1
CAUD	34.7	72.9	325.1	299.5
RIBS	2100.4	3430.4	6731.3	6212.0
STER	1894.5	4843.4	6654.6	6268.7
SCAP	580.5	288.5	207.9	776.7
PHUM	904.0	1708.7	1805.3	1684.4
DHUM	723.1	974.3	1496.6	1213.7
PRUL	588.7	553.5	907.1	817.6
DRUL	495.1	574.2	748.7	769.0
CARP	133.2	48.6	96.3	30.6
PMTC	137.1	172.8	210.1	264.7
DMTC	208.2	159.3	229.0	245.8
APHA	166.3	122.6	306.2	429.8
PFEM	1489.8	3274.3	4262.8	4806.0
DFEM	1583.4	3178.9	4558.9	4752.9

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Appendix C. Table 7. (continued)

Part A. Model SF (kcal production)

Anatomical Unit	Selected Fat (SF)			
	FYM	SAM	SAF	FAF
PTIB	795.1	1437.0	1431.5	1302.7
DTIB	587.2	827.7	779.0	1084.0
TARS	300.6	297.9	367.2	354.6
PMTT	211.2	197.5	256.8	320.2
DMTT	265.2	213.7	306.3	379.6
PPHA	209.9	169.2	219.2	366.3

[a] The values for these units are estimated subdivisions of the larger cervical unit, based upon the following proportions: ATLAS = 9 % CERV, AXIS = 11 % CERV, and C3C7 = 80 % CERV.

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Appendix C. Table 7. (continued)

Anatomical Unit	Part B. (S)SF				Part C. (S)MSF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	10.3	19.4	12.4	17.2	10.3	19.4	12.4	17.2
ATLAS	3.8	4.8	3.8	3.9	3.8	4.8	3.8	3.9
AXIS	4.5	5.9	4.7	4.7	4.5	5.9	4.7	4.7
C3C7	31.8	42.5	32.7	33.9	31.8	42.5	32.7	33.9
THOR	82.6	86.6	77.3	73.2	82.6	86.6	77.3	73.2
LUMB	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
SPEL	48.2	54.0	53.3	46.7	48.2	54.0	53.3	46.7
CAUD	0.7	0.9	2.5	2.4	0.7	0.9	2.5	2.4
RIBS	39.5	42.0	51.8	50.7	39.5	42.0	51.8	50.7
STER	35.6	59.3	51.2	51.2	35.6	59.3	51.2	51.2
SCAP	10.9	3.5	1.6	6.3	14.0	12.2	7.8	10.0
PHUM	17.0	20.9	13.9	13.7	17.0	20.9	13.9	13.7
DHUM	13.6	11.9	11.5	9.9	15.3	16.4	12.7	11.8
PRUL	11.1	6.8	7.0	6.7	13.2	11.7	9.9	9.3
DRUL	9.3	7.0	5.8	6.3	11.3	9.4	7.8	7.8
CARP	2.5	0.6	0.7	0.3	7.6	5.7	5.1	5.6
PMTC	2.6	2.1	1.6	2.2	5.7	3.9	3.8	4.6
DMTC	3.9	1.9	1.8	2.0	4.8	3.0	3.1	4.0
APHA	3.1	1.5	2.4	3.5	4.0	2.2	2.7	3.8
PFEM	28.0	40.1	32.8	39.2	29.8	40.1	35.1	39.2
DFEM	29.8	38.9	35.1	38.8	29.8	39.5	35.1	39.0
PTIB	15.0	17.6	11.0	10.6	22.4	28.6	23.1	24.8

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Appendix C. Table 7. (continued)

Anatomical Unit	Part B. (S)SF				Part C. (S)MSF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	11.0	10.1	6.0	8.8	16.7	19.3	14.5	16.8
TARS	5.7	3.6	2.8	2.9	11.2	11.5	8.7	10.0
PMTT	4.0	2.4	2.0	2.6	8.1	7.0	5.5	6.5
DMTT	5.0	2.6	2.4	3.1	6.6	4.8	4.0	4.8
PPHA	3.9	2.1	1.7	3.0	5.3	3.5	2.8	3.9

Note: (S)SF values calculated from data in Appendix C, Table 7, Part A.

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Appendix C. Table 8. Single Class, Bone Grease Fat (GRE) Model

Part A. Model GRE (kcal production)

Anatomical Unit	Bone Grease Fat (GRE)			
	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---
ATLAS	12.6	3.6	18.0	27.0
AXIS	5.4	6.3	27.0	12.6
C3C7	8.1	3.6	35.1	98.1
THOR	34.2	135.9	334.8	311.4
LUMB	150.3	205.2	219.6	216.9
SPEL	208.8	954.9	1291.5	795.6
CAUD	19.8	5.4	61.2	42.3
RIBS	50.4	326.7	689.4	812.7
STER	1.8	44.1	7.2	89.1
SCAP	36.9	79.2	182.7	190.8
PHUM	138.6	662.4	747.0	778.5
DHUM	79.2	226.8	306.9	278.1
PRUL	105.3	89.1	301.5	183.6
DRUL	178.2	264.6	517.5	375.3
CARP	133.2	48.6	96.3	30.6
PMTC	17.1	15.3	45.0	45.0
DMTC	152.1	86.4	190.8	162.0
APHA	131.4	88.2	255.6	281.7
PFEM	133.2	449.1	596.7	452.7
DFEM	343.8	703.8	1316.7	747.9

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Appendix C. Table 8. (continued)

Part A. Model GRE (kcal production)

Anatomical Unit	Bone Grease Fat (GRE)			
	FYM	SAM	SAF	FAF
PTIB	135.9	353.7	691.2	238.5
DTIB	119.7	126.0	175.5	189.9
TARS	279.0	230.4	332.1	195.3
PMTT	11.7	19.8	48.6	30.6
DMTT	158.4	144.0	244.8	189.0
PPHA	168.3	99.0	165.6	232.2

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Appendix C. Table 8. (continued)

Anatomical Unit	Part B. (S)GRE				Part C. (S)MGRE			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---	---	---	---	---
ATLAS	3.7	0.4	1.4	3.3	3.7	0.4	1.4	3.3
AXIS	1.6	0.7	2.1	1.6	1.6	0.7	2.1	1.6
C3C7	2.4	0.4	2.7	12.1	2.4	0.4	2.7	12.1
THOR	9.9	14.2	25.4	38.3	9.9	14.2	25.4	38.3
LUMB	43.7	21.5	16.7	26.7	43.7	21.5	16.7	26.7
SPEL	60.7	100.0	98.1	97.9	60.7	100.0	98.1	97.9
CAUD	5.8	0.6	4.6	5.2	5.8	0.6	4.6	5.2
RIBS	14.7	34.2	52.4	100.0	14.7	34.2	52.4	100.0
STER	0.5	4.6	0.5	11.0	0.5	4.6	0.5	11.0
SCAP	10.7	8.3	13.9	23.5	26.2	38.9	35.3	59.7
PHUM	40.3	69.4	56.7	95.8	41.7	69.4	56.7	95.8
DHUM	23.0	23.8	23.3	34.2	43.2	48.6	48.0	71.0
PRUL	30.6	9.3	22.9	22.6	46.1	38.1	43.7	58.6
DRUL	51.8	27.7	39.3	46.2	51.8	32.9	41.5	52.4
CARP	38.7	5.1	7.3	3.8	48.0	21.1	30.4	43.6
PMTC	5.0	1.6	3.4	5.5	46.1	15.1	24.9	39.1
DMTC	44.2	9.0	14.5	19.9	45.2	12.2	22.2	36.9
APHA	38.2	9.2	19.4	34.7	41.7	10.7	20.8	35.8
PFEM	38.7	47.0	45.3	55.7	100.0	73.7	100.0	92.0
DFEM	100.0	73.7	100.0	92.0	100.0	73.7	100.0	92.0
PTIB	39.5	37.0	52.5	29.3	90.6	55.4	76.3	60.7

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Appendix C. Table 8. (continued)

Anatomical Unit	Part B. (S)GRE				Part C. (S)MGRE			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	34.8	13.2	13.3	23.4	85.9	39.7	50.7	44.6
TARS	81.2	24.1	25.2	24.0	83.6	31.9	38.0	36.6
PMTT	3.4	2.1	3.7	3.8	66.3	23.5	28.3	32.6
DMTT	46.1	15.1	18.6	23.3	57.6	19.3	23.4	30.6
PPHA	49.0	10.4	12.6	28.6	53.3	14.9	18.0	29.6

Note: (S)GRE values calculated from data in Appendix C, Table 8, Part A.

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Appendix C. Table 9. Single Class, Skeletal Fat (SKF) Model

Part A. Model SKF (kcal production)

Anatomical Unit	Skeletal Fat (SKF)			
	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---
ATLAS	12.6	3.6	18.0	27.0
AXIS	5.4	6.3	27.0	12.6
C3C7	8.1	3.6	35.1	98.1
THOR	34.2	135.9	334.8	311.4
LUMB	150.3	205.2	219.6	216.9
SPEL	260.1	1001.7	1322.1	846.9
CAUD	19.8	5.4	61.2	42.3
RIBS	50.4	326.7	689.4	812.7
STER	1.8	44.1	7.2	89.1
SCAP	40.5	119.7	207.9	190.8
PHUM	555.3	1480.5	1150.2	1170.0
DHUM	374.4	746.1	841.5	699.3
PRUL	482.4	553.5	875.7	614.7
DRUL	388.8	574.2	717.3	566.1
CARP	133.2	48.6	96.3	30.6
PMTC	129.6	172.8	209.7	220.5
DMTC	200.7	159.3	228.6	201.6
APHA	149.4	104.4	266.4	298.8
PFEM	548.1	1318.5	1378.8	1109.7
DFEM	641.7	1223.1	1674.9	1056.6

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Appendix C. Table 9. (continued)

Part A. Model SKF (kcal production)

Anatomical Unit	Skeletal Fat (SKF)			
	FYM	SAM	SAF	FAF
PTIB	732.6	1259.1	1362.6	854.1
DTIB	524.7	649.8	710.1	635.4
TARS	279.0	230.4	332.1	195.3
PMTT	154.8	194.4	254.7	219.6
DMTT	208.8	210.6	304.2	279.0
PPHA	197.1	158.4	201.6	274.5

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Appendix C. Table 9. (continued)

Anatomical Unit	Part B. (S)SKF				Part C. (S)MSKF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
SKWOT	---	---	---	---	---	---	---	---
ATLAS	1.7	0.2	1.1	2.3	1.7	0.2	1.1	2.3
AXIS	0.7	0.4	1.6	1.1	0.7	0.4	1.6	1.1
C3C7	1.1	0.2	2.1	8.4	1.1	0.2	2.1	8.4
THOR	4.7	9.2	20.0	26.6	4.7	9.2	20.0	26.6
LUMB	20.5	13.9	13.1	18.5	20.5	13.9	13.1	18.5
SPEL	35.5	67.7	78.9	72.4	35.5	67.7	78.9	72.4
CAUD	2.7	0.4	3.7	3.6	2.7	0.4	3.7	3.6
RIBS	6.9	22.1	41.2	69.5	6.9	22.1	41.2	69.5
STER	0.2	3.0	0.4	7.6	0.2	3.0	0.4	7.6
SCAP	5.5	8.1	12.4	16.3	40.7	54.1	40.6	58.2
PHUM	75.8	100.0	68.7	100.0	75.8	100.0	68.7	100.0
DHUM	51.1	50.4	50.2	59.8	70.8	75.2	60.5	79.9
PRUL	65.8	37.4	52.3	52.5	68.3	57.0	56.4	66.2
DRUL	53.1	38.8	42.8	48.4	60.7	47.9	49.6	57.3
CARP	18.2	3.3	5.7	2.6	44.1	29.8	32.8	41.4
PMTC	17.7	11.7	12.5	18.8	35.7	20.8	24.3	33.5
DMTC	27.4	10.8	13.6	17.2	31.6	15.8	20.1	29.5
APHA	20.4	7.1	15.9	25.5	26.0	11.4	18.0	27.5
PFEM	74.8	89.1	82.3	94.8	84.3	89.1	100.0	94.8
DFEM	87.6	82.6	100.0	90.3	93.8	87.1	100.0	92.6
PTIB	100.0	85.0	81.4	73.0	100.0	86.0	90.7	82.8

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Appendix C. Table 9. (continued)

Anatomical Unit	Part B. (S)SKF				Part C. (S)MSKF			
	FYM	SAM	SAF	FAF	FYM	SAM	SAF	FAF
DTIB	71.6	43.9	42.4	54.3	85.8	65.0	66.6	68.5
TARS	38.1	15.6	19.8	16.7	62.0	40.3	43.2	46.2
PMTT	21.1	13.1	15.2	18.7	45.2	27.2	30.7	35.0
DMTT	28.5	14.2	18.2	23.8	36.9	20.7	24.4	29.4
PPHA	26.9	10.7	12.0	23.5	31.9	15.7	18.2	26.4

Note: (S)SKF values calculated from data in Appendix C, Table 9, Part A.

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Appendix C. Table 10. Averaged Gross-Weight-Based Model ((S)AVGFUI)

Anatomical Unit	Average (S)MUI	Anatomical Unit	Model (S)AVGFUI	Anatomical Unit	Model (S)AVGFUI
SKWT[a]	9.4	SKWT	9.4	APHA	3.0
SKWOT[a]	6.6	SKWOT	6.6	PFEM	100.0
ATLAS-AXIS	9.1	ATLAS	9.1	DFEM	100.0
C3C7	38.6	AXIS	9.1	PTIB	58.6
THOR	47.4	C3C7	38.6	DTIB	37.9
LUMB	45.1	THOR	47.4	TARS	27.5
SPEL	34.7	LUMB	45.1	PMTT	14.8
CAUD	0.9	SPEL	34.7	DMTT	8.5
RIBS	62.3	CAUD	0.9	PPHA	5.0
STER	32.4	RIBS	62.3		
SCAP	25.5	STER	32.4		
HUM	27.5	SCAP	26.5		
RUL	10.7	PHUM	27.5		
CARP-MTC	3.0	DHUM	27.5		
APHA	1.6	PRUL	19.1		
FEM	100.0	DRUL	14.9		
TIB-TARS	17.1	CARP	9.0		
MTT	2.2	PMTC	6.0		
PPHA	1.4	DMTC	4.5		

[a] Product weight used rather than Binford's (1978) and Metcalfe and Jones's (1988) method of reducing the skull value by half. This does not include brain weight.

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Appendix C. Table 11. Averaged Protein Model ((S)MAVGPRO)

Anatomical Unit	Model (S)AVGPRO	Model (S)MAVGPRO	Anatomical Unit	Model (S)AVGPRO	Model (S)MAVGPRO
SKWOT	10.9	10.9	DRUL	8.0	14.3
ATLAS	6.6	6.6	CARP	0.0	7.1
AXIS	8.1	8.1	PMTC	0.0	3.6
C3C7	59.0	59.0	DMTC	0.0	1.8
THOR	62.9	62.9	APHA	0.0	0.9
LUMB	60.0	60.0	PFEM	94.1	94.1
SPEL	51.3	51.3	DFEM	94.1	94.1
CAUD	0.9	0.9	PTIB	11.3	52.7
RIBS	100.0	100.0	DTIB	11.3	32.0
STER	42.4	42.4	TARS	0.0	16.0
SCAP	43.7	43.7	PMTT	0.0	8.0
PHUM	22.5	43.7	DMTT	0.0	4.0
DHUM	22.5	33.1	PPHA	0.0	2.0
PRUL	8.0	20.6			

Note: (S)PRO data from Appendix C, Table 2, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGPRO.

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Appendix C. Table 12. Averaged Marrow Fat Model ((S)MAVGMAR)

Anatomical Unit	Model (S)AVGMAR	Model (S)MAVGMAR	Anatomical Unit	Model (S)AVGMAR	Model (S)MAVGMAR
SKWOT	0.0	0.0	DRUL	32.7	50.3
ATLAS	0.0	0.0	CARP	0.0	36.2
AXIS	0.0	0.0	PMTC	22.1	29.2
C3C7	0.0	0.0	DMTC	7.2	18.2
THOR	0.0	0.0	APHA	2.3	10.2
LUMB	0.0	0.0	PFEM	96.3	97.2
SPEL	6.7	6.7	DFEM	52.7	98.2
CAUD	0.0	0.0	PTIB	100.0	100.0
RIBS	0.0	0.0	DTIB	69.0	84.5
STER	0.0	0.0	TARS	0.0	55.2
SCAP	2.2	36.9	PMTT	25.9	40.6
PHUM	71.5	71.5	DMTT	9.8	25.2
DHUM	63.1	69.2	PPHA	5.9	15.5
PRUL	66.8	68.0			

Note: (S)MAR data from Appendix C, Table 3, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGMAR.

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Appendix C. Table 13. Averaged White Grease Fat Model ((S)MAVGWG)

Anatomical Unit	Model (S)AVGWG	Model (S)MAVGWG
SCAP	15.3	44.4
PHUM	73.5	73.5
DHUM	28.9	59.1
PRUL	22.7	51.8
DRUL	44.6	48.2
CARP	14.3	37.6
PMTC	4.1	32.2
DMTC	23.0	29.6
APHA	26.9	28.2
PFEM	52.0	100.0
DFEM	100.0	100.0
PTIB	43.6	71.8
DTIB	22.8	56.7
TARS	41.5	49.1
PMTT	3.5	38.4
DMTT	27.7	33.0
PPHA	26.7	29.9

Note: (S)WG data from Appendix C, Table 4, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGWG.

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Appendix C. Table 14. Averaged Yellow Grease Fat Model ((S)AVGYG)

Anatomical Unit	Model (S)AVGYG
SKWOT	---
ATLAS	2.8
AXIS	1.8
C3C7	4.8
THOR	23.8
LUMB	34.5
SPEL	100.0
CAUD	5.0
RIBS	53.2
STER	4.3

Note: (S)YG data from Appendix C, Table 5, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGYG.

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Appendix C. Table 15. Averaged Total Fat Model ((S)MAVGTF)

Anatomical Unit	Model (S)AVGTF	Model (S)MAVGTF	Anatomical Unit	Model (S)AVGTF	Model (S)MAVGTF
SKWOT	16.7	16.7	DRUL	6.5	8.9
ATLAS	5.9	5.9	CARP	1.0	5.6
AXIS	7.1	7.1	PMTC	1.8	3.9
C3C7	50.7	50.7	DMTC	2.1	3.1
THOR	100.0	100.0	APHA	2.3	2.7
LUMB	99.5	99.5	PFEM	38.0	38.7
SPEL	54.0	54.0	DFEM	38.7	38.7
CAUD	1.8	1.8	PTIB	12.1	25.4
RIBS	93.0	93.0	DTIB	8.5	17.0
STER	58.6	58.6	TARS	3.2	10.1
SCAP	16.3	16.7	PMTT	2.4	6.4
PHUM	17.1	17.1	DMTT	2.8	4.6
DHUM	13.4	15.3	PPHA	2.3	3.5
PRUL	7.2	11.2			

Note: (S)TF data from Appendix C, Table 6, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGTF.

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Appendix C. Table 16. Averaged Selected Fat Model ((S)MAVGSF)

Anatomical Unit	Model (S)AVGSF	Model (S)MAVGSF	Anatomical Unit	Model (S)AVGSF	Model (S)MAVGSF
SKWOT	14.8	14.8	DRUL	7.1	9.0
ATLAS	4.1	4.1	CARP	1. 0	5.8
AXIS	5.0	5.0	PMTC	2.1	4.2
C3C7	35.2	35.2	DMTC	2.4	3.4
THOR	80.0	80.0	APHA	2.6	3.0
LUMB	100.0	100.0	PFEM	35.0	35.7
SPEL	50.6	50.6	DFEM	35.7	35.7
CAUD	1.6	1.6	PTIB	13.6	24.7
RIBS	46.0	46.0	DTIB	9.0	16.8
STER	49.3	49.3	TARS	3.8	10.3
SCAP	5.6	11.0	PMTT	2.8	6.8
PHUM	16.4	16.4	DMTT	3.3	5.1
DHUM	11.7	14.1	PPHA	2.7	3.9
PRUL	7.9	11.0			

Note: (S)SF data from Appendix C, Table 7, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGSF.

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Appendix C. Table 17. Averaged Bone Grease Fat Model ((S)MAVGGRE)

Anatomical Unit	Model (S)AVGGRE	Model (S)MAVGGRE	Anatomical Unit	Model (S)AVGGRE	Model (S)MAVGGRE
SKWOT	---	---	DRUL	45.2	48.5
ATLAS	2.4	2.4	CARP	15.0	38.2
AXIS	1.6	1.6	PMTC	4.3	33.0
C3C7	4.8	4.8	DMTC	24.0	30.4
THOR	24.1	24.1	APHA	27.8	29.1
LUMB	29.8	29.8	PFEM	51.1	100.0
SPEL	97.6	97.6	DFEM	100.0	100.0
CAUD	4.5	4.5	PTIB	43.3	71.7
RIBS	55.0	55.0	DTIB	23.2	56.9
STER	4.6	4.6	TARS	42.2	49.6
SCAP	15.4	43.6	PMTT	3.6	38.9
PHUM	71.8	71.8	DMTT	28.2	33.5
DHUM	28.6	58.5	PPHA	27.6	30.6
PRUL	23.4	51.9			

Note: (S)GRE data from Appendix C, Table 8, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGGRE.

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Appendix C. Table 18. Averaged Skeletal Fat Model ((S)MAVGSKF)

Anatomical Unit	Model (S)AVGSKF	Model (S)MAVGSKF	Anatomical Unit	Model (S)AVGSKF	Model (S)MAVGSKF
SKWOT	---	---	DRUL	50.8	59.1
ATLAS	1.6	1.6	CARP	8.3	39.2
AXIS	1.1	1.1	PMTC	16.9	29.2
C3C7	3.3	3.3	DMTC	19.2	24.2
THOR	16.8	16.8	APHA	19.1	21.6
LUMB	18.3	18.3	PFEM	94.7	100.0
SPEL	70.6	70.6	DFEM	100.0	100.0
CAUD	2.9	2.9	PTIB	94.2	97.1
RIBS	38.7	38.7	DTIB	58.9	78.0
STER	3.1	3.1	TARS	25.1	51.6
SCAP	11.8	53.7	PMTT	18.9	37.5
PHUM	95.6	95.6	DMTT	23.5	30.5
DHUM	58.7	77.2	PPHA	20.3	25.4
PRUL	57.7	67.4			

Note: (S)SKF data from Appendix C, Table 9, Part B are used to calculate the unit averages for the four bison listed as Model (S)AVGSKF.

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Appendix C. Table 19. Mixed Class, Protein Model ((S)MMCPRO)

Cows[a]				Bulls[b]			
Anatomical Unit	Model PRO	Model (S)MCPRO	Model (S)MMCPRO	Anatomical Unit	Model PRO	Model (S)MCPRO	Model (S)MMCPRO
SKWOT	1,202.4	7.2	7.2	SKWOT	1,858.8	11.1	11.1
ATLAS	982.8	5.9	5.9	ATLAS	1,208.8	7.2	7.2
AXIS	1,201.2	7.2	7.2	AXIS	1,477.2	8.8	8.8
C3C7	8,737.2	52.2	52.2	C3C7	10,744.4	64.1	64.1
THOR	7,336.4	43.8	43.8	THOR	10,134.4	60.5	60.5
LUMB	7,419.6	44.3	44.3	LUMB	8,824.4	52.7	52.7
SPEL	5,422.4	32.4	32.4	SPEL	7,922.0	47.3	47.3
CAUD	115.2	0.7	0.7	CAUD	120.4	0.7	0.7
RIBS	12,580.8	75.1	75.1	RIBS	16,749.2	100.0	100.0
STER	5,406.0	32.3	32.3	STER	6,208.8	37.1	37.1
SCAP	5,113.6	30.5	30.5	SCAP	7,622.8	45.5	45.5
PHUM	2,429.4	14.5	30.5	PHUM	3,775.8	22.5	45.5
DHUM	2,429.4	14.5	22.5	DHUM	3,775.8	22.5	34.0
PRUL	860.0	5.1	13.8	PRUL	1,247.6	7.4	20.7
DRUL	860.0	5.1	9.5	DRUL	1,247.6	7.4	14.1
CARP	0.0	0.0	4.7	CARP	0.0	0.0	7.0
PMTC	0.0	0.0	2.4	PMTC	0.0	0.0	3.5
DMTC	0.0	0.0	1.2	DMTC	0.0	0.0	1.8
APHA	0.0	0.0	0.6	APHA	0.0	0.0	0.9
PFEM	10,585.6	63.2	63.2	PFEM	13,598.2	81.2	81.2
DFEM	10,585.6	63.2	63.2	DFEM	13,598.2	81.2	81.2
PTIB	1,551.4	9.3	36.3	PTIB	1,732.6	10.3	45.8

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Appendix C. Table 19. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model PRO	Model (S)MCPRO	Model (S)MMCPRO	Anatomical Unit	Model PRO	Model (S)MCPRO	Model (S)MMCPRO
DTIB	1,551.4	9.3	22.8	DTIB	1,732.6	10.3	28.0
TARS	0.0	0.0	11.4	TARS	0.0	0.0	14.0
PMTT	6.0	0.0	5.7	PMTT	6.2	0.0	7.0
DMTT	6.0	0.0	2.8	DMTT	6.2	0.0	3.5
PPHA	0.0	0.0	1.4	PPHA	0.0	0.0	1.8

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 20. Mixed Class, Marrow Fat Model ((S)MMCMAR)

Cows[a]				Bulls[b]			
Anatomical Unit	Model MAR	Model (S)MCMAR	Model (S)MMCMAR	Anatomical Unit	Model MAR	Model (S)MCMAR	Model (S)MMCMAR
SKWOT	---	---	---	SKWOT	---	---	---
ATLAS	0.0	0.0	0.0	ATLAS	0.0	0.0	0.0
AXIS	0.0	0.0	0.0	AXIS	0.0	0.0	0.0
C3C7	0.0	0.0	0.0	C3C7	0.0	0.0	0.0
THOR	0.0	0.0	0.0	THOR	0.0	0.0	0.0
LUMB	0.0	0.0	0.0	LUMB	0.0	0.0	0.0
SPEL	51.3	5.7	5.7	SPEL	46.8	5.2	5.2
CAUD	0.0	0.0	0.0	CAUD	0.0	0.0	0.0
RIBS	0.0	0.0	0.0	RIBS	0.0	0.0	0.0
STER	0.0	0.0	0.0	STER	0.0	0.0	0.0
SCAP	0.0	0.0	22.6	SCAP	40.5	4.5	47.5
PHUM	391.5	43.2	45.1	PHUM	818.1	90.4	90.4
DHUM	421.2	46.5	47.1	DHUM	519.3	57.4	73.9
PRUL	431.1	47.6	47.6	PRUL	464.4	51.3	62.6
DRUL	190.8	21.1	34.4	DRUL	309.6	34.2	48.4
CARP	0.0	0.0	26.9	CARP	0.0	0.0	32.9
PMTC	175.5	19.4	23.1	PMTC	157.5	17.4	25.2
DMTC	39.6	4.4	13.8	DMTC	72.9	8.1	16.6
APHA	17.1	1.9	7.8	APHA	16.2	1.8	9.2
PFEM	657.0	72.6	72.6	PFEM	869.4	96.0	97.0
DFEM	308.7	34.1	70.3	DFEM	519.3	57.4	98.0
PTIB	615.6	68.0	69.2	PTIB	905.4	100.0	100.0

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Appendix C. Table 20. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model MAR	Model (S)MCMAR	Model (S)MMCMAR	Anatomical Unit	Model MAR	Model (S)MCMAR	Model (S)MMCMAR
DTIB	445.5	49.2	59.2	DTIB	523.8	57.9	79.0
TARS	0.0	0.0	40.0	TARS	0.0	0.0	49.1
PMTT	189.0	20.9	30.5	PMTT	174.6	19.3	34.2
DMTT	90.0	9.9	20.2	DMTT	66.6	7.4	20.8
PPHA	42.3	4.7	12.4	PPHA	59.4	6.6	13.7

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 21. Mixed Class, White Grease Fat Model ((S)MMCWG)

Cows[a]				Bulls[b]			
Anatomical Unit	Model WG	Model (S)MCWG	Model (S)MMCWG	Anatomical Unit	Model WG	Model (S)MCWG	Model (S)MMCWG
SCAP	190.8	24.5	62.3	SCAP	79.2	10.2	47.7
PHUM	778.5	100.0	100.0	PHUM	662.4	85.1	85.1
DHUM	278.1	35.7	74.1	DHUM	226.8	29.1	59.6
PRUL	183.6	23.6	61.2	PRUL	89.1	11.4	46.8
DRUL	375.3	48.2	54.7	DRUL	264.6	34.0	40.4
CARP	30.6	3.9	45.4	CARP	48.6	6.2	25.8
PMTC	45.0	5.8	40.8	PMTC	15.3	2.0	18.6
DMTC	162.0	20.1	38.5	DMTC	86.4	11.1	14.9
APHA	281.7	36.2	37.4	APHA	88.2	11.3	13.1
PFEM	452.7	58.2	96.1	PFEM	449.1	57.7	90.4
DFEM	747.9	96.1	96.1	DFEM	703.8	90.4	90.4
PTIB	238.5	30.6	63.4	PTIB	353.7	45.4	67.9
DTIB	189.9	24.4	46.6	DTIB	126.0	16.2	48.8
TARS	195.3	25.1	38.2	TARS	230.4	29.6	39.2
PMTT	30.6	3.9	34.0	PMTT	19.8	2.5	28.8
DMTT	189.0	24.3	31.9	DMTT	144.0	18.5	23.7
PPHA	232.2	29.8	30.8	PPHA	99.0	12.7	18.2

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 22. Mixed Class, Yellow Grease Fat Model ((S)MCYG)

Cows[a]			Bulls[b]		
Anatomical Unit	Model YG	Model (S)MCYG	Anatomical Unit	Model YG	Model (S)MCYG
SKWOT	---	---	SKWOT	---	---
ATLAS	27.0	2.8	ATLAS	3.6	0.4
AXIS	12.6	1.3	AXIS	6.3	0.7
C3C7	98.1	10.3	C3C7	3.6	0.4
THOR	311.4	32.6	THOR	135.9	14.2
LUMB	216.9	22.7	LUMB	205.2	21.5
SPEL	795.6	83.3	SPEL	954.9	100.0
CAUD	42.3	4.4	CAUD	5.4	0.6
RIBS	812.7	85.1	RIBS	326.7	34.2
STER	89.1	9.3	STER	44.1	4.6

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 23. Mixed Class, Total Fat Model ((S)MMCTF)

Cows[a]				Bulls[b]			
Anatomical Unit	Model TF	Model (S)MCTF	Model (S)MMCTF	Anatomical Unit	Model TF	Model (S)MCTF	Model (S)MMCTF
SKWOT	2697.5	16.9	16.9	SKWOT	2147.9	13.4	13.4
ATLAS	886.5	5.5	5.5	ATLAS	852.8	5.3	5.3
AXIS	1063.4	6.7	6.7	AXIS	1044.2	6.5	6.5
C3C7	7742.3	48.5	48.5	C3C7	7554.2	47.3	47.3
THOR	14212.4	89.0	89.0	THOR	11544.5	72.3	72.3
LUMB	15976.4	100.0	100.0	LUMB	10560.4	66.1	66.1
SPEL	7594.2	47.5	47.5	SPEL	6376.3	39.9	39.9
CAUD	423.7	2.7	2.7	CAUD	102.6	0.6	0.6
RIBS	13204.1	82.6	82.6	RIBS	12190.1	76.3	76.3
STER	9714.8	60.8	60.8	STER	7159.1	44.8	44.8
SCAP	2940.3	18.4	18.4	SCAP	1954.4	12.2	12.9
PHUM	2165.9	13.6	18.4	PHUM	2163.2	13.5	13.5
DHUM	1695.2	10.6	14.5	DHUM	1428.8	8.9	11.2
PRUL	845.5	5.3	9.9	PRUL	675.0	4.2	7.8
DRUL	796.9	5.0	7.5	DRUL	695.7	4.4	6.1
CARP	30.6	0.2	5.1	CARP	48.6	0.3	3.6
PMTC	264.7	1.7	3.9	PMTC	172.8	1.1	2.4
DMTC	245.8	1.5	3.3	DMTC	159.3	1.0	1.7
APHA	429.8	2.7	3.0	APHA	122.6	0.8	1.2
PFEM	6500.7	40.7	40.7	PFEM	5063.5	31.7	31.7
DFEM	6447.6	40.4	40.6	DFEM	4968.1	31.1	31.4
PTIB	1577.7	9.9	25.2	PTIB	1516.1	9.5	20.5

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Appendix C. Table 23. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model TF	Model (S)MCTF	Model (S)MMCTF	Anatomical Unit	Model TF	Model (S)MCTF	Model (S)MMCTF
DTIB	1359.0	8.5	16.9	DTIB	907.4	5.7	13.1
TARS	354.6	2.2	9.6	TARS	297.9	1.9	7.5
PMTT	322.9	2.0	6.0	PMTT	198.4	1.2	4.4
DMTT	382.3	2.4	4.2	DMTT	214.6	1.3	2.8
PPHA	366.3	2.3	3.3	PPHA	169.2	1.1	2.0

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 24. Mixed Class, Selected Fat Model ((S)MMCSF)

Cows[a]				Bulls[b]			
Anatomical Unit	Model SF	Model (S)MCSF	Model (S)MMCSF	Anatomical Unit	Model SF	Model (S)MCSF	Model (S)MMCSF
SKWOT	2105.3	17.2	17.2	SKWOT	1589.0	13.0	13.0
ATLAS	483.3	3.9	3.9	ATLAS	393.8	3.2	3.2
AXIS	570.2	4.7	4.7	AXIS	483.5	3.9	3.9
C3C7	4154.9	33.9	33.9	C3C7	3474.5	28.4	28.4
THOR	8966.3	73.2	73.2	THOR	7082.3	57.8	57.8
LUMB	12252.2	100.0	100.0	LUMB	8173.6	66.7	66.7
SPEL	5723.1	46.7	46.7	SPEL	4415.2	36.0	36.0
CAUD	299.5	2.4	2.4	CAUD	72.9	0.6	0.6
RIBS	6212.0	50.7	50.7	RIBS	3430.4	28.0	28.0
STER	6268.7	51.2	51.2	STER	4843.4	39.5	39.5
SCAP	776.7	6.3	10.0	SCAP	288.5	2.4	8.2
PHUM	1684.4	13.7	13.7	PHUM	1708.7	13.9	13.9
DHUM	1213.7	9.9	11.8	DHUM	974.3	8.0	11.0
PRUL	817.6	6.7	9.3	PRUL	553.5	4.5	7.8
DRUL	769.0	6.3	7.8	DRUL	574.2	4.7	6.3
CARP	30.6	0.3	5.6	CARP	48.6	0.4	3.8
PMTC	264.7	2.2	4.6	PMTC	172.8	1.4	2.6
DMTC	245.8	2.0	4.0	DMTC	159.3	1.3	2.0
APHA	429.8	3.5	3.8	APHA	122.6	1.0	1.5
PFEM	4806.0	39.2	39.2	PFEM	3274.3	26.7	26.7
DFEM	4752.9	38.8	39.0	DFEM	3178.9	25.9	26.3
PTIB	1302.7	10.6	24.8	PTIB	1437.0	11.7	19.0

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Appendix C. Table 24. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model SF	Model (S)MCSF	Model (S)MMCSF	Anatomical Unit	Model SF	Model (S)MCSF	Model (S)MMCSF
DTIB	1084.0	8.8	16.8	DTIB	827.7	6.8	12.9
TARS	354.6	2.9	10.0	TARS	297.9	2.4	7.7
PMTT	320.2	2.6	6.5	PMTT	197.5	1.6	4.7
DMTT	379.6	3.1	4.8	DMTT	213.7	1.7	3.2
PPHA	366.3	3.0	3.9	PPHA	169.2	1.4	2.3

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 25. Mixed Class, Grease Fat Model ((S)MMCGRE)

Cows[a]				Bulls[b]			
Anatomical Unit	Model GRE	Model (S)MCGRE	Model (S)MMCGRE	Anatomical Unit	Model GRE	Model (S)MCGRE	Model (S)MMCGRE
SKWOT	---	---	---	SKWOT	---	---	---
ATLAS	27.0	2.8	2.8	ATLAS	3.6	0.4	0.4
AXIS	12.6	1.3	1.3	AXIS	6.3	0.7	0.7
C3C7	98.1	10.3	10.3	C3C7	3.6	0.4	0.4
THOR	311.4	32.6	32.6	THOR	135.9	14.2	14.2
LUMB	216.9	22.7	22.7	LUMB	205.2	21.5	21.5
SPEL	795.6	83.3	83.3	SPEL	954.9	100.0	100.0
CAUD	42.3	4.4	4.4	CAUD	5.4	0.6	0.6
RIBS	812.7	85.1	85.1	RIBS	326.7	34.2	34.2
STER	89.1	9.3	9.3	STER	44.1	4.6	4.6
SCAP	190.8	20.0	50.8	SCAP	79.2	8.3	38.9
PHUM	778.5	81.5	81.5	PHUM	662.4	69.4	69.4
DHUM	278.1	29.1	60.4	DHUM	226.8	23.8	48.6
PRUL	183.6	19.2	49.9	PRUL	89.1	9.3	38.1
DRUL	375.3	39.3	44.6	DRUL	264.6	27.7	32.9
CARP	30.6	3.2	37.0	CARP	48.6	5.1	21.1
PMTC	45.0	4.7	33.3	PMTC	15.3	1.6	15.1
DMTC	162.0	17.0	31.4	DMTC	86.4	9.0	12.2
APHA	281.7	29.5	30.4	APHA	88.2	9.2	10.7
PFEM	452.7	47.4	78.3	PFEM	449.1	47.0	73.7
DFEM	747.9	78.3	78.3	DFEM	703.8	73.7	73.7
PTIB	238.5	25.0	51.7	PTIB	353.7	37.0	55.4

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Appendix C. Table 25. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model GRE	Model (S)MCGRE	Model (S)MMCGRE	Anatomical Unit	Model GRE	Model (S)MCGRE	Model (S)MMCGRE
DTIB	189.9	19.9	38.0	DTIB	126.0	13.2	39.7
TARS	195.3	20.5	31.1	TARS	230.4	24.1	31.9
PMTT	30.6	3.2	27.7	PMTT	19.8	2.1	23.5
DMTT	189.0	19.8	26.0	DMTT	144.0	15.1	19.3
PPHA	232.2	24.3	25.2	PPHA	99.0	10.4	14.9

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 26. Mixed Class, Skeletal Fat Model ((S)MMCSKF)

Cows[a]				Bulls[b]			
Anatomical Unit	Model SKF	Model (S)MCSKF	Model (S)MMCSKF	Anatomical Unit	Model SKF	Model (S)MCSKF	Model (S)MMCSKF
SKWOT	---	---	---	SKWOT	---	---	---
ATLAS	27.0	1.8	1.8	ATLAS	3.6	0.2	0.2
AXIS	12.6	0.9	0.9	AXIS	6.3	0.4	0.4
C3C7	98.1	6.6	6.6	C3C7	3.6	0.2	0.2
THOR	311.4	21.0	21.0	THOR	135.9	9.2	9.2
LUMB	216.9	14.7	14.7	LUMB	205.2	13.9	13.9
SPEL	846.9	57.2	57.2	SPEL	1001.7	67.7	67.7
CAUD	42.3	2.9	2.9	CAUD	5.4	0.4	0.4
RIBS	812.7	54.9	54.9	RIBS	326.7	22.1	22.1
STER	89.1	6.0	6.0	STER	44.1	3.0	3.0
SCAP	190.8	12.9	46.0	SCAP	119.7	8.1	54.1
PHUM	1170.0	79.0	79.0	PHUM	1480.5	100.0	100.0
DHUM	699.3	47.2	43.1	DHUM	746.1	50.4	75.2
PRUL	614.7	41.5	42.3	PRUL	553.5	37.4	57.0
DRUL	566.1	38.2	40.3	DRUL	574.2	38.8	47.9
CARP	30.6	2.1	30.2	CARP	48.6	3.3	29.8
PMTC	220.5	14.9	25.2	PMTC	172.8	11.7	20.8
DMTC	201.6	13.6	22.7	DMTC	159.3	10.8	15.8
APHA	298.8	20.2	21.5	APHA	104.4	7.1	11.4
PFEM	1109.7	75.0	75.0	PFEM	1318.5	89.1	89.1
DFEM	1056.6	71.4	73.2	DFEM	1223.1	82.6	87.1
PTIB	854.1	57.7	65.5	PTIB	1259.1	85.0	86.0

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Appendix C. Table 26. (continued)

Cows[a]				Bulls[b]			
Anatomical Unit	Model SKF	Model (S)MCSKF	Model (S)MMCSKF	Anatomical Unit	Model SKF	Model (S)MCSKF	Model (S)MMCSKF
DTIB	635.4	42.9	54.2	DTIB	649.8	43.9	65.0
TARS	195.3	13.2	36.5	TARS	230.4	15.6	40.3
PMTT	219.6	14.8	27.6	PMTT	194.4	13.1	27.2
DMTT	279.0	18.8	23.2	DMTT	210.6	14.2	20.7
PPHA	274.5	18.5	20.9	PPHA	158.4	10.7	15.7

[a] Data for FAF used to represent poor conditioned spring cows.

[b] Data for SAM used to represent spring bulls.

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Appendix C. Table 27. Percent of Caloric Contribution to Products Total for Carcass Units with Studentized Residuals Greater than ± 2.0 for Regressions of Averaged and Single Class Models

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Component Percent of Unit kcal Total for Single Class Model[a]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGSF	FYM(S)MSF	THOR	2.2	0.0	0.0	0.8	0.0	27.8	71.4	0.0
		STER	-3.5	0.0	0.0	0.1	0.0	10.7	71.0	18.3
	SAM(S)MSF	STER	2.6	0.0	0.0	0.9	0.0	6.5	67.8	24.8
		RIBS	-2.7	0.0	0.0	9.5	0.0	18.6	71.9	0.0
		LUMB	-2.7	0.0	0.0	2.5	0.0	7.5	37.4	52.6
	SAF(S)MSF	RIBS	3.5	0.0	0.0	10.2	0.0	40.5	49.2	0.0
		THOR	-2.0	0.0	0.0	3.3	0.0	53.5	43.2	0.0
	FAF(S)MSF	RIBS	2.4	0.0	0.0	13.1	0.0	20.0	66.9	0.0
		THOR	-3.0	0.0	0.0	3.5	0.0	42.1	54.5	0.0

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Appendix C. Table 27. (continued)

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Component Percent of Unit kcal Total for Single Class Model[a]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGTF	FYM(S)MTF	LUMB	2.6	0.0	2.3	2.8	0.0	2.3	31.3	61.3
		THOR	2.2	0.0	18.6	0.6	0.0	22.6	58.1	0.0
		RIBS	-3.2	0.0	49.0	1.2	0.0	5.2	44.6	0.0
	SAM(S)MTF	C3C7	3.2	0.0	54.0	0.0	0.0	3.4	42.5	0.0
		RIBS	2.4	0.0	71.9	2.7	0.0	5.2	20.2	0.0
		LUMB	-3.5	0.0	22.6	1.9	0.0	5.8	28.9	40.7
	SAF(S)MTF	RIBS	3.3	0.0	60.0	4.1	0.0	16.2	19.7	0.0
		C3C7	-3.2	0.0	40.2	0.5	0.0	9.3	49.3	0.0
	FAF(S)MTF	LUMB	2.7	0.0	23.3	1.4	0.0	11.7	32.6	31.1
		STER	2.1	0.0	35.5	0.9	0.0	18.6	33.7	11.3
		RIBS	-2.3	0.0	53.0	6.2	0.0	9.4	31.5	0.0
		THOR	-2.4	0.0	36.9	2.2	0.0	26.5	34.4	0.0

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Appendix C. Table 27. (continued)

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Component Percent of Unit kcal Total for Single Class Model[a]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGSKF	FYM(S)MSKF	SPEL	-2.7	0.0	0.0	80.3	19.7	0.0	0.0	0.0
		RIBS	-2.7	0.0	0.0	100.0	0.0	0.0	0.0	0.0
	SAM(S)MSKF	PHUM	3.0	0.0	0.0	44.7	55.3	0.0	0.0	0.0
		RIBS	-2.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
	SAF(S)MSKF	SPEL	2.6	0.0	0.0	97.7	2.3	0.0	0.0	0.0
		PHUM	-2.9	0.0	0.0	64.9	35.1	0.0	0.0	0.0
	FAF(S)MSKF	RIBS	4.1	0.0	0.0	100.0	0.0	0.0	0.0	0.0

[a] Intram. (intramuscular fat), Subcut. (subcutaneous fat), Interm. (intermuscular fat).
Note: See Table 8.10 for averaged and single class model comparisons for (S)MTP.

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Appendix C. Table 28. Identifying Distribution Variability that Might Account for Units with Large Studentized Residuals (Greater than ± 2.0) for Regressions of Averaged and Single Class Models

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison[b]						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGSF	FYM(S)MSF	THOR	2.2	-	-	0	-	3	3	-
		STER	-3.5	-	-	2	-	2	3	3
	SAM(S)MSF	STER	2.6	-	-	2	-	0	3	3
		RIBS	-2.7	-	-	2	-	3	3	-
		LUMB	-2.7	-	-	1	-	2	2	2
	SAF(S)MSF	RIBS	3.5	-	-	2	-	3	1	-
		THOR	-2.0	-	-	1	-	2	1	-
	FAF(S)MSF	RIBS	2.4	-	-	3	-	1	1	-
		THOR	-3.0	-	-	0	-	3	3	-

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Appendix C. Table 28. (continued)

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGTF	FYM(S)MTF	LUMB	2.6	-	0	3	-	0	0	3
		THOR	2.2	-	2	0	-	3	3	-
		RIBS	-3.2	-	0	3	-	1	0	-
	SAM(S)MTF	C3C7	3.2	-	3	0	-	2	3	-
		RIBS	2.4	-	1	1	-	0	0	-
		LUMB	-3.5	-	2	1	-	2	2	2
	SAF(S)MTF	RIBS	3.3	-	1	2	-	3	1	-
		C3C7	-3.2	-	3	2	-	0	1	-
	FAF(S)MTF	LUMB	2.7	-	3	1	-	3	2	2
		STER	2.1	-	2	3	-	3	1	2
		RIBS	-2.3	-	3	0	-	1	1	-
		THOR	-2.4	-	2	0	-	3	3	-

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Appendix C. Table 28. (continued)

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGSKF	FYM(S)MSKF	SPEL	-2.7	-	-	2	0	-	-	-
		RIBS	-2.7	-	-	3	-	-	-	-
	SAM(S)MSKF	PHUM	3.0	-	-	3	3	-	-	-
		RIBS	-2.0	-	-	2	-	-	-	-
	SAF(S)MSKF	SPEL	2.6	-	-	2	0	-	-	-
		PHUM	-2.9	-	-	2	3	-	-	-
	FAF(S)MSKF	RIBS	4.1	-	-	3	-	-	-	-
(S)MAVGMAR	FYM(S)MMAR	PFEM	-2.9	-	-	-	3	-	-	-
	SAM(S)MMAR	PHUM	2.9	-	-	-	3	-	-	-
	SAF(S)MMAR	PRUL	2.0	-	-	-	3	-	-	-
	FAF(S)MMAR	PFEM	2.1	-	-	-	2	-	-	-
		PHUM	-2.2	-	-	-	2	-	-	-

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Appendix C. Table 28. (continued)

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGWG	FYM(S)MWG	PHUM	-2.1	-	-	3	-	-	-	-
	SAM(S)MWG	PHUM	2.8	-	-	3	-	-	-	-
	SAF(S)MWG	PTIB	2.4	-	-	3	-	-	-	-
		PHUM	-2.8	-	-	2	-	-	-	-
	FAF(S)MWG	PHUM	2.4	-	-	2	-	-	-	-
(S)AVGYG	FYM(S)YG	LUMB	2.3	-	-	3	-	-	-	-
	SAM(S)YG	SPEL	2.8	-	-	3	-	-	-	-
		RIBS	-2.0	-	-	2	-	-	-	-
	SAF(S)YG	LUMB	-2.7	-	-	3	-	-	-	-
(S)AVGYG	FAF(S)YG	RIBS	2.6	-	-	3	-	-	-	-
		SPEL	-2.0	-	-	3	-	-	-	-

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Appendix C. Table 28. (continued)

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Number of Matchs in Residual Sign and Direction of Difference in Comparisons of Distribution Variability Between Model Individual and Other Three Bison						
				Protein	Intram. Fat	Grease Fat	Marrow Fat	Subcut. Fat	Interm. Fat	Cavity Fat
(S)MAVGGRE	FYM(S)MGRE	RIBS	-2.2	-	-	3	-	-	-	-
	SAM(S)MGRE	SPEL	3.4	-	-	3	-	-	-	-
		PHUM	2.0	-	-	3	-	-	-	-
	SAF(S)MGRE	PTIB	2.0	-	-	3	-	-	-	-
	FAF(S)MGRE	RIBS	3.5	-	-	3	-	-	-	-
(S)MAVGPRO	FYM(S)MPRO	RIBS	-3.3	3	-	-	-	-	-	-
		C3C7	-2.9	2	-	-	-	-	-	-
	SAM(S)MPRO	C3C7	2.7	2	-	-	-	-	-	-
		RIBS	2.3	2	-	-	-	-	-	-
		PFEM	-2.1	3	-	-	-	-	-	-
		DFEM	-2.1	3	-	-	-	-	-	-
	SAF(S)MPRO	C3C7	-3.4	3	-	-	-	-	-	-
	FAF(S)MPRO	C3C7	4.0	3	-	-	-	-	-	-

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Appendix C. Table 28. (continued)

[a] See Table 8.4 for glossary of model acronyms and Table 8.11 for averaged model comparisons with (S)MTP models.

[b] Intram. (intramuscular fat), Subcut. (subcutaneous fat), Interm. (intermuscular fat)

Note: 0 indicates the distribution value for the individual was smaller (if the residual sign is positive) or larger (if the residual sign is positive) than the other bison; 3 indicates the distribution value for the individual was smaller (if the residual sign is negative) or larger (if the residual sign is positive) than the other bison. Values 1 and 2 indicate partial agreement between the sign and the occurrence of distribution differences. Product components that were not present are indicated with a "-".

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Appendix C. Table 29. The Effect of Using Averaged Models on Kill Site Assemblages Dominated by Single Animal Classes Under the Influence of Different Recovery Strategies

Part A. Data Needed to Determine the Effect

Averaged[a] Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value			Averaged Model Over- or Underestimates Single Class Model Value		
				Averaged Model	Single Class Model	Absolute Difference	Same Value	Over-estimates Value	Under-estimates Value
(S)AVGFUI	FYM(S)FUI	RIBS	-2.9	62.3	52.3	10.0		X	
		C3C7	-2.0	38.6	31.5	7.1		X	
	SAM(S)FUI	C3C7	3.8	38.6	48.3	9.7			X
	SAF(S)FUI	LUMB	2.7	47.4	49.7	2.3			X
		C3C7	-3.0	38.6	31.5	7.1		X	
	FAF(S)FUI	RIBS	3.0	62.3	69.3	7.0			X

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value: Averaged Model	Carcass Unit Value: Single Class Model	Carcass Unit Value: Absolute Difference	Averaged Model Over- or Underestimates Single Class Model Value: Same Value	Averaged Model Over- or Underestimates Single Class Model Value: Over-estimates Value	Averaged Model Over- or Underestimates Single Class Model Value: Under-estimates Value
(S)MAVGSF	FYM(S)MSF	THOR	2.2	80.0	82.6	2.6			X
		STER	-3.2	49.3	35.6	13.7		X	
	SAN(S)MSF	STER	2.6	49.3	59.3	10.0			X
		RIBS	-2.7	46.0	42.0	4.0		X	
		LUMB	-2.7	100.0	100.0	0.0	X		
	SAF(S)MSF	RIBS	3.5	46.0	51.8	5.8			X
		THOR	-2.0	80.0	77.3	2.7		X	
	FAF(S)MSF	RIBS	2.4	46.0	50.7	4.7			X
		THOR	-3.0	80.0	73.2	6.8		X	

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value: Averaged Model	Carcass Unit Value: Single Class Model	Carcass Unit Value: Absolute Difference	Averaged Model Over- or Underestimates Single Class Model Value: Same Value	Over-estimates Value	Under-estimates Value
(S)MAVGTF	FYM(S)MTF	LUMB	2.6	99.5	100.0	0.5			X
		THOR	2.2	100.0	99.2	0.8		X	
		RIBS	-3.2	93.0	75.7	17.3		X	
	SAM(S)MTF	C3C7	3.2	50.7	62.0	11.3			X
		RIBS	2.4	93.0	100.0	7.0			X
		LUMB	-3.5	99.5	86.6	12.9		X	
	SAF(S)MTF	RIBS	3.3	93.0	97.7	4.7			X
		C3C7	-3.2	50.7	41.3	9.4		X	
	FAF(S)MTF	LUMB	2.7	99.5	100.0	0.5			X
		STER	2.1	58.6	60.8	2.2			X
		THOR	-2.4	100.0	89.0	11.0		X	
		RIBS	-2.3	93.0	82.6	10.4		X	

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value: Averaged Model	Carcass Unit Value: Single Class Model	Carcass Unit Value: Absolute Difference	Averaged Model Over- or Underestimates Single Class Model Value: Same Value	Over-estimates Value	Under-estimates Value
(S)MAVGSKF	FYM(S)MSKF	SPEL	-2.7	70.6	35.5	35.1		X	
		RIBS	-2.7	38.7	6.9	31.8		X	
	SAM(S)MSKF	PHUM	3.0	95.6	100.0	4.4			X
		RIBS	-2.0	38.7	22.1	16.6		X	
	SAF(S)MSKF	SPEL	2.6	70.6	78.9	8.3			X
		PHUM	-2.9	95.6	68.7	26.9		X	
	FAF(S)MSKF	RIBS	4.1	38.7	69.5	30.8			X
(S)MAVGGRE	FYM(S)MGRE	RIBS	-2.2	55.0	14.7	40.3		X	
	SAM(S)MGRE	SPEL	3.4	97.6	100.0	2.4			X
		PHUM	2.0	71.8	69.4	2.4		X	
	SAF(S)MGRE	PTIB	2.0	71.7	76.3	4.6			X
	FAF(S)MGRE	RIBS	3.5	55.0	100.0	45.0			X

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value: Averaged Model	Carcass Unit Value: Single Class Model	Carcass Unit Value: Absolute Difference	Averaged Model Over- or Underestimates Single Class Model Value: Same Value	Over-estimates Value	Under-estimates Value
(S)MAVGMAR	FYM(S)MMAR	PFEM	-2.9	97.2	77.1	20.1		X	
	SAM(S)MMAR	PHUM	2.9	71.5	90.4	18.9			X
	SAF(S)MMAR	PRUL	2.0	68.0	73.4	5.4			X
	FAF(S)MMAR	PFEM	2.1	97.2	100.0	2.8			X
		PHUM	-2.2	71.5	62.2	9.3		X	
(S)MAVGWG	FYM(S)MWG	PHUM	-2.1	73.5	40.5	33.0		X	
	SAM(S)MWG	PHUM	2.8	73.5	94.1	20.6			X
	SAF(S)MWG	PTIB	2.4	71.8	76.3	4.5			X
		PHUM	-2.8	73.5	56.7	16.8		X	
	FAF(S)MWG	PHUM	2.4	73.5	100.0	26.5			X

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value			Averaged Model Over- or Underestimates Single Class Model Value		
				Averaged Model	Single Class Model	Absolute Difference	Same Value	Over-estimates Value	Under-estimates Value
(S)AVGYG	FYM(S)YG	LUMB	2.3	34.5	72.0	37.5			X
	SAM(S)YG	SPEL	2.8	100.0	100.0	0.0	X		
		RIBS	-2.0	53.2	34.2	19.0		X	
	SAF(S)YG	LUMB	-2.7	34.5	17.0	17.5		X	
	FAF(S)YG	RIBS	2.6	53.2	100.0	46.8			X
		SPEL	-2.0	100.0	97.9	2.1		X	

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Appendix C. Table 29. (continued)

Part A. Data Needed to Determine the Effect

Averaged Model	Single Class Model	Carcass Unit	Studentized Residual	Carcass Unit Value: Averaged Model	Carcass Unit Value: Single Class Model	Carcass Unit Value: Absolute Difference	Averaged Model Over- or Underestimates Single Class Model Value: Same Value	Averaged Model Over- or Underestimates Single Class Model Value: Over-estimates Value	Averaged Model Over- or Underestimates Single Class Model Value: Under-estimates Value
(S)MAVGPRO	FYM(S)MPRO	RIBS	-3.3	100.0	89.1	10.9		X	
		C3C7	-2.9	59.0	48.7	10.3		X	
	SAM(S)MPRO	C3C7	2.7	59.0	64.1	5.1			X
		RIBS	2.3	100.0	100.0	0.0	X		
		PFEM	-2.1	94.1	81.2	12.9			X
		DFEM	-2.1	94.1	81.2	12.9			X
	SAF(S)MPRO	C3C7	-3.4	59.0	46.5	12.5		X	
	FAF(S)MPRO	C3C7	4.0	59.0	69.4	10.4			X

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)AVGFUI	FYM(S)FUI	RIBS		X-S			X-M			X-M	
		C3C7		V-M			V-M			V-M	
	SAM(S)FUI	C3C7			V-M			V-M			V-M
	SAF(S)FUI	LUMB			I-M			I-M			I-M
		C3C7		V-M			V-M			V-M	
	FAF(S)FUI	RIBS			V-M			V-M			V-M

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGMSF	FYM(S)MSF	THOR			I-M			I-M			I-M
		STER		X-S			X-M			X-M	
	SAM(S)MSF	STER			X-S			X-M			X-M
		RIBS		I-M			I-M			I-M	
		LUMB	I			I			I		
	SAF(S)MSF	RIBS			V-M			V-M			V-M
		THOR		I-M			I-M			I-M	
	FAF(S)MSF	RIBS			I-M			I-M			I-M
		THOR		V-M			V-M			V-M	

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGMTF	FYM(S)MTF	LUMB			I-M			I-M			I-M
		THOR		I-M			I-M			I-M	
		RIBS		XV-S			XV-M			XV-S	
	SAM(S)MTF	C3C7			X-S			X-M			X-M
		RIBS			V-M			V-M			V-S
		LUMB		X-S			X-M			X-S	
	SAF(S)MTF	RIBS			I-M			I-M			I-S
		C3C7		V-S			V-M			V-M	
	FAF(S)MTF	LUMB			I-M			I-M			I-M
		STER			I-M			I-M			I-M
		THOR		X-S			X-M			X-S	
		RIBS		X-S			X-M			X-S	

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGMSKF	FYM(S)MSKF	SPEL		XXXV-S			XXXV-M/S			XXXV-M/S	
		RIBS		XXX-S			XXX-S			XXX-M	
	SAM(S)MSKF	PHUM			I-M			I-M			I-S
		RIBS		XV-S			XV-M/S			XV-M	
	SAF(S)MSKF	SPEL			V-M			V-M			V-M/S
		PHUM		XXV-S			XXV-M			XXV-S	
	FAF(S)MSKF	RIBS			XXX-S			XXX-M/S			XXX-M/S

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGGRE	FYM(S)MGRE	RIBS		XL-S			XL-S			XL-M/S	
	SAM(S)MGRE	SPEL			I-M			I-M			I-M
		PHUM		I-M			I-M			I-M	
	SAF(S)MGRE	PTIB			I-M			I-M			I-M
	FAF(S)MGRE	RIBS			XLV-S			XLV-M			XLV-S
(S)MAVGMAR	FYM(S)MMAR	PFEM		XX-S			XX-M			XX-S	
	SAM(S)MMAR	PHUM			XV-S			XV-M			XV-S
	SAF(S)MMAR	PRUL			V-M			V-M			V-M
	FAF(S)MMAR	PFEM			I-M			I-M			I-S
		PHUM		V-M			V-M		V-M		

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGWG	FYM(S)MWG	PHUM		XXX-S			XXX-M/S			XXX-M/S	
	SAM(S)MWG	PHUM			XX-S			XX-M			XX-S
	SAF(S)MWG	PTIB			I-M			I-M			I-M
		PHUM		XV-S			XV-M/S				
	FAF(S)MWG	PHUM			XXXV-S			XXV-M			XXV-S
(S)AVGYG	FYM(S)YG	LUMB			XXXV-S			XXXV-M/S			XXXV-M/S
	SAM(S)YG	SPEL	I			I			I		
		RIBS		XV-S			XV-M/S			XV-M	
	SAF(S)YG	LUMB		XV-S			XV-S			XV-M	
	FAF(S)YG	RIBS			XLV-S			XLV-M			XLV-S
		SPEL		I-M			I-M			I-S	

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Appendix C. Table 29. (continued)

Part B. The Effect of Using an Averaged Model on a Class Dominated Bone Assemblage

			Number of Units Present Compared to the Number Expected								
			Unbiased Strategy			Bulk Strategy			Gourmet Strategy		
Averaged Model	Single Class Model	Carcass Unit	No Effect	More	Fewer	No Effect	More	Fewer	No Effect	More	Fewer
(S)MAVGPRO	FYM(S)MPRO	RIBS		X-S			X-M			X-S	
		C3C7		X-S			X-M			X-M	
	SAM(S)MPRO	SPEL			V-M			V-M			V-M
		RIBS	I			I			I		
		PFEM			X-S			X-M			X-S
		DFEM			X-S			X-M			X-M
	SAF(S)MPRO	C3C7		X-S			X-M			X-M	
	FAF(S)MPRO	C3C7			X-S			X-M			X-M

[a] see Table 8.4 for glossary of model acronyms and Table 8.12 for (S)MTP and averaged model comparisons.

Note: The effect of the change in index value has two pprts to it. The first part shows the magnitude of the index value change and the second part show the magnitude of the difference in the percent MAU expected. I = 0 to 4.9, V = 5 to 9.9, X = 10 to 14.9, ect.; -M indicates less than 10 percent MAU change, and -S indicates more than 10 percent MAU change when using the outside curves in Figure 8.4; -M/S indicates minor change for the outside curve and substantial change for the inside curve in Figure 8.4.

Appendix C. Table 30. Units with Studentized Residuals > ± 1.5 for Regressions of Averaged on Single Class Model Values

Independent Variable	Dependent Variable	Residuals ≥ 1.5 Unit	Residuals ≥ 1.5 Studentized Residual	Residuals ≤ -1.5 Unit	Residuals ≤ -1.5 Studentized Residual
(S)MAVGTP	FYM(S)MTP	PFEM	2.2	C3C7	-2.3
		DFEM	2.2	RIBS	-3.1
	SAM(S)MTP	RIBS	2.3	LUMB	-3.0
		C3C7	3.1		
	SAF(S)MTP	SPEL	1.5	SCAP	-2.1
		LUMB	1.5	PHUM	-2.1
		THOR	1.8	C3C7	-2.8
	FAF(S)MTP	STER	1.8	SPEL	-1.7
		LUMB	2.5	PFEM	-1.7
		C3C7	2.9	DFEM	-1.7
(S)AVGFUI	FYM(S)FUI			LUMB	-1.9
				C3C7	-2.0
				RIBS	-2.9
	SAM(S)FUI	RIBS	1.6	LUMB	-1.7
		C3C7	3.8		
	SAF(S)FUI	SPEL	1.7	C3C7	-3.0
		LUMB	2.7		
	FAF(S)FUI	STER	1.7		
		C3C7	1.9		
		LUMB	1.9		
		RIBS	3.0		
(S)MAVGSF	FYM(S)MSF	LUMB	1.9	STER	-3.5
		THOR	2.2		
	SAM(S)MSF	C3C7	1.8	RIBS	-2.7
		STER	2.6	LUMB	-2.7
	SAF(S)MSF	SPEL	1.7	THOR	-2.0
		RIBS	3.5		
	FAF(S)MSF	DFEM	1.7	SPEL	-1.6
		PFEM	1.8	THOR	-3.0
		RIBS	2.4		

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Appendix C. Table 30. (continued)

Independent Variable	Dependent Variable	Residuals ≥ 1.5 Unit	Residuals ≥ 1.5 Studentized Residual	Residuals ≤ -1.5 Unit	Residuals ≤ -1.5 Studentized Residual
(S)MAVGTF	FYM(S)MTF	THOR	2.2	PFEM	-1.6
		LUMB	2.6	DFEM	-1.6
				RIBS	-3.2
	SAM(S)MTF	RIBS	2.4	LUMB	-3.5
		C3C7	3.2		
	SAF(S)MTF	RIBS	3.3	STER	-1.6
				C3C7	-3.2
	FAF(S)MTF	STER	2.1	SPEL	-1.5
		LUMB	2.7	RIBS	-2.3
				THOR	-2.4
(S)MAVGSKF	FYM(S)MSKF			RIBS	-2.7
				SPEL	-2.7
	SAM(S)MSKF	SCAP	1.6	RIBS	-2.0
		PHUM	3.0		
	SAF(S)MSKF	PFEM	1.8	PHUM	-2.9
		DFEM	1.8		
		SPEL	2.6		
	FAF(S)MSKF	RIBS	4.1		
(S)MAVGGRE	FYM(S)MGRE	THOR	1.5	PHUM	-1.6
				SPEL	-1.9
				RIBS	-2.2
	SAM(S)MGRE	PHUM	2.0		
		SPEL	3.4		
	SAF(S)MGRE	PTIB	2.0	PHUM	-1.7
	FAF(S)MGRE	PHUM	1.9		
		RIBS	3.5		

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Appendix C. Table 30. (continued)

Independent Variable	Dependent Variable	Residuals ≥ 1.5 Unit	Residuals ≥ 1.5 Studentized Residual	Residuals ≤ -1.5 Unit	Residuals ≤ -1.5 Studentized Residual
(S)MAVGMAR	FYM(S)MMAR	PTIB	1.8	PFEM	-2.9
	SAM(S)MMAR	SCAP	1.7		
		PHUM	2.9		
	SAF(S)MMAR	PFEM	1.7	PHUM	-1.8
		PRUL	2.0	PTIB	-1.8
	FAF(S)MMAR	PFEM	2.1	SCAP	-1.6
				PHUM	-2.2
(S)MAVGWG	FYM(S)MWG			SCAP	-1.8
				PHUM	-2.1
	SAM(S)MWG	SCAP	1.9		
		PHUM	2.8		
	SAF(S)MWG	PTIB	2.4	PHUM	-2.8
	FAF(S)MWG	PHUM	2.4		
(S)AVGYG	FYM(S)YG	LUMB	2.3	RIBS	-1.8
	SAM(S)YG	SPEL	2.8	RIBS	-2.0
	SAF(S)YG			LUMB	-2.7
	FAF(S)YG	RIBS	2.6	SPEL	-2.0
(S)MAVGPRO	FYM(S)MPRO	PFEM	1.9	C3C7	-2.9
		DFEM	1.9	RIBS	-3.3
	SAM(S)MPRO	RIBS	2.0	PFEM	-2.1
		C3C7	2.7	DFEM	-2.1
	SAF(S)MPRO	PFEM	1.6	STER	-1.5
		DFEM	1.6	SCAP	-1.6
		SPEL	1.7	PHUM	-1.6
				C3C7	-3.4
	FAF(S)MPRO	RIBS	1.7	PFEM	-1.6
		C3C7	4.0	DFEM	-1.6
				SPEL	-1.7

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Appendix C. Table 30. (continued)

Note: See Table 8.8 for additional data on these regressions.
Note: Positive studentized residuals indicate that the averaged model value underestimates the single class model value. Negative residuals indicate that the averaged model value overestimates the single class model value.

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APPENDIX D

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CARCASS PRODUCT CALORIE YIELD IN THE TRNP BISON

The data used to caluculate the value of carcass parts in the utility models presented in Chapter 8 and applied in Chapter 9 are presented in the tables of this appendix. These data are presented as calorie rather than weight yield in order to account for differences in energy yield that are not recognized by weight values. The calorie yields were determined by multipling fat weight by 9 kcal/gm and protein weight by 4 kcal/gm.

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Appendix D. Table 1. Calorie Yield of Carcass Products in FYM Side

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
SKWOT	671.20	300.60	---	---	549.50
ATLAS[f]	408.40	68.40	12.6	0.0	189.00
AXIS[f]	499.20	83.70	5.4	0.0	231.50
C3C7[f]	3,629.60	610.20	8.1	0.0	1,682.10
THOR	4,648.80	1,005.30	34.2	0.0	4,356.50
LUMB	4,318.80	122.40	150.3	0.0	5,165.10
SPEL	3,823.60	346.50	208.8	51.3	2,300.40
CAUD	72.40	15.30	19.8	0.0	14.90
RIBS	6,639.20	2,017.80	50.4	0.0	2,050.00
STER	3,554.80	932.40	1.8	0.0	1,892.70
SCAP	3,395.20	367.20	36.9	3.6	540.00
PHUM	1,524.80	33.75	138.6	416.7	348.65
DHUM	1,524.80	33.75	79.2	295.2	348.65
PRUL[g]	699.40	3.60	105.3	377.1	106.30
DRUL	699.40	3.60	178.2	210.6	106.30
CARP	0.00	0.00	133.2	0.0	0.00
PMTC	0.00	0.00	17.1	112.5	7.45
DMTC	0.00	0.00	152.1	48.6	7.45
APHA	0.00	0.00	131.4	18.0	16.90
PFEM	7,451.20	79.65	133.2	414.9	941.65
DFEM[h]	7451.20	79.65	343.8	297.9	941.65
PTIB	844.20	0.00	135.9	596.7	62.45
DTIB	844.20	0.00	119.7	405.0	62.45

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Appendix D. Table 1. (continued)

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
TARS	0.00	0.00	279.0	0.0	21.60
PMTT	5.20	0.10	11.7	143.1	56.35
DMTT	5.20	0.10	158.4	50.4	56.35
PPHA	0.00	0.00	168.3	28.8	12.80

[a] Protein value based upon dry matter (protein plus ash) after moisture and fat extraction. Totals for limb units divided by two to determine proximal and distal portions. This overestimates the value for the distal radius and tibia and underestimates the values for the proximal ends of these units.

[b] Total intramuscular fat values for the limb units are divided by two as for protein. This represents calorie yield for extracted fat.

[c] Calorie yield for extracted fat fraction.

[d] Calorie yield for extracted fat fraction.

[e] Carcass fat excludes omental and mesenteric depots, organ fat, and those depots listed in the other columns of this table. This total is for an arbitray 75 percent of rendered fat weight rather than an extracted fat fraction.

[f] Protein, intramuscular and carcass fat values for the axis, atlas, and third through seventh cervical vertebrae units are estimates based upon division of the complete cervical unit using 9 percent of total for the atlas, 11 percent for the axis, and 80 percent for the C3C7 unit.

[g] This includes all marrow from the ulna.

[h] Bone grease value for this unit includes the patella.

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Appendix D. Table 2. Calorie Yield of Carcass Products in SAM Side

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
SKWOT	1,858.80	558.90	---	---	1,589.00
ATLAS[f]	1,208.80	459.00	3.6	0.0	390.20
AXIS[f]	1,477.20	560.70	6.3	0.0	477.20
C3C7[f]	10,744.40	4,079.70	3.6	0.0	3,470.90
THOR	10,134.40	4,462.20	135.9	0.0	6,946.40
LUMB	8,824.40	2,386.80	205.2	0.0	7,968.40
SPEL	7,922.00	1,961.10	954.9	46.8	3,413.50
CAUD	120.40	29.70	5.4	0.0	67.50
RIBS	16,749.20	8,759.70	326.7	0.0	3,103.70
STER	6,208.80	2,315.70	44.1	0.0	4,799.30
SCAP	7,622.80	1,665.90	79.2	40.5	168.80
PHUM	3,775.80	454.50	662.4	818.1	228.15
DHUM	3,775.80	454.50	226.8	519.3	228.15
PRUL[g]	1,247.60	121.50	89.1	464.4	0.00
DRUL	1,247.60	121.50	264.6	309.6	0.00
CARP	0.00	0.00	48.6	0.0	0.00
PMTC	0.00	0.00	15.3	157.5	0.00
DMTC	0.00	0.00	86.4	72.9	0.00
APHA	0.00	0.00	88.2	16.2	18.20
PFEM	13,598.20	1,789.20	449.1	869.4	1,955.80
DFEM[h]	13,598.20	1,789.20	703.8	519.3	1,955.80
PTIB	1,732.60	79.65	353.7	905.4	177.85
DTIB	1,732.60	79.65	126.0	523.8	177.85

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Appendix D. Table 2. (continued)

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
TARS	0.00	0.00	230.4	0.0	67.50
PMTT	6.20	0.90	19.8	174.6	3.05
DMTT	6.20	0.90	144.0	66.6	3.05
PPHA	0.00	0.00	99.0	59.4	10.80

[a] Protein value based upon dry matter (protein plus ash) after moisture and fat extraction. Totals for limb units divided by two to determine proximal and distal portions. This overestimates the value for the distal radius and tibia and underestimates the values for the proximal ends of these units.

[b] Total intramuscular fat values for the limb units are divided by two as for protein. This represents calorie yield for extracted fat.

[c] Calorie yield for extracted fat fraction.

[d] Calorie yield for extracted fat fraction.

[e] Carcass fat excludes omental and mesenteric depots, organ fat, and those depots listed in the other columns of this table. This total is for an arbitray 75 percent of rendered fat weight rather than an extracted fat fraction.

[f] Protein, intramuscular and carcass fat values for the axis, atlas, and third through seventh cervical vertebrae units are estimates based upon division of the complete cervical unit using 9 percent of total for the atlas, 11 percent for the axis, and 80 percent for the C3C7 unit.

[g] This includes all marrow from the ulna.

[h] Bone grease value for this unit includes the patella.

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Appendix D. Table 3. Calorie Yield of Carcass Products in SAF Side

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
SKWOT[f]	1,453.60	774.90	---	---	1,609.90
ATLAS[g]	597.20	321.30	18.0	0.0	473.90
AXIS[g]	729.60	393.30	27.0	0.0	579.20
C3C7[g]	5,306.80	2,860.20	35.1	0.0	4,213.40
THOR	7,152.00	7,177.50	334.8	0.0	9,710.60
LUMB	7,188.00	3,196.80	219.6	0.0	12,776.40
SPEL	6,541.60	2,313.00	1,291.5	30.6	5,602.50
CAUD	114.80	79.20	61.2	0.0	263.90
RIBS	11,260.40	10,093.50	689.4	0.0	6,041.90
STER	4,166.40	2,468.70	7.2	0.0	6,647.40
SCAP	4,301.60	1,585.80	182.7	25.2	0.00
PHUM	2,849.00	1,073.70	747.0	403.2	655.10
DHUM	2,849.00	1,073.70	306.9	534.6	655.10
PRUL[h]	848.80	82.35	301.5	574.2	31.40
DRUL	848.80	82.35	517.5	199.8	31.40
CARP	0.00	0.00	96.3	0.0	0.00
PMTC	0.00	0.00	45.0	164.7	0.35
DMTC	0.00	0.00	190.8	37.8	0.35
APHA	0.00	0.00	255.6	10.8	39.80
PFEM	11,405.00	1,657.35	596.7	782.1	2,883.95
DFEM[i]	11,405.00	1,657.35	1,316.7	358.2	2,883.95
PTIB	1,150.00	180.00	691.2	671.4	68.85
DTIB	1,150.00	180.00	175.5	534.6	68.85

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Appendix D. Table 3. (continued)

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
TARS	0.00	0.00	332.1	0.0	35.10
PMTT	5.20	0.45	48.6	206.1	2.05
DMTT	5.20	0.45	244.8	59.4	2.05
PPHA	0.00	0.00	165.6	36.0	17.60

[a] Protein value based upon dry matter (protein plus ash) after moisture and fat extraction. Totals for limb units divided by two to determine proximal and distal portions. This overestimates the value for the distal radius and tibia and underestimates the values for the proximal ends of these units.

[b] Total intramuscular fat values for the limb units are divided by two as for protein. This represents calorie yield for extracted fat.

[c] Calorie yield for extracted fat fraction.

[d] Calorie yield for extracted fat fraction.

[e] Carcass fat excludes omental and mesenteric depots, organ fat, and those depots listed in the other columns of this table. This total is for an arbitray 75 percent of rendered fat weight rather than an extracted fat fraction.

[f] The protein and intramuscular fat values for this animal are estimated for the SKWOT unit.

[g] Protein, intramuscular and carcass fat values for the axis, atlas, and third through seventh cervical vertebrae units are estimates based upon division of the complete cervical unit using 9 percent of total for the atlas, 11 percent for the axis, and 80 percent for the C3C7 unit.

[h] This includes all marrow from the ulna.

[i] Bone grease value for this unit includes the patella.

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Appendix D. Table 4. Calorie Yield of Carcass Products in FAF Side

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
SKWOT	1,202.40	592.20	---	---	2,105.30
ATLAS[f]	982.80	403.20	27.0	0.0	456.30
AXIS[f]	1,201.20	493.20	12.6	0.0	557.60
C3C7[f]	8,737.20	3,587.40	98.1	0.0	4,056.80
THOR	7,336.40	5,246.10	311.4	0.0	8,654.90
LUMB	7,419.60	3,724.20	216.9	0.0	12,035.30
SPEL	5,422.40	1,871.10	795.6	51.3	4,876.20
CAUD	115.20	124.20	42.3	0.0	257.20
RIBS	12,580.80	6,992.10	812.7	0.0	5,399.30
STER	5,406.00	3,446.10	89.1	0.0	6,179.60
SCAP	5,113.60	2,163.60	190.8	0.0	585.90
PHUM	2,429.40	481.50	778.5	391.5	514.35
DHUM	2,429.40	481.50	278.1	421.2	514.35
PRUL[g]	860.00	27.90	183.6	431.1	202.85
DRUL	860.00	27.90	375.3	190.8	202.85
CARP	0.00	0.00	30.6	0.0	0.00
PMTC	0.00	0.00	45.0	175.5	44.20
DMTC	0.00	0.00	162.0	39.6	44.20
APHA	0.00	0.00	281.7	17.1	131.00
PFEM	10,585.60	1,694.70	452.7	657.0	3,696.30
DFEM[h]	10,585.60	1,694.70	747.9	308.7	3,696.30
PTIB	1,551.40	274.95	238.5	615.6	448.55
DTIB	1,551.40	274.95	189.9	445.5	448.55

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Appendix D. Table 4. (continued)

Unit	Protein[a] (kcal)	Intramuscular[b] Fat (kcal)	Bone Grease[c] Fat (kcal)	Marrow[d] Fat (kcal)	Carcass[e] Fat (kcal)
TARS	0.00	0.00	195.3	0.0	159.30
PMTT	6.00	2.70	30.6	189.0	100.60
DMTT	6.00	2.70	189.0	90.0	100.60
PPHA	0.00	0.00	232.2	42.3	91.80

[a] Protein value based upon dry matter (protein plus ash) after moisture and fat extraction. Totals for limb units divided by two to determine proximal and distal portions. This overestimates the value for the distal radius and tibia and underestimates the values for the proximal ends of these units.

[b] Total intramuscular fat values for the limb units are divided by two as for protein. This represents calorie yield for extracted fat.

[c] Calorie yield for extracted fat fraction.

[d] Calorie yield for extracted fat fraction.

[e] Carcass fat excludes omental and mesenteric depots, organ fat, and those depots listed in the other columns of this table. This total is for an arbitray 75 percent of rendered fat weight rather than an extracted fat fraction.

[f] Protein, intramuscular and carcass fat values for the axis, atlas, and third through seventh cervical vertebrae units are estimates based upon division of the complete cervical unit using 9 percent of the total for the atlas, 11 percent for the axis, and 80 percent for the C3C7 unit.

[g] This includes all marrow from the ulna.

[h] Bone grease value for this unit includes the patella.

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