University of Nevada, Reno

Effects of prescribed and wild fires on pine regeneration: the role of seed dispersal by animals

A dissertation submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy in the Program of Ecology, Evolution, and Conservation Biology

By

Jennifer S. Briggs

Dr. Stephen B. Vander Wall
Dissertation Advisor
May 2003

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

**UNIVERSITY
OF NEVADA
RENO**

THE GRADUATE SCHOOL

We recommend that the dissertation
prepared under our supervision by

Jennifer Briggs

entitled

**Effects of prescribed and wildfires on pine regeneration:
the role of seed dispersal by animals**

be accepted in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

Stephen B. Vander Wall
Stephen B. Vander Wall, Ph.D., Advisor

Jeanne C. Chambers, Ph. D., Committee Member

Stephen H. Jenkins, Ph. D., Committee Member

Dennis D. Murphy, Ph. D., Committee Member

, Committee Member

Scott Slovic, Ph. D., Graduate School Representative

Marsha H. Read
Marsha H. Read, Ph. D., Associate Dean, Graduate School

May, 2003

Abstract

As large-scale wildfires are becoming frequent in semi-arid western forests after decades of fire suppression, detailed knowledge of post-fire regeneration dynamics is critical to inform management and restoration efforts. Experiments in unburned forest showed that several species of granivorous rodents (*Tamias amoenus*, *T. speciosus*, *Peromyscus maniculatus* and *Spermophilous lateralis*) cached pine seeds in microsites in which seedling emergence and survival was significantly higher than in microsites typical of wind dispersal. I examined the effects of fire on several aspects of this interaction. A laboratory study suggested that changes in the forest floor after fire may affect the mechanisms, e.g. olfaction and spatial memory, by which rodents find, cache and retrieve seeds. In ash arenas, chipmunks made greater or equal numbers of caches than in sand, retrieved high proportions of their own caches, but detected significantly fewer caches made by others. This suggests that olfaction is less effective in ash and that ash may represent a secure location for storing seeds to avoid pilferage.

In field studies before and after prescribed fires, I found that rodent communities declined for only 1 yr after the burns, with species composition remaining relatively constant. At a wildfire site, this was not the case: deer mice dominated after 2 yr of low captures. On all burned plots, animals' foraging rates reflected the size of the communities, and were significantly slower than in unburned plots for only 1-5 months after fires. The frequency of natural caching observed in burned areas was low, and difficult to detect due to drought. However, an artificial cache study found significant advantages for seeds planted both before and after fires at the depths and in the microsites (mineral soil under shrubs) often used by animals for caching. Emergence was equal, and survival greater, than that of seeds on control plots. At an older wildfire site, saplings grew significantly faster in the middle of the burned area than on the edge. These results suggest that seed-dispersing rodents can facilitate succession after fires, especially the low-intensity, patchy burns that may mimic the natural disturbance regime in yellow pine forests.

Acknowledgments

I would like to thank my advisor, Dr. Steve Vander Wall, for his continual encouragement, guidance, and patience over the last five years. He was always available and willing to assist with every aspect of my research, from design to fieldwork to analysis. However, he allowed me the freedom to develop and test my own ideas, to work independently, and to communicate and collaborate with forest managers. I learned a great deal from him both directly and indirectly, by observing his dedication to his own field research and his incredible productivity as a scientist, writer and teacher. I am also very grateful for his assistance with the numerous logistics and expenses of field research and his loans of supplies, vehicles, and field assistants as needed. Finally, I appreciate the friendship and hospitality that Steve and his wife Kathie generously extend to all their graduate students.

The other members of my committee also contributed to the development of my research and general progress. I have continually consulted Dr. Steve Jenkins (Biology and E.E.C.B.) about experimental design and statistics, especially during recent months. I thank him for writing a computer program that I used in the analyses for Chapter 1, and for numerous thoughtful responses to my questions, papers and manuscripts over the years. Dr. Jeanne Chambers (E.R.S. and U.S.F.S.) initially encouraged me to combine my interests in seed dispersal with my interests in forest management and fire, and has always reminded me to consider "the perspective of the seed" in the study of plant-animal interactions. Dr. Dennis Murphy (E.E.C.B) has helped me to develop a conservation-oriented context for my research and gave me valuable opportunities to work with local management agencies. Dr. Scott Slovic (Center for the Environmental Arts and Humanities) prompted me to look at my work in a new light and improve the ways in which I communicate my goals and findings to others.

Mo Beck, although a fellow graduate student, deserves an honorary place on my committee after generously and tirelessly helping me with countless analyses, computer

programs, and a thousand questions. Other past and present members of the Vander Wall lab, notably Julie Roth and Ted Thayer, have provided invaluable assistance and friendship over the years, especially during marathon days in the field. Many other graduate students helped me to develop ideas, learn new skills, and stay sane towards the end of each six-month field season: thanks to them all. Finally, I have been fortunate to have an incredibly energetic, insightful and entertaining series of field assistants and interns: Genevieve Torres, who was a valuable partner in this research for two seasons; and Jennifer Armstrong, Megan Blees, Molly Hendrick, Chizuko Suzuki and Richard Wilson.

I am extremely grateful to the Incline Village General Improvement District and the North Lake Tahoe Fire Department for permission to work with their prescribed burn program. Norb Szczurek and Mitch Geissinger (NLTFPD) allowed me to set up before- and after-experiments and thus provided me with an ideal study system as well as an education in how to use fire as a management tool. I also appreciated their friendship and some really tasty barbecued lunches on the burn plots over the years. I thank the Board of Directors of U.N.R.'s Whittell Forest and Wildlife Area for funding two summers of research in Little Valley. The Nevada Biodiversity Initiative, the E.E.C.B program and the Graduate Student Association at UNR also provided critical financial support.

My kind and patient relatives (the Hodge, Arnon and Briggs families) and friends encouraged me throughout my graduate program, helping me to celebrate every landmark and recover from every setback along the way. I would especially like to thank my parents and sisters for their unwavering support, interest, and enthusiasm, even from a long distance. Finally, for helping me with every possible aspect of field research, writing, academics, and everyday life, I thank my husband Rich. His friendship and partnership have made our joint progress through graduate school an adventure as well as a challenge.

Table of Contents

General Introduction

Interactions among species in ecological communities are affected by disturbances that alter probabilities of colonization and extinction (MacMahon 1980) and influence the subsequent regeneration and recovery of all processes and components of the ecosystem (Meffe and Carroll 1994). Succession, the changes in species composition and abundance flowing a disturbance, varies significantly according to the size, intensity and scale of the disturbance. Following Clements (1916), several models have attempted to describe and quantify successional processes in a wide variety of communities (e.g. Connell and Slatyer 1977, McCook 1994). Many of these models focus on plant species and their competitive interactions, as plants are the most obvious early colonists of disturbed sites (Connell and Slatyer 1977). Past research has perhaps underestimated the degree to which animals influence the course of plant succession through their herbivorous, granivorous, dispersive or pathogenic interactions with plants.

In particular, seed dispersal appears to be a much more dynamic and complex process than scientists traditionally assumed (Chambers and MacMahon 1994). Seeds and fruits of many species may be dispersed by abiotic processes such as wind or actively removed from trees by animals. But not all wind-dispersed propagules simply remain on the forest floor below or near the parent tree. Many are rapidly removed from the soil surface by animals and subjected to subsequent vertical or horizontal movements, i.e. they may be transported, deposited, and cached in a variety of sites (Chambers and MacMahon 1994).

Many studies have described the significant role of frugivorous and granivorous birds and mammals in the dispersal of seeds of trees in both temperate and tropical forests, (e.g. Howe and Smallwood 1982, Schupp et al. 1989, Vander Wall 1993, Loiselle et al. 1996, Wenny and Levey 1998). By first transporting and then either hoarding (granivores) or defecating (frugivores) seeds at a distance from the parent tree, animals may confer several benefits on seeds (if they are not later retrieved or consumed). Howe and Smallwood (1982) describe three major advantages of dispersal; seeds taken from the tree may a) escape density dependent mortality beneath the parent plant; b) colonize distant or new habitats; or c) reach microsites in which their survival is disproportionately high (Howe and Smallwood 1982). However, few studies have addressed the effects of disturbances on the nature and outcomes of these plant-animal interactions (but see Johnson et al 1997, McClanahan and Wolfe 1993), or compared the fates of seeds and seedlings dispersed by biotic vs. abiotic processes in disturbed as well as undisturbed habitat (Tomback 1996, Wunderle 1997).

In forested ecosystems, animal-mediated seed dispersal may significantly affect the ability of plant species to colonize gaps in the forest canopy created by disturbances such as fire, logging or storms. These gaps are often discrete, representing a different type of habitat than the surrounding forest matrix, and secondary succession within them can be rapid (Whitmore 1989), especially if accelerated by animal-mediated dispersal. Investigations of these processes are important in landscapes affected by frequent anthropogenic as well as natural disturbances, or in ecosystems in which managers wish to simulate pre-settlement disturbance regimes (Kilgore 1973, Hardy and Arno 1996). The studies I describe here were designed to complement and extend previous research by exploring the role of granivorous rodents in the dispersal of pine seeds following natural and prescribed fire in the eastern Sierra Nevada.

In the semi-arid yellow pine forests of many western states, rodents such as chipmunks (*Tamius* spp.) and deer mice (*Peromyscus maniculatus*) scatter-hoard such large numbers of pine seeds, many of which germinate before they are recovered and consumed (Vander Wall 1992a, 1992b), that some researchers have speculated that their activities may actually accelerate forest succession (Saigo 1969, Sherman and Chilcote 1972, Vander Wall 1993). This phenomenon was observed and appreciated, in a different type of forest, by Thoreau in the 1850s. He described the squirrels and jays in eastern deciduous woods as "forest planters…our greatest and almost only benefactors" and commented that "our oak forests, vast and indispensable as they are, were produced by a kind of accident, that is, by the failure of animals to reap the fruits of their labors" (Thoreau 1993, p. 130).

Subsequent generations of biologists and foresters, however, emphasized that these rodents are important predators as well as dispersers of pine seeds, and may consume a large proportion of the seeds they handle and cache (Tevis 1953, Smith and Aldous 1946). Many studies between 1920 and 1970 condemned and attempted to limit the "voracious" seed consumption by forest rodents and birds that "prevented the successful regeneration" of conifers by either natural reproduction or artificial seeding practices (Smith and Aldous 1946 and references therein; Ahlgren 1966). Ultimately, the long-term reproductive benefits and costs of animal-mediated dispersal for the tree are determined by the annual variation in both the seed crops of conifers and b) the population sizes of granivorous rodents. The net effect on the plant is represented by the proportion of seeds that escape consumption and survive to germination (Price and

Jenkins 1986, Schnurr et al 2002). Many other factors, such as annual precipitation and local disturbance regimes, also affect the outcome of this interaction.

Fire, a major natural and anthropogenic disturbance in western pine forests, may influence the interaction between rodents and pines both directly (e.g. by causing mortality of both animals and plants) or indirectly (e.g. by altering the nature of the available habitat or substrate). Effects vary with fire intensity; both wild and prescribed fires can create heterogeneity in forest structure and composition depending on factors such as topography, weather conditions, and fuel abundance (Kilgore 1973, Kauffman and Martin 1989). Even fires of similar intensity have different effects on different species: deer mice often colonize burned areas in higher numbers than before (Ahlgren 1966, Bock and Bock 1983, Kreftig and Ahlgren 1974) but studies of chipmunks' responses have been inconclusive or contradictory (M'Closkey 1975, McGee 1982, Sullivan et al 1999). Little is known about how the behavior of animals (most importantly their foraging and caching behavior) may be affected by postfire conditions, even if animals do remain in or near burned habitats.

In unburned ecosystems, granivorous animals make caches of seeds in a variety of microsites (Vander Wall 1993, Hutchins et al 1996, Price et al 2000) that may be selected for several different reasons. Cache sites may simply reflect preferences and patterns of habitat use by the rodents; many animals integrate attributes of vegetation such as species composition and diversity of food supply in their selection of habitat (Parmenter and MacMahon 1983). Alternatively, cache sites may be selected that increase the ability of animals to recover caches later, or decrease the probability of pilferage by other individuals (Vander Wall 1990, Leaver and Daly 2001).

The timing of a fire relative to the maturation of seed crops or to animals' burial of those seeds will influence subsequent establishment of seedlings, if depth and location of burial affect probabilities of seed mortality during and after fires. Variation among the microsites of cached seeds will also influence subsequent survival of seedlings, based on abiotic factors such as the nutrients, soil moisture and light levels available to the emerging seedlings (Callaway and Walker 1997, Chambers 2001).

Currently, both the spatial and temporal components of the fire cycle in pine ecosystems are significantly different from historical patterns, and this change poses an increasingly serious challenge for forest managers. Prior to European settlement, naturally occurring low intensity fires in western yellow-pine forests frequently burned the understory during summer and fall, clearing patches of accumulated litter, shrubs and dead wood (Weaver 1961, McKelvey et al 1996, Facelli and Pickett 1991). Estimates of median fire return intervals, derived from many studies in the Sierra Nevada, are 11 and 15 years for ponderosa and mixed conifer-pine forests, respectively (McKelvey et al 1996). Frequent, low-intensity fires expose mineral soil, release nutrients, and allow more light to reach the forest floor (Kauffmann and Martin 1988, Agee 1998). Their patchy effects often preserve some sources of seeds and shelter which may support resident or recolonizing rodent populations. Dispersal of seeds by these animals into areas cleared by fire might allow seeds to reach microsites whose abiotic characteristics promote successful establishment and growth.

As contemporary fire suppression regimes have significantly altered previous patterns of disturbance and succession, naturally occurring low-intensity fires are now rare in western states (Kilgore 1973, McKelvey et al 1996). Fuel loads, which include increasingly large proportions of insect-damaged trees, have now reached such high levels in most forests that wildfires tend to clear the understory completely (Weaver 1961) and force many species of small mammals to abandon an area due to lack of cover and food (Parmenter and MacMahon 1983) instead of remaining to exploit and shape the early stages of secondary succession (McGee 1982). For forest managers and ecologists, it is increasingly important to quantify and compare the effects of both high-intensity wildfires and lower-intensity prescribed burns on key ecosystem processes such as seed dispersal.

The objectives of this study were to assess the relative contribution of biotic and abiotic processes to the regeneration of Jeffrey pine after fire, and to examine the effects of prescribed and wild fires on several aspects of the interaction between the plant and the rodent species that disperse its seeds. I addressed the following questions in the three parts of this study:

Chapter 1: Caching of Jeffrey pine seeds by four species of forest rodents: consequences of microsite selection for seedling establishment

a) In unburned Jeffrey pine forests, how does caching behavior differ among the four most common species of scatter-hoarding rodents?

b) Do animals select cache sites randomly in their habitat, or do they use certain microsites relatively more frequently than others?

c) What are the effects of caching by animals (in terms of the size, depth and microsite characteristics of their caches) on the emergence and survival of pine seedlings?

d) What are the effects of seed dispersal by wind on seedling emergence and survival?

e) Is there evidence that animals perform "directed dispersal" of seeds to sites that are especially favorable for seedling establishment?

These questions were examined in field experiments in unburned forests.

Chapter 2: The foraging success and caching frequency of chipmunks in ash versus sand substrates

a) If a fire burns the forest floor, does the change in substrate type (i.e. the presence of ash) influence the way in which rodents find, cache and retrieve seeds?

b) Do animals cache as frequently in ash?

c) How effective are olfaction and previous experience (spatial memory) in allowing animals to recover the seeds they have buried in burned versus unburned substrates?

These questions were addressed in a laboratory experiment, and the implications of the results for the degree of caching and consumption or pilferage of caches in burned forests are discussed.

Chapter 3: Effects of fire on the interactions between Jeffrey pine and seed-caching rodents

a) How are animal communities in pine forests affected by fire?

b) How does fire affect biotic interactions between animals and seeds, such as the rate of foraging on the forest floor for buried or visible seeds, the frequency of caching, the placement of caches in different microsites, and the degree of predation on emerging seedlings?

c) How do the fates of pine seeds cached by animals vs. seeds dispersed by wind differ when they are dispersed before a fire vs. after a fire?

d) How do these processes vary at the sites of wild vs. prescribed fires?

e) Over time, how does animal-mediated dispersal contribute to forest structure after a wildfire?

Questions a)- d) were investigated at the sites of several recent prescribed burns (1999-2001) and a recent wildfire (1999); question e) was examined at the site of a wildfire which occurred in 1981.

LITERATURE CITED

Agee JK, 1998. Fire in pine ecosystems. In: Ecology and Biogeography of Pinus (Richardson DM, ed). Cambridge: Cambridge University Press; 193-218.

Ahlgren CE, 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry 64:614-617.

Bock CE, Bock JH, 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. Journal of Wildlife Managment 47:836-840.

Callaway RM, DeLucia EH, Moore D, Nowak R, Schlesinger WH, 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77:2130-2141.

Chambers JC, 2001. Pinus monophylla establishment in an expanding Pinus juniperus woodland:environmental conditions, facilitation and interaction factors. Journal of Vegetation Science 12:27-40.

Chambers JC, MacMahon JA, 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Clements FE (1916) Plant succession: An analysis of the development of vegetation. Carnegie Inst. Washington Publ. No. 42.

Connell JH and RO Slatyer (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144

Hardy CC and SF Arno, eds. 1996. The use of fire in ecological restoration. USFS Gen Tech Rept INT GTR-341. Ogden, UT

Howe HF, Smallwood J, 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Johnson WC, Adkisson CS, Crow TR, Dixon MD, 1997. Nut caching by blue jays (Cyanocitta cristata L.): Implications for tree demography. American Midland Naturalist 138:357-370.

Kauffman JB, Martin RE, 1988. Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Canadian Journal of Forest Research:455-462.

Kilgore BM, 1973. The ecological role of fire in Sierran conifer forests. Quaternary Research 3:496-513.

Krefting L, Ahlgren WA. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. Ecology 55:1391-1398.

Leaver LA, Daly M, 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia 127.

Loiselle BA, E.Ribbens, and O. Vargas, 1996. Spatial and temporal variation of seed rain in a tropical lowland wet forest. Biotropica 28:82-95.

MacMahon JA, 1980. Ecosystems over time: succession and other types of change. In: Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th annual Biology colloquium. (Waring RH, ed). Oregon State University, Corvallis, Oregon.; 27-57.

MacMahon JA (1980) Ecosystems over time: Succession and other types of change. In: Forests: Fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biology Colloquium (1979), (R H Waring, ed.), Oregon State University Press, Corvallis, OR. 1980.

McClanahan TR and RW Wolfe (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. Cons. Bio 7: 279-289

M'Closkey RM (1975) Habitat succession and rodent distribution. J. Mamm. 56: 950-955

McGee JM (1982) Small mammal populations in an unburned and early fire successional sagebrush community. J. Range Mgmt 35: 177-179

Meffe GK and CR Carroll 1994. Principles of Conservation Biology. Sinauer Assoc. Sunderland, MA

McCloskey JM, 1975. Habitat succession and rodent distribution. Journal of Mammalogy 56:950-955.

McCook LH, 1994. Understanding ecological community succession: causal models and theories, a review. Vegetatio 110:115-147.

McGee JM, 1982. Small mammal populations in an unburned and early fire successional sagebrush community. Journal of Range Management 35:177-179.

McKelvey KS, 1996. An overview of fire in the Sierra Nevada. Sierra Nevada Ecosystem Project: Final report to Congress, vol II.:1033-1040.

Price MA, Jenkins SH, 1986. Rodents as seed consumers and dispersers. In: Seed dispersal (Murray DR, ed). Orlando, FL: Academic Press; 191-235.

Price MV, Waser NM, McDonald S, 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. Journal of Mammalogy 81:97-106.

Saigo BW, 1969. The relationship of non-recovered rodent caches to the natural regeneration of ponderosa pine. Master's Thesis Oregon State University, Corvallis, OR.

Schnurr JL, Ostfeld RS, Canham CD, 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. Oikos 96:402-410.

Sherman RJaWWC, 1972. Spatial and chronological patterns of *Purshia tridentata* as influenced by *Pinus ponderosa*. Ecology 53:294-298.

Smith CF, Aldous SE, 1946. The influence of mammals and birds in retarding artificial natural reseeding of coniferous forests in United States. Annual Review of Ecology and Systematics 13:201-228.

Sullivan TP, Boateng JO, 1996. Comparison of small-mammal community responses to broadcast burning and herbicide application in cutover forest habitats. Canadian Journal of Forest Research 26:462-473.

Tevis L, 1953. Effect of vertebrate animals on seed crop of sugar pine. Journal of Wildlife Management 17:128-131.

Thoreau, HD. 1993. Faith in a seed. (Written in 1856-1860). Island Press, Covelo CA

Tomback DF, 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono 33:100-110.

Vander Wall SB, 1990. Food hoarding in animals. Chicago: University of Chicago Press.

Vander Wall SB, 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). Oecologia 96:246-252.

Weaver H, 1961. Ecological changes in the ponderosa pine forest of Cedar Valley in Southern Washing. Ecology 42:416-420.

Wenny DG, Levey DJ, 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences of the United States of America 95:6204-6207.

West NE, 1968. Rodent-influenced establishment of poderosa pine and bitterbrush seedlings in Central Oregon. Ecology 49:1009-1011.

Whitmore TC, 1989. Canopy gaps and the two major groups of forest types. Ecology 70:536-538.

Chapter 1: Caching of Jeffrey pine seeds by four species of forest rodents: consequences of microsite selection for seedling emergence and survival

ABSTRACT

Granivorous rodents play an important role in the seed dispersal of many tree species in semi-arid western forests. We quantified and compared the caching behavior of four species that are known consumers and dispersers of Jeffrey pine (*Pinus jeffreyi*) seeds in the yellow-pine forests of the Sierra Nevada: deer mice (*Peromyscus maniculatus*), golden-mantled ground squirrels (*Spermophilus lateralis*), yellow-pine chipmunks (*Tamias amoenus*) and lodgepole chipmunks (*T. speciosus*). Trials in field enclosures revealed that cache size and depth differed significantly among species, increasing with body size (n = 8-10 animals per species). Compositional analysis indicated that, as a "community", the four species did not select microsites for caching in proportion to their availability, but placed significantly more caches in mineral soil under shrubs than in any other microsite. To compare the effects of animal-mediated vs. abiotic dispersal on the emergence of pine seeds and survival of seedlings, we buried seeds in the same range of depths, microsites and substrate types that animals had used in the first experiment, as well as placing some seeds in sites that simulated dispersal by wind. Seedling emergence was significantly greater at depths typical of animal caches than at the soil surface. More seeds emerged in mineral soil than in litter, and seedlings survived for significantly longer periods, in the same microsite (mineral soil under shrubs) in which animals had placed the highest total number of caches. Thus, these animals' activities may represent a form of "directed dispersal" which could facilitate the regeneration of Jeffrey pine if seed availability is high and abiotic conditions are favorable.

INTRODUCTION

Many species of mammals and birds remove, store and consume the propagules of plants (Vander Wall 1990). If stored seeds germinate before they are retrieved, the plant receives a reproductive service from the animals' actions that may be of higher value than if dispersal had occurred by abiotic mechanisms alone. Seed burial often enhances the probability of germination and extends the time of seedling survival by allowing seeds to escape both abiotic (e.g. desiccation, heat stress) and biotic (e.g. predation) threats (Chambers 2001, Forget 1994, Schupp 1995). An understanding of plant-animal interactions such as seed dispersal can offer insights into both the evolutionary history and the future trajectories of the ecosystem-level processes to which they contribute (Nathan and Muller-Landau, 2000).

As our awareness of the dynamic, multistage nature of seed dispersal increases (Chambers and MacMahon 1994, Levey et al. 2002), researchers have assessed interactions among entire communities of seed dispersers and consumers, often including multiple taxa such as ants, beetles, mammals and birds (e.g. Levey and Byrne 1993, Hulme 1997, McAuliffe 1990), in a wide range of ecosystems (e.g. deserts, Breck and Jenkins 1997, Leaver and Daly 2001; tropical forests, Forget 1993, Wenny and Levey 1998; temperate forests, Hutchins et al. 1995; and semi-arid forests, Hutchins and Lanner 1982, Hollander and Vander Wall, submitted). Few community-level studies have been able to quantify the range of impacts of seed dispersers and consumers on reproduction of the plants they disperse, although many have discussed such consequences or examined a subset of seed fates (e.g. Hutchins and Lanner 1982, Vander Wall 1997). Studies which have linked the fates of seeds and seedlings to the activities of known dispersal agents demonstrate that the effectiveness of dispersal varies among species in terms of both quantity and quality (Schupp 1993). Certain species can provide “directed dispersal” (Howe and Smallwood 1982) of seeds to sites in which their chances of establishment are greatly enhanced (Hulme 1997,Wenny and Levey 1998, Hollander and Vander Wall, submitted).

Caches of seeds made by different species of animals may differ in at least three ways that have interactive as well as separate effects on seed emergence and seedling survival. First, the size of caches varies with physical characteristics of the animal, such as body mass and metabolic needs (Lucas et al. 1993, Price et al. 2000), size of the physical structure used to transport seeds (Bowers and Ellis 1993); and ability to defend stores from competitors (Leaver and Daly 2001, Jenkins and Breck 1998). Second, the depth of caches may vary, even within the range in which stores are classified as “scatter-hoarded”. The significantly larger larder hoards made by many species are often placed in burrows so far below the surface that germinating seeds could never emerge (Price and Jenkins 1986). The depth of scattered caches may be influenced by energetic constraints on burial and retrieval efforts, nature and hardness of substrates, facilitation of later retrieval (burial closer to the surface may enhance a cache’s detectability via olfaction, if the animal’s memory of the site declines) or minimization of losses due to pilferage or spoilage (Vander Wall 1993b).

Third, animals place caches in microsites whose characteristics vary widely, reflecting the habitat use patterns and specific behaviors of the individual cacher or of the species to which it belongs (Breck and Jenkins 1997, Price et al. 2000). The microsites in which animals bury seeds represent a suite of biotic and abiotic limitations on the future establishment of plants from those seeds (Chambers and MacMahon 1994, Vander Wall 1994, Seiwa et al. 2002). Especially in arid or semi-arid environments, both germination and survival are significantly affected by substrate type, soil moisture and temperature, nutrient availability, shading or competition from under- or over-story species, predation, and interactions among all these factors (Chambers 2001, Ibanez and Schupp 2001, Callaway et al. 1996, Shelton 1995). Dispersal by animals may expose seeds to different combinations of these conditions than they would encounter through abiotic dispersal alone, regardless of the degree to which plant propagules appear to be adapted for one or both dispersal modes.

Thus, an improved understanding of the caching behavior of all species known to scatter-hoard seeds of a given plant, combined with an analysis of seed fates at different depths, microsites and cache sizes typical of biotic vs. abiotic dispersal processes, should allow researchers to predict many ecological (and perhaps evolutionary) consequences for the regeneration dynamics of the plant. We compared the caching behavior of four species of rodents known to be important “secondary” dispersers of Jeffrey pine at our study sites in the eastern Sierra Nevada (Vander Wall 2002a; pers. obs.) and assessed the effects of their different microsite selection patterns and caching depths on seedling emergence and survival (Hollander and Vander Wall, submitted). In addition, we evaluated the ways in which the mechanisms and effects of dispersal by these species differed from those of dispersal by wind. In yellow pine forests, the dominant dispersal pathway is a two-step process in which the large, winged seeds are released from ripe cones in early autumn, fall to the forest floor (primary dispersal) and are then either consumed or removed and stored by many vertebrate species (secondary dispersal, Vander Wall 1992).

Our study had two components. First, we presented radiolabeled seeds to animals in field enclosures and recorded the characteristics and locations of the all caches they made during trials lasting 1-2 days. We used compositional analysis (Aebischer et al. 1993) to determine whether and how animals' use of microsites for caching differed from the availability of these microsites. If use was non-random, we evaluated which types of substrates and microsites were used more often than others. Second, we buried artificial caches in a range of microsites and depths that reflected the animal-dispersal patterns we observed in the caching trials, as well as in sites and at depths that simulated dispersal of seeds by wind. We tested the general hypotheses that rodent species would differ in the size, depth, and microsite placement of their caches; that use of microsites by all species would be significantly different than random; and that emergence and survival of seedlings in sites and at depths typical of animal dispersal would be significantly higher than those of seeds in sites and at depths typical of wind dispersal.

METHODS

1. Caching behavior of four rodent species

We conducted caching trials over the course of 6 seasons (June- November of 1997-2002) in the Whittell Forest and Wildlife Area (Little Valley), NV. Little Valley is located in the Carson Range of the Sierra Nevada, approximately 30 km south of Reno, NV at an elevation of 1975 m (39° 15′ 10" N, 119° 52′ 35" W). Open stands of Jeffrey pine (*Pinus jeffreyi*) with a bitterbrush (*Purshia tridentata*) understory occur on sandy, decomposed granite soils (Marla series, Johnson et al. 1997). Individuals of 4 rodent species (*Peromyscus maniculatus, Tamias amoenus, Tamias speciosus* and *Spermophilus lateralis*) were trapped at the site; *P. maniculatus* and *T. amoenus* were tested between June and September 1997-9; *T. speciosus* and *S. lateralis* were tested between June and November 2000-02. The data on *P. maniculatus* and *T. amoenus* were gathered in the course of studies published elsewhere (Vander Wall 2000, Vander Wall et al. 2001), but have not previously been reported in the context or analyzed using the methods we describe here.

We conducted trials in five 10 x 10 m fenced enclosures located throughout the valley in Jeffrey pine-bitterbrush habitat. Each enclosure contained similar proportions of bitterbrush shrubs and a few sapling Jeffrey or lodgepole pines (*Pinus contorta*). The walls of the enclosures (1 m high) were made from 5 mm wire mesh. To prevent entrance or exit by rodents, walls extended 45 cm below ground, and were lined with metal flashing 75 cm above ground. Subjects were initially released into an artificial nest bucket buried below ground. During trials conducted in late fall, we placed cotton in the nest buckets. Water was available in the enclosures at all times. At the start of all trials, we placed 150 Jeffrey pine seeds in a wooden feeder box, covered to prevent the entrance of birds but permit the entrance of rodents. Seeds had been labeled with an aqueous solution of scandium-46 (procedure described in Vander Wall, 1992). After 12 hours, we checked the feeder box and if more than 90% of seeds had been taken, the animal was removed from the enclosure. If not, the animal was allowed to forage for up to 48 additional hours. At this point, trials were terminated.

Once the animal had been removed, we surveyed the enclosure using Geiger counters to detect the locations of cached seeds and to retrieve shells of eaten seeds. If no seeds had been removed, or if all seeds had been eaten and no caches had been made, we initiated a new trial. In total, we tested 15 *P. maniculatus*, 12 *T. amoenus*, 27 *T. speciosus*, and 26 *S. lateralis*. Ten *P. maniculatus*, 10 *T. amoenus*, 9 *T. speciosus* and 4 *S. lateralis* made sufficient numbers of caches to be included in all analyses. (5 caches was the minimum sample size deemed necessary for an individual to be included in the compositional analysis; see Discussion and Aebischer et al 1993). We included the data from 4 other *S. lateralis* and one *T. speciosus* (n = 1, 3 or 4 caches) in certain analyses because the proportions of seeds they cached was comparable to the proportions cached by other subjects. The mean body mass (± 1SD) for each species, based on these 38 individuals, was 18.3 ± 2.5 g for *P. maniculatus*, 41.8 ± 4.8g for *T. amoenus*, 72.2 ± 3.7g for *T. speciosus*, and 167.1 ± 17.8g for *S. lateralis*.

At each cache site, we measured the "top" depth of the cache (distance in mm between the soil surface and the top of the buried seeds; hereafter referred to simply as "depth"). We removed and counted the seeds and recorded the microsite characteristics of each cache site (substrate type, distance to the edge of the nearest shrub canopy, understory species if present, and overstory species if present). We identified three categories of substrate: mineral soil (decomposed granite); light litter (dead plant matter, e.g. leaves or needles, 1-10 mm in depth); and heavy litter (plant matter, usually pine needles, > 10mm in depth). The understory was classified as 'open' (no plants directly above the cache); 'shrub'; or 'other' (e.g. grass, forbs). Understory species were combined, as bitterbrush accounted for approximately 90% of the understory in each enclosure. Overstory was classified as ‘open’ (no tree directly above the cache), ‘pine’ or ‘other’ (e.g. aspen).

To measure the availability of different microsite types, we created a set of randomly selected ‘cache sites’ to match the actual set of caches made by each animal. First, we randomly generated x, y co-ordinates of points in the enclosure in which each animal had been tested. We eliminated all points that fell in areas of the enclosure not actually used for caching by that animal (i.e. outside a line drawn within 0.5 m of the outermost cache sites). We then located each randomly selected point, and recorded the same characteristics of the microsite (substrate, understory and overstory) as we had measured for the actual caches. To represent the total availability of different types of microsites in the entire area accessible to each animal, we combined the sets of random points sampled within each of the five enclosures. An individual animal’s choice of cache sites could then be compared to the proportions of microsite types available within its enclosure (reflected by the data from the random points) in a compositional analysis (Aebischer et al. 1993). Sample sizes of random points were similar in each enclosure: 148, 175, 178, 185, and 186 random points representing the caches of 8, 8, 5, 6 and 11 animals respectively. At least one individual of each species was tested in each enclosure. Sample sizes for ‘available’ habitat were identical for animals tested in the same enclosure. No overstory data were gathered in deer mouse trials, so sample sizes were lower (between 84 and 125) in that category than in the others.

Analyses

Cache size and depth

We performed a MANOVA, followed by separate univariate ANOVAs, to test the hypotheses that mean cache size and mean minimum depth of caches would differ among the four species. Tukey's pairwise comparisons were used to identify any significant differences between all possible pairs of species. All caches made by all animals were included, unless minimum depths had not been recorded due to disruption of the cache site during excavation. Caches with missing depth data were excluded from all subsequent analyses, and animals with more than 25% missing depth data were excluded completely.

Microsite use: differences among species

We performed compositional analyses (Aebischer et al. 1993) to compare species' use of different microsites relative to their availability, in the three categories substrate, understory and overstory. The individual subject was used as the unit of replication in all comparisons within and among species (Aebischer et al. 1993). For each animal, proportions of utilized and available microsite types were first converted to log-ratios within categories. The proportion of caches made in one type of microsite was used as the denominator in all log-ratios within that category. A "difference" matrix was generated for each species by subtracting the log-ratios representing available cache sites from the log-ratios representing utilized cache sites, for each microsite type in each category for each animal (Aebischer et al. 1993). To reflect the variation among animals in caching frequency (the range was 1- 109), these differences in log-ratios were weighted by the square root of the number of caches the animal had made (Aebischer et al. 1993).

Microsite use and preferences for each species

We examined the "difference" matrices for each species separately to identify significant departures from random use of microsites in each category, i.e. to test the general null hypothesis that the difference values were equivalent to zero (Aebischer et al. 1993). As departures from multivariate normality were identified (by visual inspections of plots of the data) in the many of the difference matrices we generated, we used Monte Carlo simulations to assess whether microsite use was significantly different from random. Positive and negative signs were assigned with equal probability to each value in 999 simulations of the original data.

If the Monte Carlo simulations revealed a significant departure from random use of microsites, we performed the second step of the analysis: ranking the microsite types according to 'preference' for each species (Aebischer et al. 1993). Throughout this paper, we use the term "preferred" to describe more frequent use of a microsite, either in relation to its availability or in relation to the frequency of use of another type of microsite.

For all subjects, log-ratios of proportions of caches made in each type of microsite were calculated for all possible pairs of microsite types within a category (unlike Step 1, above, in which one microsite type served as the denominator in all ratios). The differences between the log-ratios representing availability vs. use were then analyzed in post-hoc 1-sample t-tests, to identify significant differences from an expected mean of zero. The signs (i.e. positive or negative) of all t-values obtained from comparisons of all pairs of microsite types were entered in a matrix for each species. In any given column, we counted the number of either positive or negative signs to obtain the relative rank of the microsite type in that column with respect to all the other microsite types (Aebischer et al. 1993). A positive and a negative sign in the same column cancelled each other out. The significance of the difference between any two ranks was assessed by comparing all the p-values obtained from the respective sets of t-tests (e.g. Table 2). In other words, one rank was deemed to be significantly higher than another if it had a) a higher number of positive signs and b) those positive signs represented statistically significant t-tests.

Microsite use and preferences for all species combined and for combinations of categories

The data from all individuals were combined to assess whether the overall 'community' of animal dispersers selected cache sites according to their availability. If a departure from random use was detected in any of the three microsite categories, preferences were ranked as before. Finally, the entire series of analyses was repeated using the data for two microsite categories combined: substrate plus understory. In other words, we calculated the proportions of caches that each animal had made in the six 'combined' categories mineral soil-under shrub, mineral soil-open, light litter-under shrub, light litter-open, heavy litter-under shrub, heavy litter-open. As above, we assessed whether use of these categories (by each species and by all species combined) differed significantly from random, and ranked categories in order of preference if so.

2. Seedling emergence and survival

We conducted a field study between fall 2000 and spring 2002 near Incline Village, NV (39° 16′ 30" N, 119° 57′00" W) to compare the fates of seeds buried at different depths and in different microsites. This site is in the Tahoe Basin, 8-10 km northwest of Little Valley; our study plots were located in mixed conifer forest (dominated by Jeffrey pine) at a mean elevation of 2450 m. Understory species in this more mesic forest are predominantly tobacco brush (Ceanothus velutinous), huckleberry oak (Quercus douglasii), and greenleaf manzanita (Arctostaphylos patula) (Walter 2001); the bitterbrush which is so common in yellow-pine forests on the eastern slope of the Carson Range is rare or restricted to open sunny slopes on the western side of the ridge. The dominant soil types on our study plots were granitic in origin: Umpa very stony loam and Tahoma stony sandy loam (Walter 2001).

On each of four arbitrarily selected plots (20 ha) in the Wood Creek and Second Creek drainages, I established a series of artificial caches in different types of microsites. To investigate the possible effects of cover, substrate and depth of burial on the survival of seeds and emergence of seedlings, I used a split plot design with two additional factors (Figure 1). Within each treatment and control plot, there was a split between two substrate types (mineral soil and litter), and within each of these categories there was a cover factor with 2 levels (under shrub and open, i.e. shrub interspace) and a depth factor with 3 levels (seeds were placed on the soil surface, i.e. 0mm, or buried at 5 mm and 25 mm). All levels were completely crossed, although the sample sizes within the cover factor were unbalanced as the two dominant shrubs at the study site were used as cover in equal proportions. The number of subsamples under each of the two shrub types was the same as that in the open category. On each plot, I established seven replicates of all the substrate/cover treatment combinations (Figure 1). Within each of these replicates, I established 3 subsamples of each of the three depth treatments. These subsamples were arrays of caches, placed inside protective wire mesh cages in a randomized order.

Each array of 9 caches was made inside a 30-cm square cage of 5-mm wire mesh, with walls were buried at least 10 cm below ground. The walls above ground were approximately 10 cm high, and the roof of the cage was securely fastened to prevent access by animals. The 9 caches in each array represented three replicates of three depth treatments, arranged in a randomized order within the cage. The "surface" treatment consisted of three seeds placed on the soil surface, to mimic abiotic dispersal. Three other caches each contained three seeds buried 5 millimeters below the soil surface: this represented shallow caches made by animals, but could possibly occur via abiotic burial if wind-dispersal seeds became entrapped in plant material (Vander Wall and Joyner 1998b). The final series of 3-seed caches in the set was buried 25 mm below the soil surface, to mimic the deeper caches made by larger animals and to represent a depth closer to the "optimal" range for emergence for Jeffrey pine (Vander Wall 2002a).

When preparing caches at the 5 mm depth, we placed the seeds in a shallow depression on the substrate surface and scattered 5 mm of either soil or litter over them. When burying caches at 25 mm in litter, we first removed all existing litter from the area within the cage, buried the seeds 5 mm deep in the exposed soil, then replaced the original litter (shrub or pine matter depending on location of the cage) to a standard depth of 20 mm. Equal proportions of huckleberry oak and tobacco brush were used for under-shrub treatment, because these shrubs are co-dominant at the sites. On all sites, each replicate was located in an area where the 6 combinations of substrate and cover described above occurred in close proximity to each other. I attempted to place all cages in level areas (to minimize effects of erosion over winter) and to place the under-shrub cages at a consistent distance under shrub canopies, with the outside edge of the cage just below the edge of the shrub canopy.

We planted seeds in late October 2001. A few weeks after snowmelt the following spring (beginning 25 May 2002), we checked all cages for emergence of seedlings. We recorded emergence if we could see a shoot from a buried seed protruding above the soil/litter surface, or emerging from a seed lying on the surface. We checked the seedlings' status and noted cause of death, if applicable, at approximately monthly intervals until the end of the growing season (November) or the death of the seedlings, whichever occurred first.

Analyses

We used logistic regression (Proc Logistic in SAS, 2000) to evaluate the effects of cover (open vs. under shrub), substrate (mineral soil vs. litter) and depth (surface, 5 mm and 25 mm) on emergence of seedlings. As all seeds were members of 3-seed caches, we did not code by cache within replicates, to limit inflation of the number of parameters in the model. The total sample size (excluding any cache arrays accidentally disturbed before emergence) was 4335 seeds. Dummy variables representing the four different sites and the seven different replicates (blocks) of treatments within each site were included in the original model, but dropped if they did not contribute significantly to the model's fit. We followed the procedure recommended by Burnham and Anderson (1998) for model selection: several reduced models were compared to a 'global' model that contained all parameters and interaction terms. Parameters were dropped if they did not have a significant main effect or were not part of a significant interaction, if they had little biological relevance (e.g. four-way interactions between a site, cover, depth and substrate), or if their inclusion or exclusion did not significantly reduce the Akaike Information Criterion (AIC) value of a model (a reduction of more than 2 points was considered to be a significant improvement in the fit of the model; Allison 1995, Burnham and Anderson 1998). The final model, which was used for estimation of parameters and post-hoc contrasts, had the lowest AIC value while containing the highest number of biologically meaningful parameters, i.e. it represented the best fit to the data.

We assessed the effects of the same factors on the lifespan of all seedlings that emerged using survival analysis (Proc Lifereg in SAS, 2000) with interval censoring and a Weibull distribution (Allison 1995). The response variables were the lower and upper limits on the time a seedling was known to have been alive, expressed as days since a common 'starting point' (arbitrarily assigned to be March 3, 2001). For example, a seedling that was healthy on 30 July, 2001, but was found to be dead when checked on 9 September, 2001, received a code of 153, 194. Model selection and post-hoc contrasts were performed as above.

RESULTS

Caching behavior of four rodent species

Cache size and depth differed significantly among species (MANOVA for species: Wilk's lambda = 0.387, $F_{6,64} = 14.26$, $p < 0.0001$). In a separate univariate ANOVA on cache size, Tukey's pairwise comparisons showed that the mean cache size of *S. lateralis* was significantly different ($p < 0.02$) from that of all other species, but that the other three species' mean caches were not significantly different from each other (Fig. 1a). Tukey's pairwise comparisons of cache depth among species also showed that the mean depths of *S. lateralis* caches were significantly greater than those of all the other species ($p < 0.02$), which were not significantly different from each other (Fig. 1b).

Cache microsite selection: differences among species

Compositional analysis showed that the four species used microsites significantly differently, with respect to availability, in all three microsite categories (MANOVAs for substrate: Wilk's lambda = 0.537, df = 9,73; F = 2.37; p = 0.02; understory: Wilk's lambda = 0.485, df = 6,62; F = 4.50; p = 0.001; overstory: Wilk's lambda = 0.518; df = 4,44; F = 4.28; p = 0.005). However, in some of these comparisons, the data (difference matrices for each species, described above) violated certain assumptions of the MANOVA, e.g. via a significant departure from univariate normality (Kolmogorov-Smirnov tests; $p < 0.05$), which can predict departures from multivariate normality (Manly 1991). Visual inspections of histograms of the difference matrices suggested that they did not have a multivariate normal distribution. As it was not practical to further transform these log-ratios, we present these results to be interpreted with caution; we used randomization trials to assess significance levels in all further tests (Aebischer et al. 1993).

Cache microsite selection: patterns observed for each species

Fig. 2 displays the patterns of departures from random use in the three microsite categories, i.e. the mean differences in log ratios (use - availability) for each species. Values for each individual were weighted by number of caches, but variation among individuals was often considerable. Thus, significant species-specific preferences for microsite types, revealed in the following analyses (Table 3), are reflected by means in Fig. 2 for which the standard deviations do not include zero, or do not extend very far past zero. Randomization trials showed that deer mice used substrate types (mineral soil, light litter and heavy litter) randomly with respect to availability but used understory types non-randomly (Table 1). Post-hoc t-tests comparing the use of all possible pairs of understory types found that deer mice preferred under-shrub microsites to open microsites, and preferred open microsites to "other" microsites (this category included sites under grasses, forbs, etc) (Table 3). Differences between all three of these ranking were significant at the 0.05 level recommended by Aebischer et al. (1993).

Yellow pine chipmunks used microsite types within all three microsite categories non-randomly (Table 1). When preferences were ranked within categories (Table 3), results showed that this species used mineral soil substrate significantly more often than light litter and used heavy litter significantly less than light litter. The ranks of heavy litter and "other" substrates (e.g. logs, grass) were interchangeable. In the understory category, there was a non-significant preference for under-shrub microsites over open microsites.

Lodgepole chipmunks also used substrate types and understory types non-randomly (Table 1). Within the substrate category, relative use was in the order light litter > mineral soil > or = heavy litter > or = other (Table 3). In the understory category, relative use was in the order shrub > open > or = other. Ground squirrels used substrate types randomly but used understory types and overstory types non-randomly (Table 1). Order of use of understory types was open > other > or = shrub; overstory types were ranked open > other > pine (Table 3).

Cache microsite selection: all species combined

To identify any general patterns of microsite use by all individuals combined, we performed the same analyses on the entire data set (Table 2). Within the substrate category, mineral soil was significantly preferred over light litter; light litter was used more than "other" substrates but these two ranks were statistically interchangeable; and heavy litter was used significantly less than all other substrates. Microsites under shrubs were used significantly more often than open sites, with "other" sites used least. In the overstory category, there was a significant preference for open sites, followed by "other" sites; sites under pine saplings were least preferred.

Cache microsite selection: combined substrate/understory categories

When each species' use of combined categories (i.e., substrate + understory) was examined, only deer mice were found to have used these combinations non-randomly

(Table 1, $p = 0.009$). Use of combined categories was random for the three other species (Table 1). However, when we analyzed the combined-category use by all species combined, we found that, as a "community", animals' use of these microsites differed from random ($p < 0.001$). Mineral soil-under shrub microsites were used significantly more often, relative to availability, than any other combination (Table 4); the full ranking order was mineral soil-under shrub >light litter-under shrub > or = mineral soil-open> light litter-open>heavy litter-open > or = heavy litter-shrub.

Seedling emergence and survival

Emergence

Of the 4335 seeds planted, 739 (17%) produced seedlings. Logistic regression revealed that the probability of seedling emergence was significantly affected by substrate (Wald = 66.67, $p < 0.0001$), cover (Wald = 9.81, $p = 0.002$) and depth (5-mm vs. surface: Wald = 32.10, $p < 0.0001$; 25-mm vs. surface: Wald = 228.77, $p < 0.0001$). Across all treatment combinations, a higher percentage of seeds emerged in mineral soil (54.3%) than in litter (31.1%) and at depths of 5 and 25 mm than at 0 mm (45.1 % vs. 4.7%, Table 5). If interactions between factors were significant, we used post-hoc contrasts to identify the categories in which the odds of emergence differed significantly. A significant interaction between cover and substrate (Wald = 6.96, $p = 0.008$) showed that emergence was similar in mineral soil under shrubs and in mineral soil in the open (Table 5) but that emergence was 7.7 times higher in the litter substrate under shrubs than in the open ($p <0.0001$).

The interaction between substrate and the 5-mm burial depth was also significant (Wald = 11.50, $p = 0.007$), reflecting the fact that seeds planted at 5 mm in mineral soil were 7.23 times more likely to emerge than seeds planted at 5 mm in litter ($p < 0.0001$). Two additional interactions, between site 3 and substrate, and site 3 and the depth of 25 mm, were significant (Wald = 28.82, $p < 0.0001$ and Wald = 5.50, $p = 0.02$, respectively). There was an unusually low value (9 %) for emergence of seeds at the 25mm burial depth. If this value was deleted, an ANOVA using arcsine-transformed data found there was a significant difference between mean germination (30%) at the 5 mm depth vs. the 25 mm depth (21.5%) ($P < 0.02$). In general, the sites showed significantly different patterns of emergence (all p-values < 0.02 in the logistic regression) so they were retained as blocking factors.

Post-hoc contrasts performed between the microsite categories described in Experiment 1 (Table 5) showed that both soil microsites (open and under-shrub) were significantly more favorable than sites in heavy litter under shrubs, which received the next highest rank (odds ratio for open soil vs. heavy litter under shrubs: 1164.2, $p < 0.00001$). Seeds in heavy litter under shrubs were significantly more likely to emerge than in light litter under shrubs (odds ratio 1.24, $p < 0.05$), which in turn was a significantly more favorable site than heavy litter in the open (1.59, $p < 0.05$). It should be noted that light litter and heavy litter, by definition, represent different depths of caches (5 and 25 mm respectively). The lowest emergence occurred in light litter in the open: only 9 of 426 seeds planted in this category emerged.

Seedling survival

The survival analysis was performed on the 739 seedlings that emerged, of which 645 had known maximum dates of emergence and death. For 96 seedlings, the lower boundary was unknown, i.e. the seedling was dead at the time of the first check. No factor had a significant main effect on survival time (see similar mean maximum survival times for many categories in Table 6; but note that the analysis used a more precise measure, survival interval, as the response variable). However, survival patterns at two sites were significantly different ($p < 0.0001$) from the other two. The interaction between cover and substrate type was highly significant ($p < 0.0001$). There was a significant interaction between cover and the 25-mm depth ($p = 0.026$), but not between cover and 5 mm depth, showing that the deepest burial extended survival time in under-shrub microsites but not in the open (Table 5). The main effect of burial was not significant, i.e. if seedlings emerged from surface seeds, their mean maximum survival time (122 days, Table 6) was not significantly shorter that of seeds establishing from 5mm or 25 mm (140 vs. 144 days, respectively).

Contrasts between the categories identified in Experiment 1 showed that seedlings survived significantly longer in mineral soil sites under shrubs compared with mineral soil sites in the open (odds ratio 1.87, $p < 0.0001$). The next three lower categories (Table 6) were not statistically different from each other in terms of survival, (all odds ratios ≈ 1.0, $p > 0.05$), but they were all significantly more favorable than the lowest-ranked category, light litter under shrub (odds ratios > 1.16, $p < 0.05$). The longest-surviving seedlings were all found in the mineral soil-under shrub microsite. One surface seed, 10 seeds planted at 5 mm and 12 seeds planted at 25 mm produced seedlings that were still alive at the end of the growing season (14 October, 2001). These represented 2.8 %, 5. 4% and 6.8%, respectively, of all the seeds that had germinated in the same depth, substrate and cover treatments (Table 5), and represented a total of 0.6 % of the 4335 seeds originally planted. At the time of the final check (18 November), 16 of these 23 seedlings were still alive, but by June 2002 of the following season, they had all died. The almost universal cause of death was dessication; only a few cages were disturbed by animals, ants or humans. Tables 5 and 6 show the degree to which the rankings for the microsites in terms of animal preference match the rankings for the same microsites in terms of favorability for seedling emergence and survival.

DISCUSSION

Our general hypotheses that the four rodent species would differ in terms of the size, depth, and microsite characteristics of their caches were supported by the results of our first experiment, and results of the second experiment suggested that variation in all these factors strongly influences emergence and survival of pine seedlings. In fact, the microsite category in which both emergence and survival were highest (under shrubs in mineral soil) was also the microsite in which animals made significantly more caches than any other. When considered separately, most species' use of microsites differed significantly from the distribution expected by random chance. The pattern of cache distribution for all species combined was also significantly different from random, suggesting that community-level effects may outweigh the patterns of cache site selection shown by individual species and animals. Under natural conditions, this balance would obviously depend on interactions between many factors, such as relative population sizes, access to seeds, and interactions between individuals. Although these were standardized in this experiment, at least two effects should remain consistent under natural conditions: burial at 5 or 25 mm significantly improved the emergence success of seeds relative to those placed on the forest floor, and burial in mineral soil enhanced both emergence and survival.

There are several possible explanations for the inter- and intraspecific variation we observed in cache depth, cache size, and selection of microsites, and many consequences of these differences. First, depth of caching generally increased with mean body size of species, although *T. speciosus* and *S. lateralis* individuals showed considerable variation in cache depth. Like Vander Wall (1993a) and Hollander and Vander Wall (submitted), we found that larger caches were buried significantly more deeply. Variation in cache depth (and size) may affect the detectability of buried seeds, as their olfactory signal declines in proportion to depth below ground (Reichmann and Oberstein 1977, Vander Wall 1993b).

The most effective depth for caching, from the animal's perspective, may represent a balance between facilitating its own storage and retrieval of seeds and minimizing pilferage by other animals who have no knowledge of the cache site (Vander Wall 1991, 1993, Clarke and Kramer 1994, Leaver and Daly 2001). Shallow caches may be energetically more efficient to make and recover, e.g. by olfaction, but be more vulnerable to discovery by conspecifics. In our caching trials, the range of depths at which most animals cached was so narrow that it overlapped only with the shallower depth used in the seedling emergence study, and fell at the upper end of the 'optimal' range of emergence (10- 40 mm) found for Jeffrey pine (Vander Wall 2002a). 95% of the 680 caches were between 0 and 19.5 mm. Fifty three percent were buried between 3 and 7 mm deep, whereas only 2% were buried between 22 and 28 mm, by 4 *T. speciosus* and 8 *S. lateralis*. 4 ground squirrels in our study demonstrated a mean caching depth well below (over 60 mm deep) the range of depths from which Jeffrey pine successfully emerges and all of the deer mice made a majority of their caches at depths between the surface and 10mm, from which seedling establishment is lower than optimal (Vander Wall 2002a),.

From the plant's perspective, germination and survival are often significantly enhanced by burial within a narrow range of depths (Chambers 2001,Vander Wall 1993b). In semi-arid systems, unfavorable abiotic conditions such as desiccation and heat stress limit emergence success if burial does not occur or is too shallow (this study; Hollander and Vander Wall, submitted; Hutchins and Lanner 1982) but emerging shoots cannot reach the soil surface if seeds are buried too deeply (Chambers 2001, Seiwa et al. 2002). In our study, depths of 5mm and 25 mm were both significantly more favorable for emergence, in all microsites, than the surface depth. Surprisingly, the survival of seedlings that did establish from surface seeds was not consistently lower than that of all buried seeds, but varied with microsite. Some surface seeds (especially those in soil and/or under shrubs) fared as well or better than seeds buried in other microsites. The seedling study was conducted during a very dry summer, with total precipitation of 24.4 mm at the sites between 1 May and 30 October 2001 (Bugge, pers. comm.). In years with higher rainfall, differences in the favorability of different sites and depths might be easier to detect, and longer-term changes might become apparent.

The second attribute of caches that may affect emergence and survival, cache size, was not assessed in our emergence study. However, results of the caching trials showed that, like depth, mean cache size varied in proportion to species' mean body mass. Such variation reflects constraints on the amount of seeds that can be carried in one load (Vander Wall et al 1998, Bowers and Ellis 1993). Saigo (1969) reported a capacity of 77 ponderosa pine seeds for *T. amoenus* and 130 for *S. lateralis*, but deer mice can carry only one to four Jeffrey pine seeds at a time (Vander Wall 2001). Metabolic needs may vary at different times within annual cycle (Kenagy et al. 1989) and might also affect cache size if animals respond to external cues such as the ripeness or availability of seed crops by changing the size and number of their caches. On a daily basis, Lucas et al. (1993) found that body mass and satiation levels in birds affected their decision to cache versus eat available food items almost from one minute to the next. Our ability to assess animals' physiological needs, or even patterns of activity during trials, was very limited in this study as we did not wish to disrupt caching behavior by direct observation. Periodic checks to see if seeds had been removed from the feeders, and assessment of the signs of digging and seed consumption at the end of each trial, gave us some idea of the animals' activity patterns.

The two larger-bodied species showed much greater variation in cache size among individuals, and a much lower propensity to cache in general during this experiment. Fewer individuals tested made any caches at all, and those individuals made fewer caches each (n =1-15) than did deer mice (n = 8-109 caches) or yellow pine chipmunks (n = 19 - 44). Time of year, with respect to seed availability, did not appear to influence caching propensity, as approximately 40% of all subjects made more than 5 caches in trials conducted before pine cones opened in early fall. We did not examine possible year effects on caching tendencies as we felt these were unlikely to have influenced behavior in the captive conditions of the 2-day caching trials, and different species were tested in different years in any case.

Individuals of different species often cached similar proportions of seeds in very different numbers of caches. The most striking example was that from the 150 seeds available, one *S. lateralis* made 1 cache of 65 seeds, one *T. speciosus* made 11 caches totaling 68 seeds, one *T. amoenus* made 23 caches totaling 65 seeds, and one *P. maniculatus* made 53 caches totaling 64 seeds. Thus, we felt justified in including 4 - 8 *S. lateralis* in our analyses, but we note that the effects of such large cache sizes may be far fewer potential sites of establishment for the plant, i.e. a lower "quantity" of dispersal (Schupp 1995, Hollander and Vander Wall submitted) and a higher risk of post-dispersal predation on any seedlings emerging in such large, conspicuous clumps (Saigo 1969).

As *S. lateralis* did not often demonstrate the behavior of interest (scatter hoarding) under the conditions of the experiment, our predictions about its "natural" behavior, use of microsites, and effectiveness as a disperser of pine seeds, must be limited. Captivity in the enclosure probably restricted the movements of this large-bodied species much more significantly than the others (McNab 1963). Many individuals tended to ignore all seeds for 1-2 days (often while running around enclosure walls, climbing fences or making burrows along edges) then eat all seeds in a short period of time without caching many, or any at all. We included these caches in the compositional analyses only for the sake of completeness and only after weighting all animals' microsite use patterns by the number of caches it made.

Our comparison of substrate selection revealed that two out of four species used substrates in proportion to their availability, and that the others showed significant preferences for mineral soil (*T. amoenus*) and light litter (*T. speciosus*). All species made significantly fewer caches in heavy litter than expected. These results are consistent with Sherman and Chilcote's (1972) report that very few rodent caches of pine or bitterbrush in their study area were emerging from heavy litter. Vander Wall (1993) also found more pine seed caches in mineral soil; Saigo (1969) noted increased caching in areas where disruption/disturbance of litter had occurred. These authors suggested that animals may "prefer" to manipulate loose, friable soils, or that they simply spend less time in closed-canopy forests which have a deep layer of litter on the floor (see also Vander Wall 1994, 2003). It is also possible that animals' ability to retrieve caches using olfaction, memory or both is limited in heavy litter and enhanced in mineral soil, perhaps because the hydrophobic heavy litter could 'insulate' seeds from imbibing moisture after a rainfall, when there is usually a strong increase in the olfactory signals released by dampened seeds (Vander Wall 2003). It does not appear that frequent use of mineral soil sites is an artifact of frequent use of under-shrub sites, as the areas under shrubs tend to contain a layer of plant litter.

Variation in animals' use of substrates for caching has both abiotic and biotic consequences for the seeds. We found that seeds in mineral soil had a much greater probability of emerging than seeds in litter, regardless of presence of understory. In the absence of abundant moisture, germinating seeds benefit from burial in mineral substrates where plant matter does not form a barrier to the radicle (Facelli and Pickett 1991, Chambers 2001). Breck and Jenkins (1998) identified several ecological consequences of substrate choice when they found that three species of heteromyid rodents preferred to cache Indian ricegrass seeds in rocky substrates at an ecotone at their Great Basin study site, while a fourth species cached more seeds in the sandy substrate. Studies in more mesic environments have found that burial in litter occurs more frequently and not only has abiotic benefits (creating a favorable microclimate for the germinating seed, Forget 1994) but reduces risk of predation, pilferage, infection by pathogens and other biotic phenomena (Hayashida 1989, Forget 1994).

The interactive effects of substrate type and cover on seedling fates suggest that it is more valid to examine these categories together instead of separately. The only seedlings to survive the first growing season were in mineral soil substrate under shrubs, the combination of microsites that was significantly preferred when cache site selection was analyzed for the entire set of animals we tested. Caching under shrubs has been documented in other studies (conducted in unenclosed conditions) at both the Little Valley (Vander Wall 1994, 2002b) and Incline Village sites (Briggs unpublished data). This suggests that, at least in the short term, the behavior of this community of animal dispersers may have positive effects on the pine. Reasons for apparent cache site preferences, and the geographic variation in pine/shrub distribution they may produce, include several types of behavior and movement patterns that may be only indirectly related to food hoarding. Cache sites may be chosen simply as by-products of habitat use, e.g. caching occurs when animals are foraging in areas rich in preferred resources (Forget 1994, Pyare et al. 1997); interacting with or avoiding potential sympatric competitors (desert rodent community; Thompson 1982); avoiding aerial predators (Brown et al. 1988) or generally exploiting a structurally complex environment, which includes shrubs, for its favorable abiotic microclimate and diversity of food resources (Parmenter and MacMahon 1983).

In arid ecosystems, placement of seeds in shaded microsites generally increases seedling survival (Chambers 2001) even if, as in our study, rates of emergence are similar in open and under-shrub microsites. We found that seedlings under shrubs survived for almost twice as long (odds ratio 1.9, $p < 0.001$) as seedlings in the open. In an experiment on pinyon pine, Vander Wall (1997) found 36% of initial caches under shrubs, but these represented 69% of all caches still alive the following spring. Similarly dramatic effects were found by Chambers (2001), Hollander and Vander Wall (submitted) and Ibanez and Schupp (2001), suggesting that in the short term, survival of seedlings may be severely constrained by abiotic factors such as soil moisture, soil and ambient temperatures, and exposure to light. If so, seedling survival is significantly enhanced by placement in the shade of a "nurse plant" (Ibanez and Schupp 2001, Callaway et al. 1995). Short-term biotic effects may include escape from certain seed predators (Fuller and Hay 1981, Callaway 1995), but there is less evidence in drier, temperate forests that biotic processes impair establishment from buried seeds as much as abiotic processes do (Callaway and Walker 1997, Schupp 1995, 1998).

Over the longer term, however, negative biotic effects such as competition, even with a former 'nurse plant', may start to influence seedlings in under-shrub microsites (Callaway and Walker 1997). Many studies have shown that the presence of a shrub understory suppresses tree growth for a variety of reasons: decrease in availability of water to seedlings (Callaway et al. 1996, Dunne and Parker 1999), short-term reduction in soil nutrients (Busse et al. 1996), shading and root competition (Conrad and

Radesovich 1982). However, other results, some even from the same studies continued over a longer period (Busse et al. 1996) or expanded to include an additional species (Callaway et al. 1996), have identified positive interactions between shrub species and young trees (see also Callaway 1992). As our study was conducted in an unusually dry year, we cannot predict whether the consequences of animals' placement of pine seeds under shrubs will be positive or negative in the longer term.

The species of shrubs investigated, which were not the same in the two parts of our study, may also have different effects on Jeffrey pine seedlings based on physiological and possibly chemical factors such as water use efficiency, nitrogen-fixing ability (Johnson et al. 1995) and allelopathic potential (Yoder-Williams and Parker 1987). We feel justified in presenting these early results because we are not aware of any evidence for significantly different effects of bitterbrush, tobacco brush and huckleberry oak on pine seedlings, and because we have documented animals' caching under all three species of shrub (Vander Wall 2002b, Briggs unpublished data). However, future work is needed to explore possible longer-term interactions, and should also examine another variable that we could not consider fully here: the overstory component of the microsite and the contribution of mature trees to the abiotic environment of a young seedling.

In general, our results confirm that granivorous rodents can affect emergence and early survival of Jeffrey pine seeds and seedlings through variation in several aspects of caching behavior: size, depth, substrate type and understory characteristics of caches. Species-specific differences in food hoarding behavior may reflect niche partitioning within a guild of species sharing a common resource and habitat, as other workers have found for seed specialists (Hutchins et al. 1996, Thompson 1982). When assessed as a community, animals made more caches in a type of microsite, mineral soil under shrubs, in which seed emergence was significantly higher (and short-term seedling survival, even in a very dry year, was greater) than in any other combination of microsites. Of the four species, yellow pine chipmunks appeared to place the greatest number of caches in the range of depths, substrates and microsites that were found to enhance seedling survival. Seeds in sites typical of wind-dispersal, i.e. on the forest floor in open areas, fared significantly worse in all comparisons; however, one seedling that emerged from a surface seed (out of 1445) did survive until the end of the first growing season under a shrub in mineral soil.

Although short in duration, our results suggest the type of directed dispersal process described by Howe (1986) and reevaluated both theoretically (e.g. Callaway and Walker 1997, Wenny 2001, Strykstra et al. 2002) and empirically (e.g. Wenny and Levey 1998, Hoshizaki et al. 1999) in a variety of systems. When seeds reach safe sites (Janzen 1971, Callaway 1996) for germination and survival through the actions of animals that intend to use them as a future food source, a "diffuse mutualism" occurs (Wenny 2001) which is positive for both partners when a surplus of seeds coincides with favorable abiotic conditions for seedling establishment (Vander Wall 1993a, Chambers 2001). Under these conditions, many researchers have speculated that the activities of animals may facilitate and accelerate the process of succession (Sherman and Chilcote 1972, Vander Wall 1993a, Pyare et al. 1997, MacMahon 1980). In coniferous forests, seed dispersal by animals may be especially important after natural or anthropogenic disturbances which change the nature of the forest floor (Kauffman and Martin 1988) or understory (Parmenter and MacMahon 1983), presenting new combinations of substrates and microsites and, consequently, providing new opportunities for animal-mediated seed dispersal (McClanahan and Wolfe 1991, Luken 1990).

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Allison, P. D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Inc., Cary, NC.

Bower, M. A. and A. E. Ellis. 1993. Load size variation in the Eastern chipmunk, Tamius striatus, : the importance of distance from burrow and cover. Ethology 94: 72-82.

Breck, S. W., and S. H. Jenkins. 1997. Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. Ecography 20:253-263.

Brown, J. S., B. P. Kotler, R. J. Smith and W. O. Wirtz. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76: 408-415

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York.

Busse, M. D., P. H. Cochran, and J. W. Barret. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Science Soc. Am. J. 60:161-1621.

Bugge, J. 2003. Personal Communication. Annual precipitation for Wood Creek canyon, Incline Village, NV.

Callaway, R. M. 1992. Effect of shrubs on recruitment of Quercus douglasii and Quercus lobata in California. Ecology 73: 2118-2128

Callaway, R. M., E. H. DeLucia, D. Moore, R. Nowak, and W. H. Schlesinger. 1996. Competition and facilitation: contrasting effects of Artemisia tridentata on desert vs. montane pines. Ecology 77: 2130-2141.

Callaway RM and LR Walker (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965

Chambers, J. C. 2001. Pinus monophylla establishment in an expanding Pinus juniperus woodland: environmental conditions, facilitation and interaction factors. Journal of Vegetation Science 12:27-40.

Chambers, J. C., and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Clarke, M. F. a. D. L. K. 1994. The placement, recovery and loss of scatter hoards by eastern chipmunks, Tamias striatus. Behavioral Ecology 5:353-361.

Dunne, J. A., and T. V. Parker. 1999. Species-mediated soil moisture availability and patch establishment of Pseudotsuga menziesii in chaparral. Oecologia 119:36-45.

Facelli J. M. and S.T. A. Pickett (1991) Plant Litter: effects on community structure. Bot. Rev. 57:1-32

Forget, P. M. 1993. Postdispersal Predation and Scatterhoarding of Dipteryx- Panamensis (Papilionaceae) Seeds by rodents in Panama. Oecologia 94:255-261.

Forget, P. M. 1994. Recruitment Pattern of Vouacapoua-Americana (Caesalpiniaceae), a Rodent-Dispersed Tree Species in French-Guiana. Biotropica 26:408-419.

Hay, M. E., and P. J. Fuller. 1981. Seed escape from Heteromyid rodents: the importance of microhabitat and seed preference. Ecology 62:1395-1399.

Hayashida, M. 1989. Seed dispersal by red squirrels and subsequent establishment of Korean pine. Forest Ecology and Management 28:115-129.

Hollander, J. K. a. S. B. V. W. 2002. Effectiveness of six species of rodents as dispersers of single-leaf pinyon pine (Pinus monophylla). Submitted.

Hoshizaki, K., W. Suzuki, and T. Nakashizuka. 1999. Evaluation of secondary dispersal in a large seeded tree Aesculus turbinata: a test of directed dispersal. Plant Ecology 144:167-176.

Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pp. 123-189 in D. R. Murray, ed. Seed dispersal. Academic Press, Orlando, FL.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Hulme, P. E. 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia 111:91-98.

Hutchins, H. H. and R. M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55: 192-201.

Hutchins, H. H., S. A. Hutchins, and B. Liu. 1996. The role of birds and mammals in Korean pine regeneration dynamics. Oecologia 107:120-130.

Ibanez, I., and E. W. Schupp. 2001. Positive and negative interactions between environmental conditions affecting Cercocarpus ledifolius seedling survival. Oecologia 129:543-550.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465-492.

Jenkins, S. H., and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79:1221-1233.

Johnson, D. W. 1995. Soil properties beneath ceanothus and pine stands in the eastern Sierra Nevada. Soil Sci. Soc. Am. J. 59:918-924.

Johnson, D. W., R.B Susfalk and R.A Dahlgren. 1997. Nutrient fluxes in forests of the eastern Sierra Nevada mountains, United States of America. Global Biogeochemical Cycles 11:673-681.

Johnson,W. C., C. S. Adkisson, T. R. Crow, and M. D. Dixon. 1997. Nut caching by blue jays (Cyanocitta cristata L.): Implications for tree demography. American Midland Naturalist 138:357-370.

Kauffman, J. B. and R. E. Martin. 1989. Fire behavior, fuel consumption, and forest floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Can. J. For. Res. 19: 455-462

Kotler, B. P. and Brown, J. S. 1988. Environmental heterogeneity and the coexistence of desert rodents. Ann. Rev. Ecol. Syst. 19: 281-307

Kenagy, G. J., S. M. Sharbaugh, and K. A. Nagy. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269-282.

Leaver, L. A., and M. Daly. 2001. Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice. Oecologia 127

Levey, D. J. and M. M. Byrne. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74: 1802-1812.

Levey, D. J., W. R. Silva, and M. Galetti. 2002. Seed dispersal and frugivory: ecology, evolution and conservation. CABI, New York.

Lucas, J. R., L. J. Peterson, and R. L. Boudinier. 1993. The effects of time constraints and changes in body mass and satiation on the simultaneous expression of caching and diet-choice decisions. Animal Behavior 45:639-658.

Luken, J. O. 1990. Directing ecological succession. 251 pp. Chapman and Hall, London, UK

MacMahon, J. A. 1980. Ecosystems over time: Succession and other types of change. In: Forests: Fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biology Colloquium (1979), (R H Waring, ed.), Oregon State University Press, Corvallis, OR. 1980.

McClanahan, T. R. and R. W. Wolfe. 1991. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Cons. Bio 7: 279-289

McAuliffe, J. Paloverdes, pocket mice, and bruchid beetles: interrelationships of seeds, dispersers and seed predators. SouthWestern Naturalist 35: 329-337

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133-140

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278-285.

Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145-156.

Price, M. V. and S. H. Jenkins. 1986. Rodents as seed consumers and dispersers. Pp 191-235 in Seed Disperal, Murray DR (ed). Academic Press, Sydney, Australia

Price, M. V., N. M. Waser, and S. McDonald. 2000. Seed caching by heteromyid rodents from two communities: Implications for coexistence. Journal of Mammalogy 81:97-106.

Reichman, O. J., and D. Oberstein. 1977. Selection of Seed Distribution Types by Dipodomys Merriami and Perognathus Amplus. Ecology 58:636-643.

Pyare, S., J. A. Kent, D. L. Noxon, and M. T. Murphy. 1993. Acorn preference and habitat use in eastern chipmunks. The American Midland Naturalist 130:170-183.

Saigo, B. W. 1969. The relationship of non-recovered rodent caches to the natural regeneration of ponderosa pine. Master's Thesis, Oregon State University, Corvallis, OR.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51:71-78.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108:15-29.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of botany 82:399-409.

Seiwa, K., A. Watanabe, T. Saitoh, H. Kanno, and S. Akasaka. 2002. Effects of burying depth and seed size on seedling establishment of Japanese chestnuts, Castanea crenata (vol 164, pg 149, 2002). Forest Ecology and Management 168:323-323.

Shelton, M. G. 1995. Effects of the amount and composition of the forest floor on emergence and early establishment of loblolly pine seedlings. Can. J. For. Res. 25:480-486.

Sherman, R. J. and W. W. Chilcote. 1972. Spatial and chronological patterns of Purshia tridentata as influenced by Pinus ponderosa. Ecology 53:294-298.

Strysktra, R. J., R. M. Bekker, and J. Van Andel. 2002. Dispersal and life span spectra in plant communities: a key to safe site dynamics, species coexistence and conservation. Ecography 25:145-160.

Thompson, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology 63: 1303- 1312.

Tomback DF, 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono 33:100-110.

Vander Wall SB, 1992a. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73:614-621.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.

Vander Wall, S. B. 1991. Mechanisms of cache recovery by yellow pine chipmunks. Animal Behaviour 41: 851- 863.

Vander Wall, SB. 1992b. Establishment of Jeffrey pine from animal caches. Western Journal of Applied Forestry.

Vander Wall, S. B. 1993a. Cache site selection by chipmunks (Tamias spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (Pinus jeffreyi). Oecologia 96:246-252.

Vander Wall, S. B. 1993b. A model of caching depth: implications for scatter hoarders and plant dispersal. American Naturalist 141:217-232.

Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush; dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911-1926.

Vander Wall, S. B. 1997. Dispersal of singleleaf pinon pine (Pinus monophylla) by seed-caching rodents. Journal of Mammalogy 78:181-191.

Vander Wall, S. B., and J.W. Joyner. 1998. Recaching of Jeffrey pine (Pinus jeffreyi) seeds by yellow pine chipmunks (Tamias amoenus): potential effects on plant repoductive success. Can. J. Zool. 76:154-162.

Vander Wall, S. B., and J. W. Joyner. 1998b. Secondary dispersal by the wind of winged pine seeds across the ground surface. American Midland Naturalist 139:365-373.

Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck, and J. R. Roth. 2001. Scatter-hoarding behavior of deer mice (Peromyscus maniculatus). Western North American Naturalist 61:109-113.

Vander Wall, S. B. 2002. Secondary dispersal of Jeffrey pine seeds by rodent scatter-hoarders: the roles of pilfering, recaching and a variable environment in D. J. Levey, W. R. Silva and M. Galetti, ed. Seed dispersal and frugivory: ecology, evolution and conservation.

Vander Wall, S. B. 2002b. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83:3508-3516.

Vander Wall, S. B. 2003. How rodents smell buried food: a model based on the behavior of pesticides in soil. In press, Journal of Mammalogy.

Walter, G. 2001. Prescribed burn plan- Incline Village General Improvement District burn units, 2000-2002. Unpublished document, on file with the North Lake Tahoe Fire Department and Incline Village General Improvement District, Inlcine Village, NV.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3:51-74.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences of the United States of America 95:6204-6207.

West, N. E. 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in Central Oregon. Ecology 49:1009-1011.

TABLE 1. Significance of randomization trials used to determine whether species' use of microsite types, within the categories substrate, understory, overstory, and (substrate+understory), was random with respect to availability. A p-value greater than 0.05 indicates random selection of cache sites in that category.

	Microsite category			
Species	Substrate	Understory	Overstory	Combined
P. maniculatus	0.11	< 0.0001	n/a	0.009
T. amoenus	0.03	0.001	0.001	0.09
T. speciosus	0.01	0.008	0.06	0.36
S. lateralis	0.11	0.03	0.01	0.36
All species	< 0.0001	< 0.0001	< 0.0001	< 0.0001

TABLE 2. Ranking matrix for microsite types used for caching by all four species combined. Within each of the three categories (substrate, understory and overstory), the relative use of each microsite type is represented by t-values obtained from a post-hoc comparison of the pair of substrate types shown in the appropriate row and column headings. Asterisks indicate that the difference between two types was significant at the 0.05 level. Microsite types were ranked in order of preference (bottom row), based on the number of positive t-values in a column. The highest ranking microsite type in each category was given the highest number. Asterisks indicate a significant difference between a rank and the next one below it.

	Substrate			
	MS	LL	HL	Other
MS		-1.27	-4.49*	-2.48*
LL	1.27		-4.54*	1.29
HL	4.49*	4.54*		3.23*
Other	2.48*	1.29	-3.23*	
Rank	3*	2	0	1*

	Understory		
	Shrub	Open	Other
Shrub		0.02	-3.16*
Open	-0.02		-3.02*
Other	3.16*	-3.02*	
Rank	2*	1*	0

	Overstory		
	Pine	Open	Other
Pine		17.32*	6.79*
Open	-17.32*	-11.9*	
Other	-6.79*	11.9*	
Rank	0	2*	1*

TABLE 3. Summary of caching microsite preferences (derived from ranking matrices) for each species, and for all species combined. Codes for substrate categories are mineral soil (MS), light litter (LL) and heavy litter (HL). In each microsite category, the highest-ranked type is indicated by the highest number, while a 0 value represents the lowest-ranked type. Asterisks indicate a significant difference between a ranking and the next ranking below it.

	Microsite category									
	Substrate				Understory			Overstory		
Species	MS	LL	HL	Other	Shrub	Open	Other	Pine	Open	Other
P.maniculatus	use was random				2*	1*	0	no data		
T. amoenus	3*	2*	0	1	2	1	0	1*	2*	0
T. speciosus	2	3*	1	0	2*	1*	0	use was random		
S. lateralis	use was random				0	2*	1	0	2*	1
All combined	3*	2	0	1*	2*	1*	0	0	2*	1*

TABLE 4. Ranking matrix for combined substrate-understory categories used for caching by all four species combined. The relative use of each combined category is represented by t-values obtained from post-hoc comparisons of that category with all others. Asterisks indicate that the difference between a pair was significant at the 0.05 level. The combined categories were ranked in order of preference (bottom row), based on the number of significant positive t-values within a column, and the highest-ranking category was given the highest number (5). Asterisks indicate a significant difference between a rank and the next one below it. Adjacent ranks with no asterisks are qualitatively different.

Combined categories	MS-shrub	LL-shrub	HL-shrub	MS-open	LL-open	HL-open
MS-shrub		-1.32	-6.15*	-1.33	-2.70*	-4.53*
LL-shrub	1.32		-5.43*	-0.24	-1.62	-4.26*
HL-shrub	6.15*	5.43*		4.16*	2.79*	1.09
MS-open	1.33	0.24	-4.16*		-1.61	-3.96*
LL-open	2.70*	1.62	-2.79*	1.61		-2.24*
HL-open	4.53*	4.26*	-1.09	3.96*	2.24*	
Rank	5*	4	0	3*	2*	1

TABLE 5. Emergence of Jeffrey pine seedlings from 4335 seeds planted in combinations of 3 different treatments: depth (0 mm, 5 mm and 25 mm), substrate (mineral soil, MS; light litter, LL, heavy litter, HL) and cover (under shrub, open). Values represent the percentage of seeds emerging from the total planted in a given category; categories are ranked from 5 (high) to 0 in order of favorability for emergence ("Rank: plant") and in order of relative use by animals as cache sites ("Rank: animal"). Asterisks show significant differences between a rank and the next one below it.

	Under shrub[+]			Open[++]			
Depth	MS	LL	HL	MS	LL	HL	Mean
Surface	8.0	1.8	-[‡]	7.0	2.0	-	4.7
5 mm	38.5	7.3	-	35.0	2.0	-	20.7
25 mm	36.4	-	15.5	38.0	-	9.0	24.7
Mean	27.6	4.6	15.5	26.7	2.0	9.0	
Rank: plant	5	2*	3*	4*	0	1*	
Rank: animal	5*	4	0	3*	2	1	

[+] Sample size was 468 seeds in each of the 6 combinations of treatments

[++] Sample size was 240 seeds in each of the 6 combinations

[‡] No seeds were planted in this combination of treatments; heavy litter was defined as >10mm in depth.

FIGURE LEGENDS

FIGURE 1. Schematic diagram of the design of the seedling emergence and survival study. This design was replicated on 4 separate sites. Each site, as shown, contained 7 blocks of 6 cache arrays each, representing all possible combinations of the 2 treatment categories substrate (mineral soil or litter) and understory (Flammable shrub (F. shrub), Non flammable shrub (Nf. Shrub), and Open). Each cache array contained 3 replicate 3-seed caches at each of 3 depths (0 mm, 5 mm and 25 mm).

FIGURE 2. The mean cache size (+1SD) (A) and mean cache depth (B) of four species of rodents: Peromyscus maniculatus (PM), Tamias amoenus (TA), T. speciosus (TS) and Spermophilous lateralis (SL). Data represent 10 P. maniculatus, 10 T. amoenus, 9 T. speciosus, and 4 S. Lateralis individuals, which made a total of 378, 324, 83 and 39 caches, respectively.

FIGURE 3. Use of microsites for caching, relative to availability, by 4 species of rodents: Peromyscus maniculatus (PM), Tamias amoenus (TA), T. speciosus (TS) and Spermophilus lateralis (SL) (n = 6-10 per species). Values are mean differences between log ratios for utilized and available microsite types (+/- SD). A mean of 0 indicates random use. Means were calculated after weighting by the number of caches an individual made. Asterisks indicate significantly higher use of one microsite type relative to the others within that category.

FIGURES

Figure 1

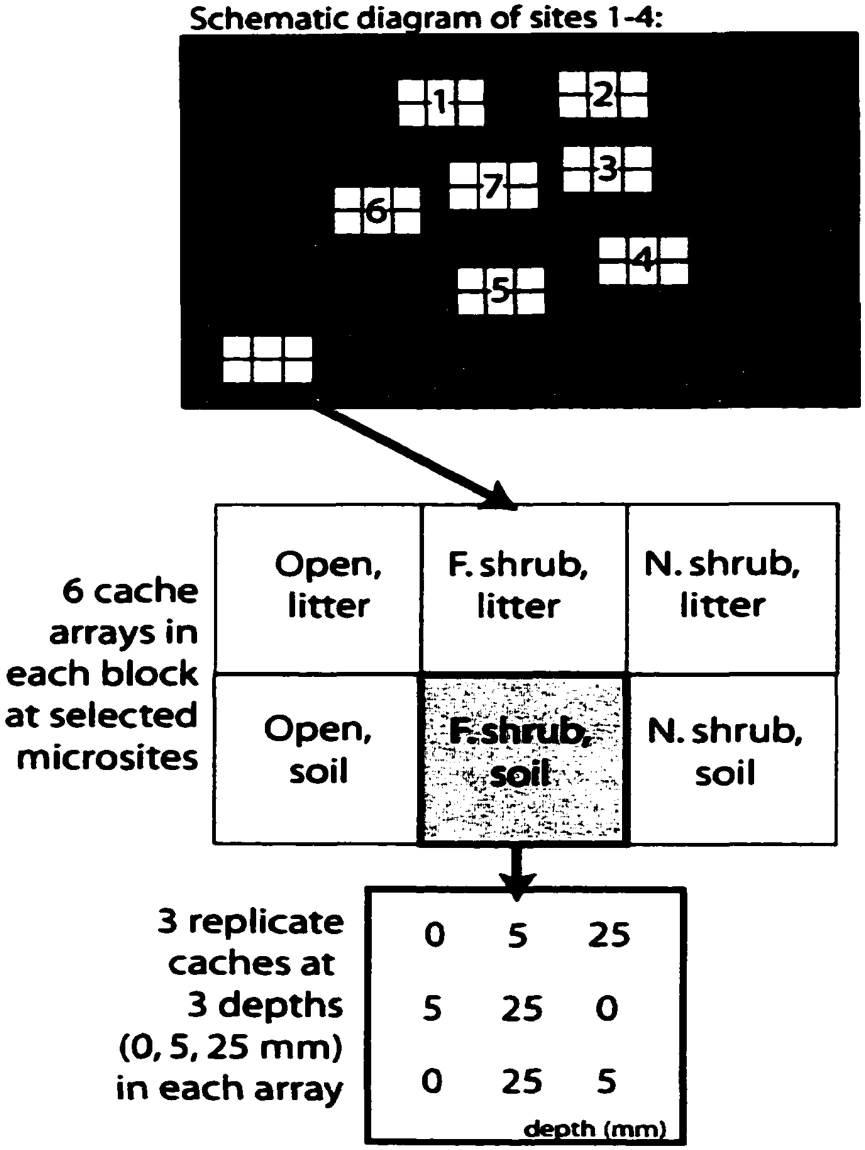


Figure 2

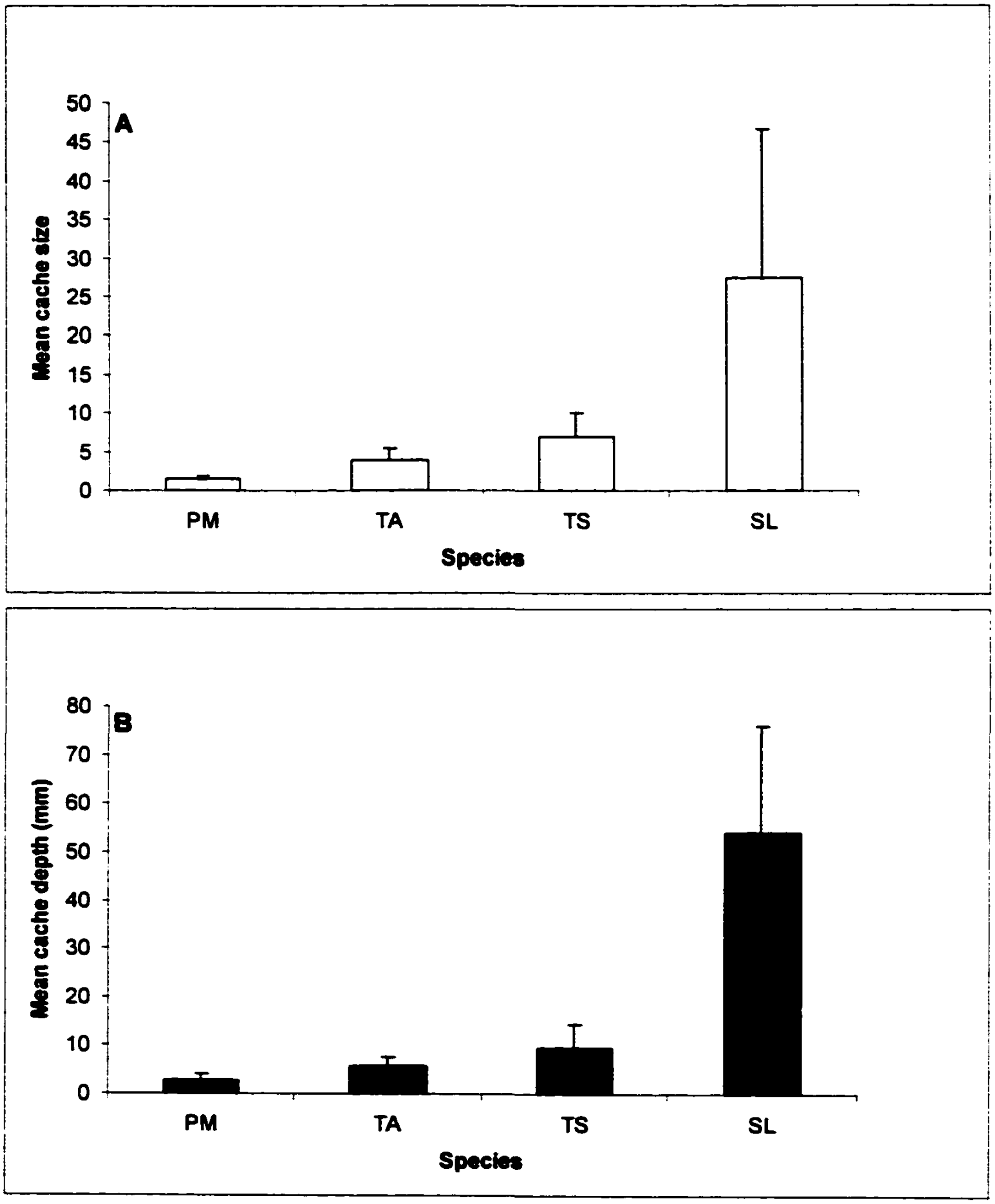
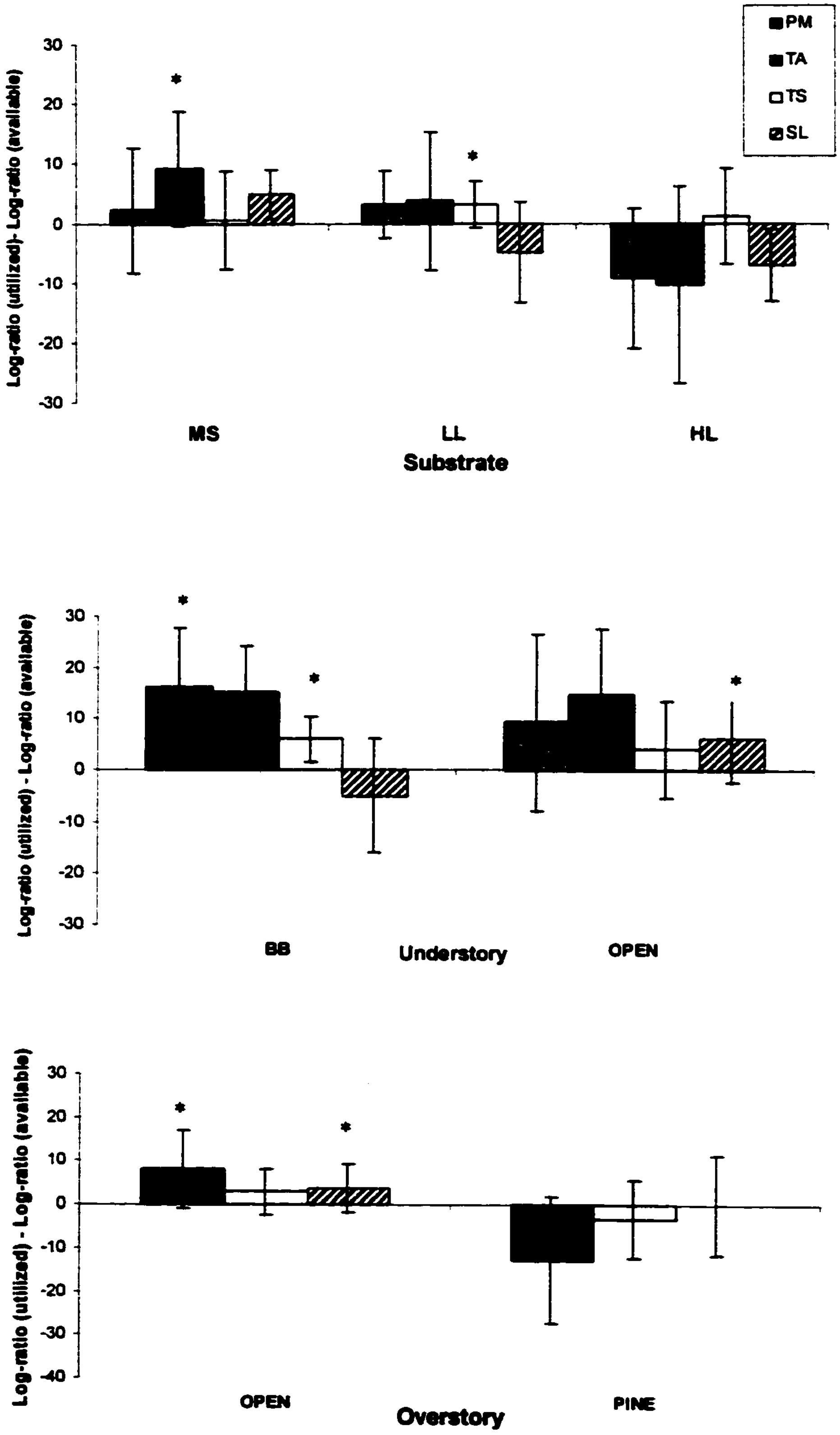

A
Mean cache size
0
5
10
15
20
25
30
35
40
45
50
PM
TA
TS
SL
Species
B
Mean cache depth (mm)
0
10
20
30
40
50
60
70
80
PM
TA
TS
SL
Species

Figure 3


■PM
■TA
□TS
▨SL
Log-ratio (utilized)- Log-ratio (available)
30
20
10
0
-10
-20
-30
*
*
MS
LL
HL
Substrate
Log-ratio (utilized) - Log-ratio (available)
30
20
10
0
-10
-20
-30
*
*
*
BB
Understory
OPEN
Log-ratio (utilized) - Log-ratio (available)
30
20
10
0
-10
-20
-30
-40
*
*
OPEN
Overstory
PINE

Chapter 2: The foraging success and caching behavior of chipmunks (Tamius amoenus and T. speciosus) in ash and sand substrates

ABSTRACT

Many factors in the physical environment affect the ability of food-hoarding rodents to find and recover food. We predicted that, after a wildfire, the presence of ash would impair rodents' ability to detect pine seeds on the forest floor using olfaction. We performed a lab experiment to compare the foraging success, caching frequency, and cache recovery of chipmunks (6 *Tamius amoenus* and 6 *T. speciosus)* in ash versus sand substrates. Initial results supported our hypothesis: chipmunks found only 2.3% of 108 caches of Jeffrey pine (*Pinus jeffreyi*) seeds that we buried in ash, but found 98% of caches in sand. However, chipmunks made as many or more of their own caches in ash compared to sand (48 vs. 52% for *T. amoenus*, 73 vs. 27% for *T. speciosus*.) When we exposed the same subjects to sets of caches of which they were a) knowledgeable and b) naïve, they found significantly higher proportions of their own caches in ash substrates (62%) than caches made by other animals (25%). However, when foraging in sand, they found high proportions of both their own caches and those of others (86 vs. 81%). These results suggest that olfaction is less effective in ash than in sand, that spatial memory enables chipmunks to recover their own caches in ash, and that caching in ash may allow animals to avoid pilferage of stored food. As chipmunks are important dispersers of seeds, changes in their foraging patterns or competitive interactions after fire could significantly affect pine regeneration.

INTRODUCTION

The storage and recovery of food by animals is influenced by many factors in the physical and social environment (Vander Wall, 1990). In variable environments, species that store food for later consumption demonstrate several behaviors that appear to optimize the ratio of costs and benefits associated with this strategy (Andersson and Krebs, 1978). First, they select cache sites that permit them to recover a high proportion of stored food (Vander Wall, 1990), considering environmental factors such as vegetation structure (Petit et al., 1989), climate (Brotons, 2000), accessibility during winter (Vander Wall and Hutchins, 1983), and proximity to landmarks (Collet et al., 1986; Cheng and Sherry, 1992; Kamil and Jones, 1997; Barkley and Jacobs, 1998). These factors limit loss of food from spoilage, reduced seasonal access, and erosion of spatial memory (Vander Wall and Smith, 1987). Second, animals use diverse behavioral strategies that limit pilferage by members of their own or other species (Hampton and Sherry, 1994). Such behaviors include active defense (Clarke and Kramer, 1994), optimal spacing of caches (Stapanian and Smith, 1978; Clarkson et al., 1986), selection of inaccessible or cryptic sites (Petit et al., 1989; Preston and Jacobs, 2001), and avoidance of possible competitors when caching (Stone and Baker, 1989; Heinrich and Pepper, 1998).

Animals may also augment their food supplies, and effectively increase the adaptive value of food-hoarding (Andersson and Krebs, 1978), by pilfering from the stores of others whenever possible. Inevitably, some of the strategies animals use to find food and recover their own stored food are the same as those they use to discover and exploit the stores of other animals. Olfaction and directed searching are common examples (Vander Wall, 1991). Thus, behaviors that minimize an individual's costs of recovering its own food stores (such as caching closer to the nest or selecting memorable and accessible sites) can simultaneously increase the food's vulnerability to theft by others (Clarke and Kramer, 1994). Successfully balancing these conflicting pressures may be especially critical for scatter-hoarding birds and mammals, which make many small caches throughout their habitat instead of concentrating most or all stored food in a defensible larder. These species use several strategies--olfaction, memory, directed searching and exploratory digging at preferred sites (Balda et al., 1987; Vander Wall, 1982, 1991)--either singly or in combination when they are looking for food, selecting cache sites, recovering caches, pilfering, and avoiding pilferage.

In this paper we focus primarily on the interplay between memory and olfaction in the placement and recovery of caches by chipmunks. We consider the opportunities for inter- and intra-specific pilferage arising from animals' differential use of memory and olfaction in different environmental conditions. Previous research on the use of olfaction by rodents suggests that some forest-dwelling species may be sensitive to changes in the moisture levels of the substrates (and seeds) in which they forage (Vander Wall, 1993, 1995, 2000). In dry soils, or when searching for dry seeds, yellow-pine chipmunks (*Tamius amoenus*) and deer mice (*Peromyscus maniculatus*) had much lower foraging success both in the lab and in the field (Vander Wall, 1993, 2000). Spatial memory seems to be necessary for animals to recover food stores in arid environments when olfaction is less effective (Vander Wall, 2000).

In many forested ecosystems in the semi-arid western states, animals experience annual dry seasons and frequent wildfires that severely alter many physical properties of their habitat. Although some granivorous rodents are able to remain in, or rapidly recolonize, burned areas (Bock and Bock, 1983; Briggs unpublished data), conversion of the forest floor to ash may strongly influence the foraging environment for these animals. Not only is the moisture content of ash low, it may have an additional negative effect on the olfactory capacity of animals either by masking the smell of seeds with its own strong smell, or by absorbing organic odorants that would otherwise be released from the seeds and provide an olfactory signal (Vander Wall, 2003).

We tested chipmunks caught in an eastern Sierran pine forest in a lab experiment that compared their caching and cache recovery behavior in ash and sand substrates. We quantified the effects of substrate type and spatial memory on the caching and recovery of Jeffrey pine (*Pinus jeffreyi*) seeds by two species of chipmunk: yellow pine (*Tamias amoenus*) and lodgepole chipmunks (*T. speciosus*). As the habitats and diets of these species overlap locally, our results have implications for the possible changes in foraging strategy and frequency of pilferage that may occur in post-fire environments. Granivorous rodents like chipmunks are important dispersers and consumers of pine seeds in the Sierra Nevada (Tevis, 1953; Vander Wall, 1992b), and many pine trees establish from their caches (Vander Wall, 1992a). Thus, changes in the nature and degree of inter-and intra-specific competition for seeds after fire could significantly affect pine regeneration.

We tested the following hypotheses: 1) Naive chipmunks will find more seeds buried in sand substrate than seeds buried in ash substrate. The ash may bind odorant molecules and the strong smell of ash may mask the olfactory signal given by the seeds. 2) Chipmunks will make more caches in sand than in ash. In these animals' natural environment, ash is a less familiar substrate than soil: the last fire in the area occurred in

1982. Their behavior may also reflect an awareness that caches made in ash will be harder to relocate using olfaction. 3) Chipmunks will retrieve a significantly higher proportion of their own caches made in ash than caches made by other animals in ash. They will be able to use spatial memory as well as olfaction to recover their own caches, but must rely on olfaction alone to find the caches of others. 4) Chipmunks will retrieve similar proportions of their own and others' caches made in sand, if the cached seeds are moist. Olfaction is likely to be effective in sand substrate. 5) No significant differences will be observed between the two species of chipmunks in caching frequency or cache recovery success in ash and sand.

METHODS

The experiment was conducted from January to April, 2002 in a laboratory at the University of Nevada, Reno, using yellow pine chipmunks and lodgepole chipmunks trapped the previous fall in the Carson Range, Washoe County, Nevada. Animals were kept in an animal care facility and fed a diet of mixed wild bird seeds and rodent chow between trials. The experiment comprised 5 phases: 1) acclimation trials, in which subjects foraged for moistened pine seeds that we had buried in a sand-filled test arena, 2) foraging trials in sand- and ash-filled compartments of the arena, 3) caching trials, in which subjects could bury seeds in sand or ash, 4) retrieval of caches made in phase 3, and 5) foraging by naive subjects for caches made by other animals in sand and ash. All chipmunks were tested in each phase in the same order, and all the trials in one phase were completed before the next phase was initiated. 17 individuals were tested in total; 6 *T. amoenus* and 6 *T. speciosus* completed all 5 phases of the experiment.

We conducted experiments in an arena comprised of two wooden enclosures (dimensions 88 x 232 x 30 cm) connected by a tunnel 7 cm in diameter and ≈150 cm long. Each enclosure was divided into three compartments, separated by partitions with holes allowing animals to move freely from one compartment to another (Fig. 1). The six compartments were filled to a depth of ≈3 cm with either sand or an ash-sand mixture (75% ash) depending on the phase of the experiment. At the start of each trial, animals were placed in a nest box, connected to the arena, to which they could return at any time. Foraging trials lasted 11 hr and caching trials lasted 8 hr. Water was available in two of the six compartments (hereafter called 'boxes'), and small rocks and sticks were placed in each box to provide some heterogeneity.

As chipmunks cannot easily detect dry seeds buried in dry substrates (Vander Wall, 1993, 1998), we increased the moisture content of the Jeffrey pine seeds used in acclimation and foraging trials by placing seeds in a hydration chamber (100% RH) for 11 hours before we buried them. The mean moisture content of the seeds (± 1 SD) after hydration was 14.8 ± 1.9%, well above the threshold moisture level of around 5 % at which chipmunks have been shown to detect Jeffrey pine seeds in dry substrates (Vander Wall, 1998, 2003). We tested whether seeds retained a comparable level of moisture in both substrates throughout the foraging trials by burying sample caches in the arena, then removing two caches from each substrate at hourly intervals. After weighing, oven-drying and re-weighing the seeds, we found that seeds lost moisture at a similar rate in the two substrates. There was a sharp decline during the first hour, followed by a gradual decrease in moisture over time (mean water loss over 9 hr = 7.4 ± 1.1 % in ash and 6.4 ± 1.1 % in sand). The moisture content of seeds in both substrates did not fall below the 5

% threshold, and was similar after 9 hr (6.6 % in ash, 6.3 % in sand). Thus, moisture levels of seeds probably did not change enough to affect subjects' foraging success in either substrate.

The design of the arena allowed us to record the removal and caching of seeds at the end of each trial. The bottom of each box in the arena consisted of a 6 mm wire mesh screen, stretched over a removable plywood floor. When the floor was removed, the sand or ash in the box drained through the screens into receptacles situated below. Any cached or undiscovered seeds on the screens could be counted and mapped.

Phase 1: Acclimation

Before each subject was tested, we deprived it of food for 12 hr to increase its motivation to forage during the trial. It was then allowed approximately 11 hr to explore the arena and search for buried seeds. During this phase, each of the six boxes in the arena contained sand in which we had made three caches of two Jeffrey pine seeds at a depth of 1.5 cm. This depth is typical of chipmunk caches in the field (Vander Wall, 1993b). We also placed a single seed on the sand surface in each box, to indicate to the animal that food was present in the arena.

Cache sites were chosen arbitrarily within each box, with the following restrictions: caches were spaced at least 30 cm apart and at least 10 cm from the edges of the box or from rocks and sticks. Previous observations of subjects in lab conditions have shown that they often dig near walls and objects when exploring a new, restricted environment (Vander Wall, pers. obs.). After making the caches, we leveled and brushed the surface of the substrate to remove traces of disturbance.

At the end of each foraging trial the subject was removed from the arena, all cache sites were checked and the presence or absence of the original caches was recorded. If a subject had not found any of the 36 buried seeds, it was tested a second time in exactly the same way after an interval of 1 wk. If it failed to find any buried seeds in the second trial, it was dropped from the experiment.

Phase 2: Foraging for caches in ash and sand

In foraging trials, the sand substrate in boxes 1, 3, and 5 was replaced with the ash-sand mixture (Figure 1b). Cache size and depth were the same as in Phase 1; however, the locations of caches were different. Placement of the rocks and sticks was also altered, and no seeds were placed on the surface of the substrates. In all other respects, trials were conducted as in Phase 1.

Phase 3: Caching seeds in ash and sand

During caching trials, the substrate in each box was the same as in the previous phase (alternately ash and sand) but no buried seeds were present. Instead, a glass dish containing 12 Jeffrey pine seeds was placed on the substrate surface in the center of each box (72 total seeds). Animals were not deprived of food before these trials. Each animal was left in the test arena until it had removed all of these seeds, or until 8 hr had elapsed, whichever occurred first. We drained the sand and ash out of the boxes and recorded the number and size of all caches made in each box.

All animals completed one caching trial in early February and a second trial in early March. The two sets of trials were conducted in the same manner, but in the March trials we introduced new rocks and sticks, altered their placement in the boxes relative to the previous arrangement, and taped pictures to the compartment walls. These changes were intended to reduce the chance that subjects would search in vain for caches they had made in the first trial. Two distinct sets of objects (rocks, sticks and pictures) were used in the March trials: half of the subjects were arbitrarily assigned to be tested when the arena contained Object Set A and half when it contained Object Set B. The results of both the February and March trials were used in the analyses of caching behavior. However, only the caches made by each subject in the March trial were reestablished in Phases 4 and 5 of the experiment.

Phase 4: Retrieval of caches in ash and sand by knowledgeable subjects

Phase 4 was initiated 1 week after completion of Phase 3. We re-established the Object Set (A or B) that had been present for each subject in its second caching trial. Each animal was deprived of food for 10-12 hr and then allowed 11 hr to forage for the caches it had made in that trial. These caches had been replaced in the arena in their original locations, but they differed from the originals in several respects. To standardize the conditions experienced by each animal, each cache consisted of two hydrated seeds buried 1.5 cm deep. If an animal had made many (>25) caches in a box, or placed caches very close to each other, some of these caches were not reestablished in an effort to standardize the numbers of caches available to each subject. Caches were eliminated if they were closer than 5 cm to another cache, but at least two thirds of each animal's original caches in each box were retained, to reduce the chance that the animal would stop foraging if it discovered that many of its caches were gone. At the end of each trial, all cache sites were checked and the presence or absence of the seeds was recorded.

Phase 5: Foraging for cached seeds in ash and sand by naive subjects

For this final phase, the visual environment of the arena was changed again. All subjects previously tested when the arena contained Object Set A were now exposed to Object Set B, and vice versa. The alterations of the landscape were again intended to suggest to animals that they should not 'expect' their recent caches to be present in the boxes. In each trial, the arena in fact contained a set of caches in locations unfamiliar to the individual being tested. For all subjects, the total number of caches, and the relative proportions of caches in ash and sand, were the same as those present for that animal in Phase 4. For example, a subject that had searched for 5 of its own caches in sand and 12 in ash in Phase 4 was presented with 5 caches in different sites in sand, and 12 caches in different sites in ash.

For each subject, the new set of cache locations was randomly selected from the pooled set of all caches made by the individuals of the same species that had cached when the opposite 'Object Set' was in place in Phase 4. Thus, in contrast to the arbitrary cache sites we used in Phase 2, we now buried seeds in actual cache sites previously chosen by other animals but unknown to each naive forager. However, to minimize the number of caches that naive animals could discover using random search or previous memory rather than olfaction, the following exceptions to the randomly generated cache distributions were made: a) caches were not placed < 5 cm from sites previously used by the subject being tested; b) no more than one cache per box was made near a corner, at the edge of a box, or at the edge of a rock or stick, because these sites had regularly been excavated by many subjects in previous phases; and c) caches made in corners (common for *T. speciosus*) were moved 5 cm away from those corners. At the end of each trial, all cache sites were checked and the presence and absence of seeds was recorded. Any subject (there were 3) that had retrieved ≤ 1 cache during the trial was retested a week later in exactly the same way, after being deprived of food for 24 hr instead of 12 hr.

Analyses

T-tests were used to compare the number of caches found by *T. amoenus* and *T. speciosus* in Phase 1, and the size of caches made by *T. amoenus* and *T. speciosus* in Phase 3. Chi-squared tests were used to determine whether each species' caching frequency in the two substrates (ash and sand) differed from the expected 50:50 distribution. For all other analyses, we used repeated-measures ANOVA. First, to compare foraging success in Phases 1 and 2, we compared the number of caches found in boxes 1, 3, 5 with the number found in boxes 2, 4, 6 in Phase 1 (when all boxes contained sand) versus Phase 2 (when boxes 1, 3 and 5 contained ash). Species and box set (1, 3, and 5 or 2, 4 and 6) were the between-subjects factors, and phase of experiment (1 or 2) was the within-subjects factor.

We performed repeated-measures ANOVAs on the results of Phase 3 to examine the effects of species, substrate, trial and box on: a) mean number of caches made, and b) mean number of seeds cached. Finally, we assessed the effects of experience on foraging success by comparing the proportion (arc-sine transformed) of caches found by individuals when they were either knowledgeable or naïve of cache locations, in Phases 4 and 5, respectively. Species and substrate (ash or sand) were the between-subject factors, and experience was the within-subjects factor.

RESULTS

Phase 1: 9 of the 12 subjects found 80-100% of the caches of moistened seeds buried in sand (Fig. 2a). 3 subjects found 30% of the 18 available caches. The mean number of caches found by *T. amoenus* (12.3) was not significantly different from the mean number found by *T. speciosus* (15.4); (t-test, $t = 1.13$, $df = 9$, $P = 0.29$).

Phase 2: When boxes 1, 3, and 5 contained ash instead of sand, the success rate of animals foraging in those boxes declined (Fig. 2b), although observations of footprints showed that all 12 animals had explored 80-100% of the boxes. Overall, subjects in Phase 2 only found 3 of the 108 caches buried in ash (2.8 %), compared to 98 % (106 of 108) of those in sand. Repeated-measures ANOVA identified a highly significant decrease in the mean number of caches that individuals found in Phase 2 versus Phase 1 ($F_{1, 10} = 165.97$, $P < 0.0001$). The number of caches found in the two substrates was significantly different ($F_{1, 10} = 14.15$, $P = 0.004$) and there was a significant interaction between substrate type and phase of experiment ($F_{1, 10} = 417.65$, $P < 0.0001$) which showed that the number of caches found in boxes 1, 3 and 5 differed between Phase 1 and 2 (when the sand was replaced with ash), but the number found in boxes 2, 4, and 6 (sand in both phases) did not differ. Foraging success of the two species was not significantly different ($F_{1, 10} = 2.62$, $P = 0.14$).

Phase 3: Repeated-measures ANOVA did not identify a significant overall difference between the number of caches made in trial 1 and trial 2 ($F_{1, 10} = 0.22$, $P =$

0.647), nor were the interactions between trial and substrate or species significant, so data from trials 1 and 2 (Fig. 3a and b) were pooled for analyses. Also, no significant box effect was identified when box was used as a blocking factor ($F_{5,50} = 1.31$, $P = 0.27$), although an interaction between box and trial was nearly significant ($F_{5,50} = 2.36$, $P = 0.053$).

The mean number of caches placed in ash was significantly greater than the mean number placed in sand for all individuals combined ($F_{5,50} = 7.35$, $P = 0.02$). Ten of the 12 subjects (4 *T. amoenus* and all *T. speciosus*) placed most of their caches in ash substrate (Fig. 2a). The number of caches made by *T. amoenus* was significantly greater than that made by *T. speciosus* ($F_{1,10} = 12.30$, $P = 0.006$). *T. amoenus* made 33.8 ± 26.7 caches in ash and 36.8 ± 17.9 in sand; *T. speciosus* made 18.7 ± 12.25 in ash and 6.8 ± 7.7 in sand (values are mean ± 1 SD). Although there was too much variation among individuals to identify a statistically significant difference in the two species' use of ash and sand substrates (species x substrate interaction: $F_{5,50} = 0.34$, $P = 0.88$), chi-squared analyses showed that, for *T. speciosus*, the distribution of caches between the two substrates was significantly different ($X^2 = 32.95$, df = 1, $P < 0.001$; Fig. 4). The distribution was not significantly different for *T. amoenus* ($X^2 = 0.77$, df = 1, $p > 0.25$, Fig. 4).

The analysis using number of seeds cached (rather than number of caches) as the response variable showed that *T. speciosus* and *T. amoenus* cached similar numbers of seeds overall (344 vs. 343, respectively, in Trial 1; 297 vs. 350 in Trial 2; $F_{1,10} = 0.67$, $P = 0.43$). This suggests that the larger size of caches made by *T. speciosus* was responsible for the significant difference between species in mean number of caches made (Fig. 3a and b). In fact, the mean cache size was significantly greater for *T. speciosus* (6.1 ± 2.1 seeds) than for *T. amoenus* (1.5 ± 0.2 seeds) (t-test: t = 5.52, df = 10, $p < 0.001$). There was a significant effect of substrate on number of seeds cached ($F_{1, 10} = 14.77$, P = 0.003). This ANOVA identified a significant effect of box on number of seeds cached ($F_{5, 50} = 4.87$, P = 0.001) as well as an interaction between box and species ($F_{5, 50} = 3.02$, P = 0.02). Also, although the main effect of trial was not significant ($F_{1, 10} = 2.78$, P = 0.13), there was a significant interaction between trial and substrate ($F_{1, 10} = 8.30$, P= 0.02), showing a change in number of seeds placed in the two substrates in the two trials.

T. amoenus and *T. speciosus* used certain types of cache sites with varying frequency. In ash, both species placed similar proportions of caches along or touching the walls of compartments (16.5% vs. 17.9%). However, *T. amoenus* placed very few (< 5%) of their caches in corners or under objects in ash compartments, while *T. speciosus* placed 39.7 % of caches in these types of sites. In sand, *T. amoenus* placed fewer caches along or touching walls than did *T. speciosus* (10.9% vs. 20.5%), and also cached near corners and objects much less frequently (3.3% vs. 22.9%). These data were not analyzed statistically because of the large variation between species and individuals in number of caches made.

Phases 4 and 5: A significant experience x substrate interaction ($F_{1, 10} = 14.63$, P = 0.003) revealed that knowledge of cache sites increased foraging success in the ash substrate only. In sand, knowledgeable vs. naive subjects of both species found similar mean proportions of caches (81% vs. 72% for *T. speciosus*, 91% vs. 90% for *T. amoenus*; Fig. 5). Thus, the analysis revealed no main effects of experience ($F_{1, 10} = 3.33$, P =

0.10) or species ($F_{1,10} = 2.99$, $P = 0.11$). However, the main effect of substrate was highly significant ($F_{1,10} = 61.82$, $P < 0.0001$): subjects found a lower proportion of caches in ash compared to sand (Fig. 5),. The interaction between substrate and species was also highly significant ($F_{1,10} = 27.55$, $P = 0.0004$), reflecting the greater overall success rate achieved by *T. speciosus* vs. *T. amoenus* when foraging in ash (Fig. 5). Knowledgeable *T. speciosus* retrieved more (91% on average) of their own caches made in ash than did knowledgeable *T. amoenus* (33%). The difference between the two species in mean percentage of caches found in ash by naïve animals was also great (37% vs. 13%).

DISCUSSION

The results of Phases 1 and 2 showed that, as predicted, chipmunks found significantly fewer caches in ash compared to sand, and that *T. amoenus* and *T. speciosus* did not differ in foraging success during these phases. However, the results of caching trials in Phase 3 caused us to reject our hypothesis that animals would prefer to make caches in sand. When the substrate use of each species was examined separately, *T. amoenus* was found to have placed approximately equal proportions of their caches in sand and ash (48% vs. 52%), while *T. speciosus* placed 73% of caches in ash and 27% in sand. Thus, we rejected the possibility that the results of Phase 2 could be explained by animals' avoidance of ash. However, the high frequency of caching in ash, combined with the low foraging success in ash, suggested that we might have identified an unexpected process.

In designing Phases 4 and 5, we sought to distinguish between four alternative explanations for the results of Phases 2 and 3. First, animals might not have foraged actively in the ash boxes because previous experience in the acclimation trials had exposed them only to seeds buried in sand. This possibility could be discounted in Phases 4 and 5, because in these trials subjects foraged for their own caches, many of which they had made in ash. Although there was considerable individual variation, all subjects made some caches in ash (> 6 for 11 of 12 subjects). Thus, if a 'training effect' had influenced the results of Phase 2, it was no longer relevant in Phases 4 and 5.

Second, animals might not have foraged actively in ash boxes because they were satiated after consuming the seeds they had found in sand. This seemed unlikely, as the mean numbers of seeds consumed by *T. amoenus* and *T. speciosus* in the acclimation trials were 18 and 29, respectively (out of a possible 42 available). In Phase 2, 36 seeds were present (18 in sand and 18 in ash), but animals found and ate an average of only 15 (*T. amoenus*) and 17 (*T. speciosus*). Thus, most individuals, especially *T. speciosus*, were not likely to have been fully satiated when they stopped finding seeds, or by the end of Phase 2. A third possibility was that animals did not find seeds in ash because the caches were made at arbitrary locations and not in sites where chipmunks would actually cache and forage. This may have affected the results, but in Phases 4 and 5 we avoided this issue by presenting the animals with caches in sites that they or others had actually used.

A fourth explanation for our results seemed the most likely: animals could not smell the seeds we had buried in ash, but treated the ash compartments as relatively secure locations for their own caches, which they could retrieve using spatial memory. All the predictions that we generated from this hypothesis were supported by the results of Phases 4 and 5. Animals foraging in ash found significantly more of their own caches than caches of which they had no knowledge, suggesting that memory was important in relocation. In sand, their success in finding known and unknown caches of moistened pine seeds did not differ significantly, presumably because olfaction could be effectively used in these conditions and memory did not contribute significantly to successful retrieval (Vander Wall, 2000). And, a significantly higher proportion of caches overall was found in sand compared to ash, indicating that seeds placed in ash are harder to detect by both knowledgeable and naive foragers, and may be less vulnerable to pilferage. Inspection of the ash boxes after trials indicated that many naive animals had searched extensively in certain areas, e.g. digging along the edges, corners and objects in these boxes, but often failed to locate seeds 1-5 cm away. Taken together, these results support the hypothesis that memory is the key factor allowing animals to retrieve seeds buried in a substrate that masks the olfactory signal of the seeds, thereby making ash a more secure location for the placement of caches.

The results of Phase 5 led us to reject the hypothesis that *T. speciosus* and *T. amoenus* would have similar foraging success. However, the conclusion that *T. speciosus* was more successful overall may be erroneous for two reasons. First, although *T. speciosus* recovered three times as many of their own caches in ash than did *T. amoenus*, they were searching for fewer (a mean of 17 versus 27) caches, and may have been hungrier during foraging trials as a result. Their greater body mass (≈75 g, vs. 45 g for *T. amoenus*) probably also increased their motivation to forage.

Second, although naive *T. speciosus* also found approximately three times more 'unknown' caches in ash than did naive *T. amoenus*, this result reflects the unusual behavior of two individuals. Initially, these animals did not appear to forage at all in Phase 5, and found no seeds in any boxes, so they were re-tested a week later after being deprived of food for 24 instead of 12 hours. During their second trials, both animals systematically excavated all 6 boxes and found 92% and 67% respectively of the caches present in the ash. This behavior resembled exploratory digging (Vander Wall, 1982), did not appear to involve the use of olfaction, and was very different from that of the other animals in the study as well as from their own behavior in earlier phases. This search strategy probably would not have been as effective in a field situation, and we conclude that there is insufficient evidence that *T. speciosus* are more successful foragers than *T. amoenus*.

Although the constraints of our experimental design probably contributed to the higher success of *T. speciosus*, this species' apparent preference for sites close to possible 'landmarks' may also have been important. More *T. speciosus* caches (a total of 58 % in ash and 43 % in sand) were placed in corners and along the edges of objects or boxes, while *T. amoenus* made far fewer caches in these types of sites (23 % in ash, 14 % in sand). Although these data were not analyzed statistically due to the variation in sample sizes and the lack of independence of caches made by the same individual, the trends have interesting implications, especially if they persist in the field. Similar cache placement strategies among *T. speciosus* may explain their higher success rate in locating caches made by conspecifics in Phase 5; Vander Wall (1982) found evidence for this type of directed search in nutcrackers but few studies have since confirmed the phenomenon, even though there is a great deal of evidence that many species use landmarks in the placement and recovery of their own caches (Collet et al., 1986; Cheng and Sherry, 1992;

Kamil and Jones, 1997; Barkley and Jacobs, 1998). *T. amoenus* may have selected cache sites relative to a set of landmarks of which we were not aware (eg. cues in the larger room environment: Brodbeck, 1994), but their lower success in locating cache sites used by conspecifics suggests that they did not consistently cache or search for seeds in preferred sites. Vander Wall (2000) also found no difference in the success rate of yellow-pine chipmunks and deer mice when they foraged for the caches of hetero- or con-specifics. Additional tests would be needed to address whether the level of intra-specific pilferage is higher in *T. speciosus* under natural conditions.

We observed considerable variation in behavior among individuals, as well as between species, throughout the study. This may have influenced our analyses in Phases 4 and 5 because subjects had different retrieval and foraging tasks based on what they had done with seeds in the caching trial. We could not standardize the numbers or even proportions of caches for which animals searched in the two substrates without potentially affecting the knowledgeable animals' foraging decisions: e.g. if we did not re-set enough of an animal's original caches, the lack of positive feedback might have caused it to become frustrated and cease foraging (Balda, 1980). The consequence of our design was that each individual might have had different levels of motivation and experience when searching for each cache. Despite this variation, the effect of experience on success in ash was similar for 9 of 12 subjects; the exceptions were one of the *T. speciosus* described above who used extensive random searches when naive, one *T. speciosus* who did not forage at all in Phase 5 even when re-tested, and one *T. amoenus* who did not forage in ash whether knowledgeable or naive. Thus, the results for most subjects supported our hypothesis that foraging success improves in ash when animals are knowledgeable of cache sites.

As subjects did not place all of their caches in ash in Phase 3, nor retrieve all of their ash caches in Phase 4 when they had knowledge of the cache sites, we can infer that there may be a cost associated with retrieval in ash. Studies of caching and retrieval in captive Clark's nutcrackers led Bednekoff and Balda (1997) to speculate that the costs of different choices affect the performance levels of the birds in different situations. Initially, nutcrackers retrieved caches most accurately early in trials and were less accurate in later retrieval attempts (Kamil and Balda, 1990). However, when costs of retrieval were imposed by experimenters, the nutcrackers made fewer errors (Bednekoff and Balda, 1997). For our subjects, olfaction is probably the most effective foraging technique under certain conditions. Presumably, less accuracy in retrieval is required in sand, because olfaction can be used to assist memory. Bednekoff and Balda's (1997) results suggest that if we increased the cost of caching in sand (e.g., by increasing pilferage there) animals might place higher proportions of caches in ash even though those caches are more difficult to retrieve. Alternatively, if we allowed animals to look only for the seeds they had buried in ash, their accuracy of retrieval in this substrate should increase. Tests of these possibilities could predict the response to pilferage in field situations.

Studies of pilferage in black-capped chickadees (Hampton and Sherry, 1994; Baker and Anderson, 1995) have shown the birds stop using cache sites that are regularly robbed. Merriam's kangaroo rats (*Dipodmys merriami*) responded to pilferage by increasing the degree to which they larder-hoarded, rather than scatter-hoarded food

(Preston and Jacobs, 2001). Emery and Clayton (2001) demonstrated that lab-raised western scrub jays *(Aphelocoma californica)* altered their caching behavior in response to their own experience of pilfering from others plus their own memory of being watched while caching. Although we tested individuals one at a time, we used adult animals trapped in the wild that presumably had considerable experience caching and pilfering seeds. Thus, while we did not directly test the effects of social context on caching behavior, our subjects' actions may reflect an 'awareness' of the competitive environment in the field.

In our study, animals never experienced returning to identical environments from which all their original caches had been removed, but there were two situations in which their behavior may have represented a response to pilferage. First, in preparation for the second caching trial of Phase 3, we removed all caches made by subjects in the first trial. Although the placement of landmarks was then altered in an attempt to make the arena look 'different', some animals adopted a different caching strategy in their next trial, possibly in response to the removal of their previous caches. Five *T. amoenus* placed more caches in ash boxes in Trial 2 than in Trial 1, four *T. speciosus* cached in one sand box that none of them had used in the first trial, and one *T. speciosus* made many (50) small caches instead of fewer (14) large ones. Further tests would be necessary to examine whether such shifts in strategy became more pronounced, or widespread, as the level of 'pilferage' increased. Secondly, in our attempt to standardize the sample size of caches for recovery in Phase 4, we did not reestablish a proportion of the caches made by five animals. During Phase 4, four out of these five animals re-cached some of their recovered seeds, compared to only one out of the other seven subjects whose entire set of caches had been reestablished. Barkley and Jacobs (1998) found a significant increase in re-caching by Merriam's kangaroo rats after conspecifics pilfered 75% of their caches. Although we did not directly test our subjects' response to pilferage by conspecifics, our results suggest that some individuals may modify their behavior rapidly after experiencing losses of their food stores.

The results of this study support and extend Vander Wall's finding (2000) that seed-caching animals change their foraging strategy according to variation in the physical environment. He discovered that yellow-pine chipmunks and deer mice found many more caches of Jeffrey pine seeds when recent rainfall or watering had dampened the soil, and concluded that the time they allot to caching vs. pilfering of seeds in natural environments varies with the weather. When searching for seeds, animals seem to rely on memory and olfaction to different extents depending on the context: their knowledge of the cache sites and the moisture content of the seeds or soil (Vander Wall, 2000). Our repeated-measures analysis demonstrated the contrasting effects of knowledge or lack of knowledge on the foraging success of the same individuals. In Vander Wall's study (2000), different subjects were used in the 'naive' and 'knowledgeable' groups, so the change in individual success in different conditions could not be demonstrated as directly. Our results also indicate that the nature of a substrate, rather than its moisture content alone, can influence the strength of the olfactory signal of seeds. We found that the two substrates themselves had similar mean levels of moisture: 0.2% for ash and 0.1% for sand (n = 3 samples for each substrate, taken from the arena and dried at 75 C for 72 hr). We do not know the specific mechanism by which ash reduces the olfactory signal of seeds, but it may either mask the smell of seeds with its own strong smell, or absorb organic odorants that would otherwise be released from the seeds and provide an olfactory signal (Vander Wall 2002).

Our findings suggest that animals may alter their caching behavior in response to spatial as well as temporal variation in the environment. Vander Wall's results (2000) describe a short-term change in foraging strategy following rainfalls or seasonal climate changes. The present study indicates that animals could also respond to large-scale, long-term changes in their physical environment such as those produced by fires. When pine seeds are available and viable in the years following a fire, they are often buried in the soft, ashy substrate via abiotic processes (dispersal through wind or gravity) more readily than is usual in unburned forest (pers. obs.). Previous studies (Briggs unpublished data; Vander Wall and Joyner, 1998) have shown that in unburned forests, Jeffrey pine seeds falling on the forest floor are not often buried and do not often germinate or survive. The finding and caching of these initially wind-dispersed seeds by animals appears to be critical for their successful establishment, especially if animals place the seeds in favorable microsites such as under the canopy of shrubs (Vander Wall, 1993b). However, our results suggest that following a fire, chipmunks' abilities to find seeds in an ashy substrate using olfaction are significantly reduced. Thus, although seeds may readily be buried in ash, either by abiotic processes or by the frequent caching observed in this study, animals may not recover, consume or rebury them to the same degree that they do in unburned forest. The effects of these changed dynamics on the regeneration of pines may be significant.

LITERATURE CITED

Andersson M, Krebs J, 1978. On the evolution of hoarding behaviour. Anim Behav 26:707-711.

Baker MC, Anderson P, 1995. Once-pilfered sites not avoided by black-capped chickadees. Anim Behav 49:771-785.

Balda RP, 1980. Recovery of cached seeds by a captive *Nucifraga caryotactes*. Z Tierpsychol 52: 331-346.

Balda RP, Bunch KG, Kamil AC, Sherry DF and Tomback DF, 1987. Cache site memory in birds. In Foraging Behavior, ed. Kamil AC, Krebs JR, Pulliam HR. New York: Plenum Press.

Barkley CL, Jacobs LF, 1998. Visual environment and delay affect cache retrieval accuracy in a food-storing rodent. Anim Learning Behav 26:439- 447.

Bednekoff PA, Balda RP, 1997. Clark's nutcracker spatial memory: many errors might not be due to forgetting. Anim Behav 54:691-698.

Bednekoff PA, Balda RP, Kamil AC, Hile AG, 1997. Long-term spatial memory in four seed-caching corvid species. Anim Behav 53:335-341.

Bock CE, Bock JH, 1983. Response of birds and deer mice to prescribed burning in ponderosa pine. J Wildl Mgmt 47:836-841.

Brodbeck DR, 1994. Memory for spatial and local cues: a comparison of a storing and a non-storing species. Anim Learn Behav 60:395-402.

Brotons L, 2000. Individual food-hoarding decisions in a nonterritorial coal tit population: the role of social context. Anim Behav 60:395-402.

Cheng K, Sherry DF, 1992. Landmark-based spatial memory in birds (*Paris atricapillus* and *Columba livia*): the use of edges and distance to represent spatial positions. J Comp Psych 106:331-341.

Clarke MF, Kramer DL, 1994. The placement, recovery and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. Behav Ecol 5:353-361.

Clarkson K, Eden SF, Sutherland WJ, Houston AJ. 1986. Density dependence and magpie food hoarding. J Anim Ecol 55:111-121.

Clayton NS, Krebs JR, 1994. Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 174:371-379.

Collett TS, Cartwright BA, Smith BA, 1986. Landmark learning and visuo-spatial memory in gerbils. J Comp Physiol A 158:835-851.

Emery NJ, Clayton NS, 2001. Effects of experience and social context on prospective caching strategies by scrub jays. Nature 414:443-446.

Hampton RR, Sherry DF, 1994. The effects of cache loss on choice of cache sites in black-capped chickadees. Behav Ecol 5:44-50.

Heinrich B, Pepper JW, 1998. Influence of competitors on caching behavior in the common raven, *Corvus corax*. Anim Behav 56:1083-1090.

Hitchcock CL, Sherry D, 1995. Cache pilfering and its prevention in pairs of Black-capped Chickadees. J Avian Biol 26:187-192.

Kamil AC, Balda RP, 1990. Differential memory for cache sites by Clark's nutcracker (*Nucifraga columbiana*). J Exp Psych: Anim Behav Proc 16:162-168.

Kamil AC, Jones JE, 1997. The seed-storing corvid Clark's nutcracker learns geometric information about landmarks. Nature 390:276-279.

Petit DR, Petit LJ, and Petit KE, 1989. Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. Condor 91:766-776.

Preston SD, Jacobs LF, 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Behav Ecol 12:517-523.

Shettleworth SJ, Krebs JR, 1982. How marsh tits find their hoards: the role of site preference and spatial memory. J Exp Psych: Anim Behav Proc 8:354-375.

Stapanian MA, Smith CC, 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896

Stone ER, Baker MC, 1989. The effects of conspecifics on food caching by Black-capped Chickadees. Condor 91:886-890.

Tevis L, 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. J Mammal 34:316-324.

Tomback DF, 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123-161.

Tomback DF, 1986. Post-fire regeneration of Krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono 33:100-110.

Vander Wall SB, 1982. An experimental analysis of cache recovery in Clark's nutcracker. Anim Behav 30:84-94.

Vander Wall SB, 1990. Food Hoarding in Animals. Univ. Chicago Press, Chicago.

Vander Wall SB, 1991. Mechanisms of cache recovery by yellow pine chipmunks. Anim Behav 41:851-863.

Vander Wall SB, 1992. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73:614-621.

Vander Wall SB, 1993a. Seed water content and the vulnerability of buried seed to foraging rodents. Amer Midl Nat 129:272-281.

Vander Wall SB, 1993b. Cache site selection by chipmunks (*Tamias spp.*) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). Oecologia 96:246-252.

Vander Wall SB, 1995. Influence of substrate water on the ability of rodents to find buried seeds. J Mammal 76:851-856.

Vander Wall SB, 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behav Ecol 11:544-549

Vander Wall SB, 2003. How rodents smell buried seeds: a model based on the behavior of pesticides in soil. J. Mammal.

Vander Wall SB and Hutchins HE, 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the post-fledging period. Can Field-Nat 57:208-214

Vander Wall SB and Joyner JW, 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamius amoenus*): potential effects on plant reproductive success. Can J Zool 76:154-162

Vander Wall SB and Smith KG, 1987. Cache-protecting behavior of food-hoarding animals. In Foraging Behavior, ed. Kamil AC, Krebs JR, Pulliam HR. New York: Plenum Press.

FIGURE LEGENDS

Figure 1. Diagram of experimental arena. During Phase 1, all 6 compartments contained sand. A nest was adjacent to compartment 4 and a tunnel connected compartments 3 and 4. Sources of water are represented by rectangles. In Phases 2-5, the sand in compartments 1, 3 and 5 was replaced with ash.

Figure 2. Mean number of artificial caches found by 6 *T. amoenus* (empty bars) and 6 *T. speciosus* (filled bars) in compartments 1-6. Error bars represent 1 SD. 3 caches were present in each compartment. A. Phase 1: All compartments contained sand. B. Phase 2: Compartments 1, 3 and 5 contained ash, and compartments 2, 4, and 6 contained sand.

Figure 3. Placement of caches by 6 *T. amoenus* (empty bars) and 6 *T. speciosus* (filled bars) in ash and sand compartments during Phase 3. Data are from both trials combined; error bars represent 1 SD. A. Mean number of caches made in each box. B. Mean number of seeds placed in each box.

Figure 4. Proportion of caches placed in ash and sand substrates by 6 *T. amoenus* (empty bars) and 6 *T. speciosus* (filled bars) during Phase 3. Data are from both caching trials combined.

Figure 5. Effects of experience on mean proportion of caches found by chipmunks in ash and sand during Phases 4 and 5. Filled bars represent caches found in ash, empty bars represent caches found in sand. Error bars represent 1 SD. A. *T. speciosus* (n = 6). B. *T. amoenus* (n = 6).

FIGURES

Figure 1

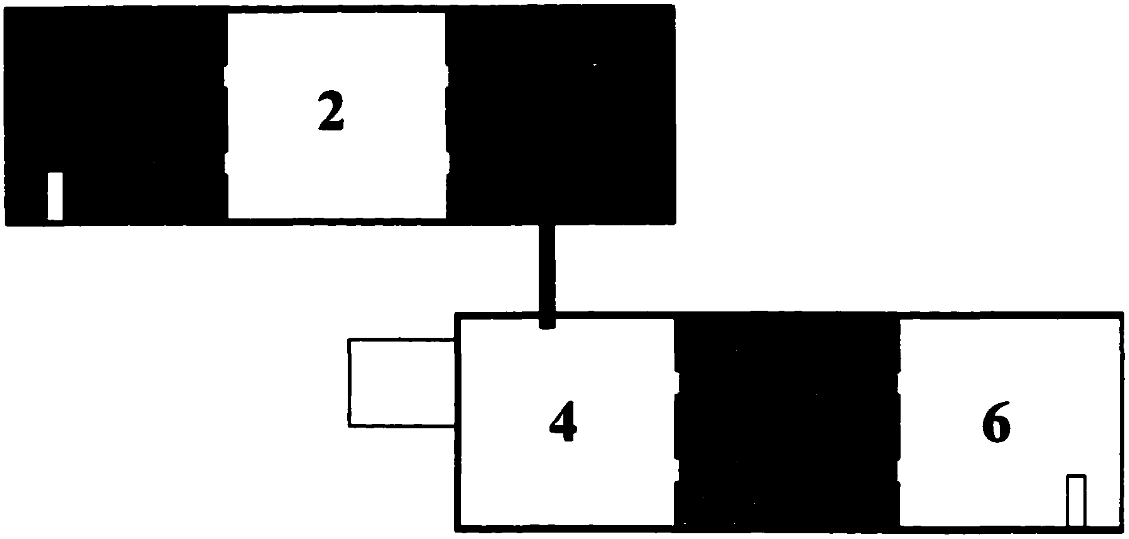


Figure 2

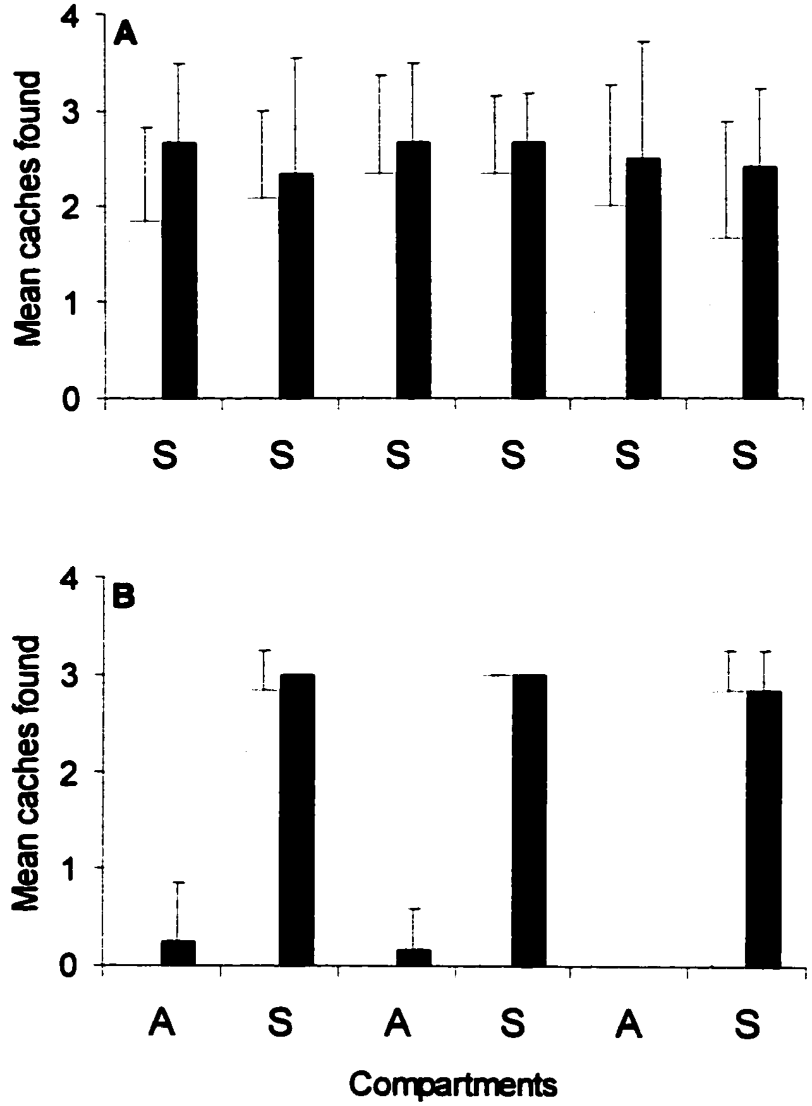


Figure 3

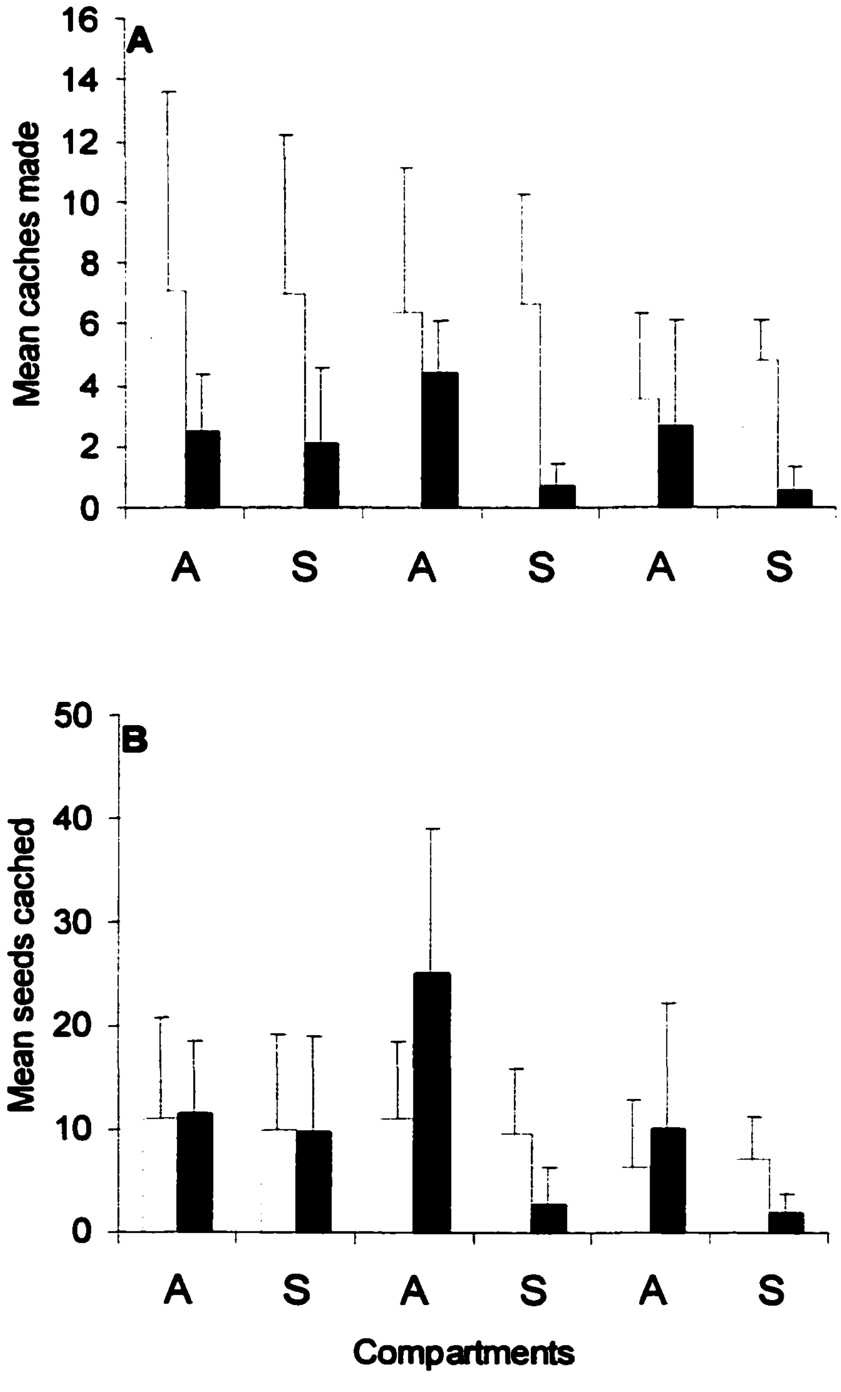

A
Mean caches made
0
2
4
6
8
10
12
14
16
A
S
A
S
A
S
B
Mean seeds cached
0
10
20
30
40
50
A
S
A
S
A
S
Compartments

Figure 4

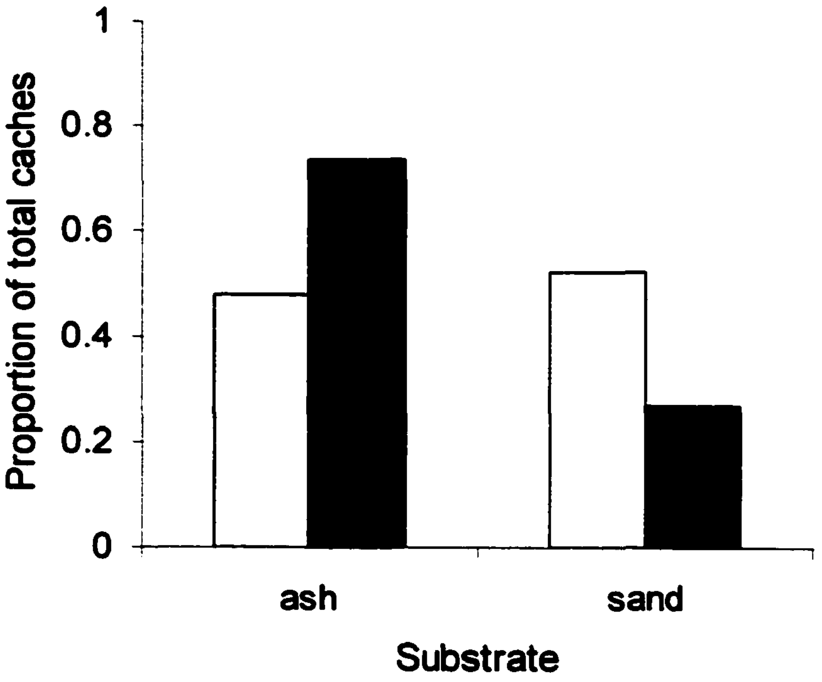
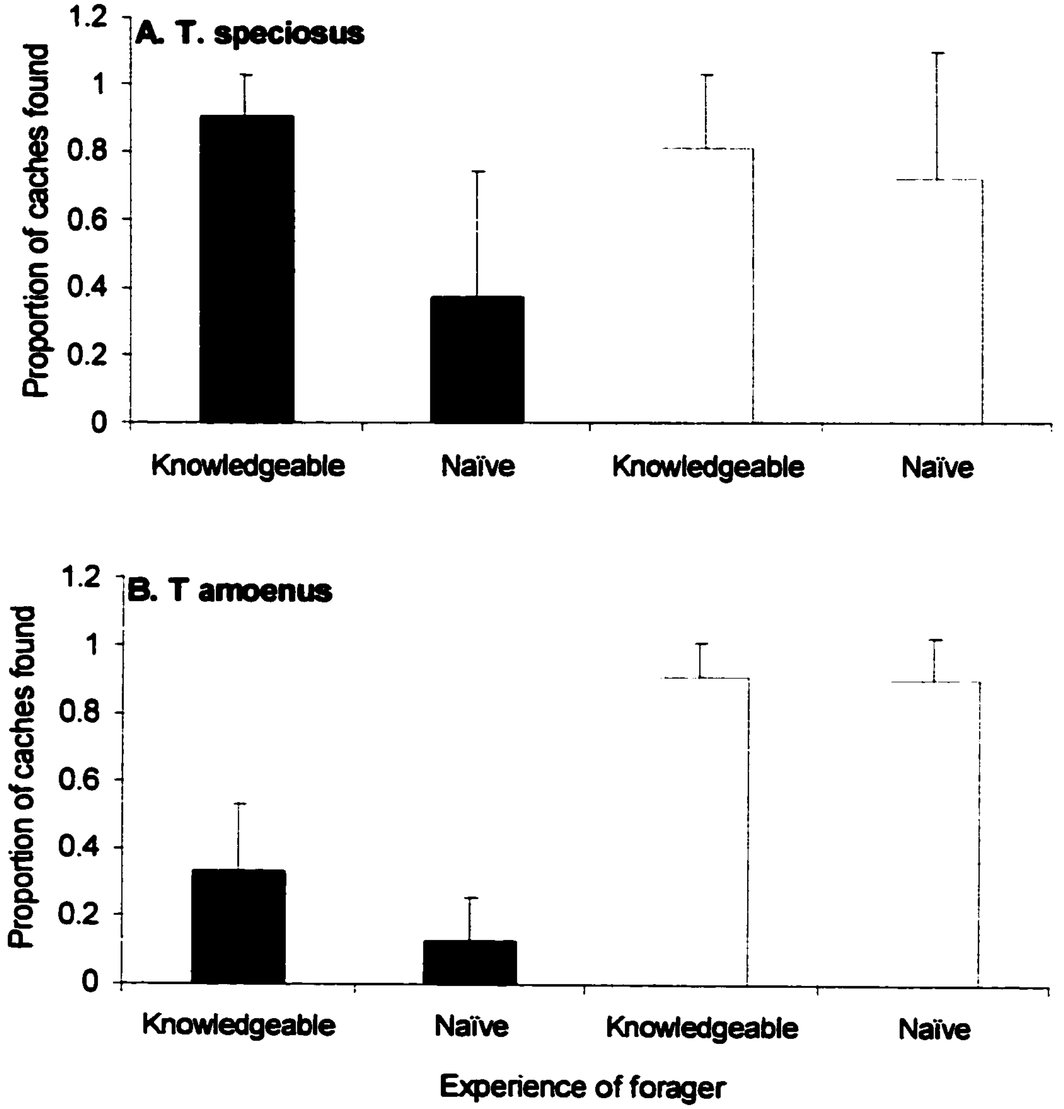


Figure 5


A. T. speciosus
B. T amoenus
Proportion of caches found
1.2
1
0.8
0.6
0.4
0.2
0
Knowledgeable
Naïve
Knowledgeable
Naïve
Experience of forager

Chapter 3: Effects of prescribed and wild fire on the dispersal of Jeffrey pine seeds by forest rodents

ABSTRACT

Animal-mediated dispersal of seeds to sites that enhance the probability of seedling establishment and survival may be especially critical after disturbances. This study examined the interactions between rodents and Jeffrey pine seeds after prescribed and wild fires. The abundances of rodents declined only in the first season after prescribed fires, and for 2-3 years at the site of a small wildfire. At the wildfire site, deer mice dominated center and edge areas until 3.5 yr post fire. No species differences were apparent at the prescribed burn site. The rates at which animals foraged for seeds on the forest floor declined significantly for only a few months after the burn. During the 3 yr study, frequency of establishment of natural caches and seedlings was very low, partly due to extremely low precipitation and low cone crops in one or more years. Survivorship of new seedlings was at most 12 months. Thus, it was difficult to conclude whether animal presence and activity would contribute to higher levels of predation or seed dispersal (caching) after the burn. However, the fates of artificial caches made before burns, in sites typical of animal versus wind-dispersal, showed significant advantages of animal-mediated dispersal after fires. Emergence of seeds placed on the forest floor before burns was extremely low in all types of microsite. Seeds placed in litter failed to emerge after the burns except from the deepest depth (25 mm). Seedlings emerged in similar proportions on burned plots and unburned plots, suggesting that seed germination and emergence was not significantly inhibited by heat during or after fires. Seedling survival was higher on the burned plots than on the control, especially in certain

microsites (mineral soil under shrubs) and at burial depths of 5 mm or 25 mm. Seeds planted in ashy substrates after fires emerged from caches in significantly higher numbers than seeds planted on control plots. At an older (20 yr) wildfire site, higher densities of seedlings and caches were found on the edges of the burn, and significantly higher growth rates were recorded for saplings in burned areas. Taken together, these results suggest that 1) burial of seeds in mineral soil and under shrubs enhances both emergence and survival after fire; 2) seed-caching rodents recolonize both low- and higher-density burned areas relatively soon after fires, and continue to forage for surface seeds; 3) some seed caching occurs on freshly burned plots but survival of seedlings is limited by low precipitation; 4) the edges and center of burned areas represent favorable environments for seedling establishment in terms of both quality (e.g. more mineral soil exposed on the forest floor; higher levels of light, potential future shading from shrubs) and quantity (fire increases the availability of these favorable microsites). Thus, seed caching animals may play a key role in facilitating pine regeneration on burned sites if abiotic conditions are favorable, and an important role even if they are not. Understanding the relative importance of biotic and abiotic seed dispersal processes after fire can inform forest management practices as well as allowing insight into possible coevolutionary relationships between plants, their animal dispersers, and the typical disturbance regime in an area.

INTRODUCTION

The activities of animals often influence and sometimes facilitate the succession of plant communities (MacMahon 1980, Wunderle 1997). These effects may arise from seed dispersal (Jensen and Nielsen 1986), herbivory (Weltzin et al 1997) or physical alterations of the habitat (e.g. burrowing, Andersen and MacMahon 1985), among other behaviors. Following a major natural or human-caused disturbance, the nature and outcomes of such plant-animal interactions may change significantly. However, large-scale ecosystem processes and disturbances are difficult to examine experimentally with replicates and controls, even though there is a critical need for such studies to improve the ecological basis for the management and conservation of biodiversity in forests (Simberloff 1999). Two recent studies of seed dispersal by birds following fire, for instance, were necessarily post-hoc (e.g. Johnson et al's investigation of nut caching by jays on a burned prairie plot, 1997) and observational in nature (Tomback's study of whitebark pine seedlings presumed to have been cached by Clark's nutcrackers at a wildfire site in Yosemite National Park, 1996).

Large-scale wildfires are becoming increasingly frequent after decades of fire suppression in western forests (Kilgore 1973, Parsons and Debendetti 1979). As dispersal of pine seeds by granivorous rodents and birds often makes a significant contribution to regeneration in unburned forests (Saigo 1969, Hutchins and Lanner 1982, Vander Wall 1994, Chapter 1), it is important to investigate the ways in which fire may influence this process. In general, "secondary" dispersal by animals of seeds that fall from a parent tree (Vander Wall 1992) may benefit the seed in several ways (Howe and Smallwood 1982). Transport away from the parent plant may reduce competition for light and resources (the escape hypothesis; Howe and Smallwood 1982), or allow access to new or distant habitat (the colonization hypothesis). Animals, especially rodents, often cache seeds in microsites that specifically enhance seedling survival (directed dispersal hypothesis; Howe and Smallwood 1982; Schupp 1993). Finally, burial greatly improves a seed's chances of germination and establishment, and reduces its vulnerability to predation or desiccation on the soil surface (Vander Wall 1992, 1993).

In the semi-arid yellow pine forests of many western states, rodents such chipmunks (*Tamias* spp.) and deer mice (*Peromyscus maniculatus*) scatter-hoard such large numbers of seeds, many of which germinate before they are recovered and consumed (Vander Wall 1992a, 1992b), that some researchers have speculated that their activities may actually accelerate forest succession (Saigo 1969, Sherman and Chilcote 1972, Vander Wall 1993). However, as these rodents are important predators as well as dispersers of pine seeds, and as seed crops vary annually, long-term reproductive benefits and costs to the plant are determined by the relationship of rodent population density to seed crop density each year.

Fire may significantly alter the relationship between pines and granivorous rodents in many ways: 1) by causing direct mortality (if very intense) of both plants (future seed sources) and animals (future seed dispersers); 2) by either enhancing or destroying favorable habitat for the animals; 3) by altering the availability and nature of sites for caching of seeds by animals as well as destinations for wind dispersed seeds; 4) by altering the abiotic conditions that affect seed germination, seedling emergence and survival (e.g. substrates, nutrients and light; and 5) by influencing the biotic conditions that affect emergence, survival and growth (e.g. competition with other plants, changes in foraging and caching behavior of animals). The relative magnitudes of these direct and indirect effects depend on the spatial and temporal scale of the fires.

In addition to elucidating the ecological effects of a major disturbance on a key ecosystem process, an improved understanding of biotic and abiotic dispersal after fire could inform management decisions about the use and timing of prescribed fire to improve ecosystem health. Additionally, there is potential for animal-mediated seed dispersal to be used in restoration after wildfires, as has been suggested or attempted after other types of disturbance (Chambers and MacMahon 1994,Wunderle 1997, Duncan and Chapman 2002). In this study, I used before- and after experiments and observations on replicated treatment and control plots at the site of a prescribed burn program, as well as at 2 wildfire sites. I examined the effects of fire on the interaction between granivorous rodents and Jeffrey pine by addressing the following questions:

a) How are animal communities in pine forests affected by fire?

b) How does fire affect biotic interactions between animals and seeds, such as the rate of foraging on the forest floor, the frequency of caching, the placement of caches in different microsites, and the degree of predation on emerging seedlings?

c) How do the fates of pine seeds cached by animals vs. seeds dispersed by wind differ when they are dispersed before a fire vs. after a fire?

d) How do these processes vary at the sites of wild vs. prescribed fires?

e) Over time, how does animal-mediated dispersal contribute to forest structure after a wildfire?

METHODS

Research sites

To examine the short-term effects of prescribed fires on animal communities, pine seeds and seedlings, and plant-animal interactions, I performed three before- and after fire studies on replicate plots at the site of a prescribed burn program at Incline Village, NV. To compare the effects of prescribed fire with the effects produced by a wildfire, I performed the same studies (postfire only) at the site of a 200 ha wildfire at Floriston, CA. This area burned in July 1999; the prescribed burns began in October 1999. All of these sites were studied through November 2002. To examine the longer-term effects of a wildfire on forest structure and pine regeneration, I conducted a fourth study at the site of a wildfire which burned 10,000 ha in 1981 near Little Valley, NV.

Prescribed burns

At Incline Village, several sites were burned every fall between 1999 and 2002 by the North Lake Tahoe Fire Department, on lands owned and managed by the Incline Village General Improvement District (Walter 1999, 2001). Sites were 7-38 ha in area and located in mixed-conifer forest, dominated by Jeffrey pine, within the Wood Creek and Second Creek canyons (39°16'N, 119° 58'W). Most were located between residential neighborhoods and adjoining undeveloped Forest Service land. Table 1 summarizes the names (arbitrarily assigned) and sizes of the burned sites, the dates of the burns and characteristics of the sites. The prescription for these prescribed burns (Walter 1999, 2001) required retention of at least 30 % of shrub understory on a site, plus 40% of total fuels.

I established experimental plots as close to the center of each burned site as possible, while maximizing distance from the nearest road, residence or trail in an attempt to reduce possible disturbance by humans or domestic pets. I established control plots in the nearest unburned, undisturbed forest to the burned site. I conducted pre-fire experiments in the period (generally late August-mid October) after pinecones opened but before plots were burned, as described below. Post-fire studies were initiated soon after the burns each fall or the following spring, 2-4 weeks after snowmelt. Studies began in August 1999 and continued until November 2002.

Wildfires

I began studies at the Floriston wildfire site (39°23'27" N, 120°10'46" W) in November 1999, 5 months after the wildfire occurred on July 9, 1999. I established 3 study plots at this site: a center plot, equidistant from both fire lines; an edge plot, 200 m from the center plot and 20 m from the nearest fireline; and an unburned plot, 50 m from the fireline and 70 m from the edge plot. The sites for the edge and center plots were selected to match characteristics of the adjacent unburned vegetation as closely as possible; although much of the understory had been completely burned, and to represent relatively level ground and friable soils. Much of the burned area and surrounding forest was steep and rocky, but all study plots were located on level plateaus. Studies continued at this site until Fall 2002. In the descriptions below of Studies 1-3, the methods apply to all experiments conducted at Floriston as well as Incline, with the obvious caveat that only post fire studies were performed at Floriston. The timing of certain studies, and the years in which they were performed, varied as shown in Table 1.

I studied some longer-term effects of fire at the Little Valley wildfire site in the Carson Range (39°15'11" N, 119°50'36" W). A severe wildfire burned approximately 10,000 ha east of the valley in August 1981 over an elevation range of 1575 m to 2050 m and burned mostly Jeffrey pine- dominated forest on steep east-facing slopes. My study took place in 2001 and 2002 on a series of transects located on the edges of the burned area, through the center of the burn and in adjacent unburned forest, within a range of elevations (1700 m to 1950 m) as described below.

Study 1. Rodent communities

At prescribed burn sites, on each treatment and each control plot, I established a 5 x 5 trapping grid with 25 Sherman live traps spaced 12 m apart. The grid was approximately 50 m square. I conducted trapping sessions on all plots a few weeks prior to the burns (in September), in the late spring the year after a burn (June) and every September thereafter until 2002. During each trapping session, I baited traps with sunflower seeds and checked them twice a day for 3 consecutive days. Individuals were ear-tagged and their physical condition, sex and weight were recorded.

At the Floriston wildfire site, three similar 5 x 5 trapping grids were established, on the center, edge and unburned plots. Trapping sessions were conducted as described above, beginning in May 2000 (10 months after the fire) and continuing every fall and spring until October 2002.

Study 2. Seed removal from forest floor

In mid-September to mid-October, after cones opened on the pine trees, I established seed removal transects on all plots. Transects were located across the side of the plot furthest from the nearest road or trail, and in most cases overlapped the trapping grid at some points. Each transect consisted of 25 filled Jeffrey pine seeds placed on the forest floor at known 'stations' 5-7 m apart (following methods in Vander Wall 1994). This distance appears sufficient to ensure that the fates of each seed are independent (Vander Wall, 1994, pers. obs). Stations were inconspicuously marked with unique symbols such as rocks and sticks, and seeds were 'tethered' to small twigs at each location by brown threads glued to the seed wings. I checked each transect daily for approximately 1 wk after setting out the seeds, and at irregular intervals thereafter. I recorded the first date at which each seed was missing (i.e. last date present, first date observed to be missing). As seeds could not blow away, their absence indicated removal by a foraging animal. I recorded that the seed had been eaten if shell fragments remained at the site. After burns, I established new seed removal transects on the burned areas as soon as possible (generally within 9-21 days after the fire). If winter snows came early, I waited until the following fall to conduct post-burn transects. I made post-burn transects in approximately the same places every year.

Analyses

I used survival analyses (Proc Lifereg with a Weibull distribution in SAS, 2000) to assess the effects of treatment (burn versus control) and time since burn on the length of time seeds remained on the forest floor. The response variables were the lower and upper bounds of time until removal Time since burn (pre-burn, post 1 mo, 1 yr, 2 yr, and 3 yr) varied between plots, depending on the timing of the burns and our subsequent access to the plots; I lumped plots together in the analyses if I had sampled them at the same intervals (Table 1) but I used plot as an additional predictor variable in the model.

For transects at the Floriston site, there were three levels of treatment (center, edge, and unburned plots) and two times since burn: 5 mo and 3 yrs).

I followed the procedure recommended by Burnham and Anderson (2002) for model selection: several reduced models were compared to a 'global' model that contained all parameters and interaction terms. Parameters were dropped if they did not have a significant main effect or were not part of a significant interaction, if they had little biological relevance (e.g. four-way interactions), or if their inclusion or exclusion did not significantly reduce the Akaike Information Criterion (AIC) value of a model (a reduction of more than 2 points was considered to be a significant improvement in the fit of the model; Allison 1995, Burnham and Anderson 2002). For each study, after comparing different possible models, I selected one final model to use in estimation of parameters and post-hoc contrasts. Final models had the lowest AIC value while containing the highest number of biologically meaningful parameters, i.e. they represented the best fit to the data.

To compare the survival of seeds statistically in different categories, (e.g. on control plots before the burn versus 1 mo after the burn, or on treatment plots at 1 mo after the burn versus 3 yr after the burn, I calculated the difference between the parameter estimates for each category. The exponential of this difference represents the relative difference in "lifespan" (time until removal) of seeds in the two categories (Allison 1995).

Study 3. Effects of microsite and burial depth on pine establishment after fire

3a) Frequency of natural seedling emergence

Before the fires, on each treatment and nearby control plot, I established a permanent 40 x 40m vegetation sampling plot. It was placed roughly in the center of the treatment plot, in a stand of mature pines with an understory characteristic of the plot as a whole. Control plots were situated in the nearest unburned forest in vegetation similar to that of the treatment sampling plots. I established a 5 x 5m subplot in each corner of the 40 x 40m plots, and a fifth 5 x 5m subplot in the center. In each of these subplots, I searched for pine seedlings or saplings less than 1 m tall, growing singly or in clumps.

Clumps of seedlings were defined as caches if they were growing within 1 cm. I recorded the following characteristics of all seedlings and caches: height in cm; approximate age (a minimum and maximum age was estimated for each seedling by counting the number of annual growth scars); substrate (mineral soil, light litter less than 1 cm deep, or heavy litter, e.g. pine needles over 1 cm deep); understory species (if present directly above the seedling); and overstory species (if present directly above the seedling. I monitored these seedlings for several years in spring/fall surveys, noting whether they survived the burns, and the cause of death if and when they died. In June of each year, I searched the entire 40 x 40m sampling plots on the burns, and the 5 subplots on the controls, for new emerging seedlings. I recorded their characteristics as above. I repeated the surveys every spring and fall, on both treatment and control plots, but on control plots I just surveyed the sub-plots. Thus a total area of 125 m^2 was searched on each control plot before and after the burns occurred on the treatment plots; 125 m^2 was searched on each treatment plot before the burn, and 1600 m^2 was searched on each treatment plot after it was burned. At the end of the final season (2002) I recorded the final height and calculated the growth rate of all living seedlings. These data were not analyzed statistically, because sample sizes and survival were too low (Table 2).

3b) Artificial caches made before burns

On each of three plots scheduled to be burned (B1 in fall 2000, B2 and SB in fall 2001), I established a series of artificial caches in different types of microsites before the burns and on nearby plots not scheduled to be burned. To investigate the possible effects of burning, cover, substrate and depth of burial on the survival of seeds and emergence of seedlings, I used a split, split plot design with two additional factors (Figure 1). The main split was treatment versus control. Within each treatment and control plot, there was a second split between two substrate types (mineral soil and litter), and within each of these categories there was a cover factor with 2 levels (under shrub and open, i.e. shrub interspace) and a depth factor with 3 levels (seeds were placed on the soil surface, i.e. 0mm, or buried at 5 mm and 25 mm). All levels were completely crossed, although the sample sizes within the cover factor were unbalanced as the two dominant shrubs at the study site were used as cover in equal proportions. The number of subsamples under each of the two shrub types was the same as that in the open category. On each treatment and control plot, I established either seven (in 2000) or five (in 2001) replicates of all the substrate/cover treatment combinations. Within each of these replicates, I established 3 subsamples of each of the three depth treatments. These subsamples were arrays of caches, placed inside protective wire mesh cages in a randomized order (Fig 1).

Each array of 9 caches was made inside a 30-cm square cage of 5-mm wire mesh. with walls buried at least 10 cm below ground. The walls above ground were approximately 10 cm high, and the roof of the cage was securely fastened to prevent access by animals. The 9 caches in each array represented three replicates of three depth treatments, arranged in a randomized order within the cage. The "surface" treatment consisted of single seeds placed on the soil surface, to mimic abiotic dispersal. Three other caches each contained three seeds buried 5 millimeters below the soil surface: this represented shallow caches made by animals, but could possibly occur via abiotic burial if wind-dispersal seeds became entrapped in plant material (Vander Wall and Joyner 1998b). The final series of 3-seed caches in the set was buried 25 mm below the soil surface, to mimic the deeper caches made by larger animals and to represent a depth closer to the "optimal" range for emergence for Jeffrey pine (Vander Wall 2002a).

When preparing caches at the 5 mm depth, we placed the seeds in a shallow depression on the substrate surface and scattered 5 mm of either soil or litter over them. When burying caches at 25 mm in litter, we first removed all existing litter from the area within the cage, buried the seeds 5 mm deep in the exposed soil, then replaced the original litter (shrub or pine matter depending on location of the cage) to a standard depth of 20 mm. Equal proportions of huckleberry oak and tobacco brush were used for under-shrub treatment, because these shrubs respond very differently to burning based on the flammability of their leaves. Huckleberry oak is extremely flammable (Walter 2001; pers. obs.) whereas tobacco brush is more fire resistant and requires intense heat and higher flame lengths to ignite and burn (Geissinger pers. comm.; pers. obs.) The sample sizes on plot B1 and its control plot (2000) at each of the three depths were 21 caches in the soil/open microsite, 21 in litter/open sites, 21 caches in soil/under flammable shrubs and 21 in litter/under nonflammable shrubs. The sample sizes on plots B2, SB and their controls (2001) were 15 caches in each of the categories described above. On all sites, each replicate was located in an area where the 6 combinations of substrate and cover described above occurred in close proximity to each other. I attempted to place all cages in level areas (to minimize effects of erosion over winter) and to place the under-shrub cages at a consistent distance under shrub canopies, with the outside edge of the cage just below the edge of the shrub canopy.

I planted seeds in late September in both years (2000 and 2001). Burns occurred between 5 Oct and 5 Nov in both years. A few weeks after snowmelt the following spring (25 May 2001 and 2002), I checked all cages for emergence of seedlings. I recorded emergence if we could see a shoot from a buried seed protruding above the soil/litter surface, or emerging from a seed lying on the surface. I checked the seedlings' status and noted cause of death, if applicable, at approximately monthly intervals until the end of the growing season (November) or the death of the seedlings, whichever occurred first.

3c) Artificial caches made after burns

After burns were completed and surfaces cooled in 2001, I made a second series of artificial caches on 3 burned plots to assess the effects of the ash substrate and the altered understory on seedling establishment. I established twelve cache arrays (mesh cages containing 9 caches each) per plot in the same manner as in the study described above, but these cages were set up every 2 m along a 25-m transect across a severely burned portion of the plot. I placed half of all cache arrays under severely burned shrubs and half in open areas; however, it was difficult to tell what the previous understory conditions had been. Sample sizes were lower than in the pre-burn study because of difficulties accessing the burned sites in the short time after the surface had cooled but before winter storms began. A set of caches was also established in similar conditions on the adjacent control plots.

Analyses. I performed logistic regressions on seedling emergence in the pre- and post-fire artificial cache studies (3b and 3c). In the pre-fire study, the response variable in the model was probability of emergence. The initial predictor variables were treatment (versus control); burned microsite (versus unburned microsite, within the treatment only); depth; substrate; cover (open, flammable shrub, nonflammable shrub); and site (blocking factor). I included the burned/unburned microsite factor because fire behavior varied within all treatment plots during burns, and some replicates escaped being directly burned). In the post fire study, fewer factors were included in the model, as all cache sites were burned and it was impossible to distinguish between different substrate types and shrub species. The remaining factors were treatment, depth and cover.

I used logistic regression (Proc Logistic in SAS, 2000) to evaluate the effects of cover (open versus under shrub), substrate (mineral soil versus litter) and depth (surface, 5 mm and 25 mm) on emergence of seedlings. As all buried seeds were members of 3-seed caches, I did not code by cache within replicates, to limit inflation of the number of parameters in the model. Dummy variables representing the different sites were included in the original model.

Study 4. Sapling densities and growth rates at the site of a 1981 wildfire

On the site of the wildfire, I established five 300-m vegetation sampling transects through each of three types of habitat-- burned, edge of burn and unburned forest. These habitats, hereafter referred to as "zones", were defined according to the following criteria.

'Burned' transects were located in areas containing no living overstory trees within 50 m of the transect line. 'Edge' transects were placed within 30- 60m of a burned area, and contained living overstory trees that showed signs of significant scorching on the trunks. In these areas the fire had burned the understory but had not killed the overstory. 'Unburned' transects were established in closed-canopy forest at least 100 m from the edge of a burn (and usually much further away), in areas where trees showed no signs of having been scorched or otherwise affected by the 1981 fire. The locations of all transects were determined in relation to the edge transects, which were placed around the borders of an arbitrarily defined portion of the wildfire site. Burned and unburned transects were then established in the closest appropriate areas near each edge transect. Thus, 5 groups (blocks) of transects, were created near the edges of the fire.

Along each transect, I used the Point-Centered Quadrat method (Cottam and Curtis 1956) to record multiple variables around each of 10 points spaced 30 m apart (Briggs et al. in prep.). Here I present the results for a subset of these variables: density of overstory trees (>40 cm dbh) and understory trees (< 40 cm cbh); density of shrubs (radius in cm); and density and growth rates of seedlings and saplings growing in clumps and singly.

Density of seedlings, trees and shrubs was calculated by measuring the distance to the closest individual to the central point, in each of 4 quadrats established in the 4 cardinal directions from the transect line (Cottam and Curtis 1956). For trees and shrubs, distances were measured to the center of the trunk or shrub. No individual was counted in more than one quadrat. The following formula was used to calculate density of features on a transect using the distance measurements: Density (individuals/m^2) = 1/ (mean distance)^2 x (correction factor) (Warde and Petranka 1981). Mean distance represented the sum of all the distances to the closest trees within each of the 40 quadrats in the 10-point transect, divided by the number of quadrats that actually contained trees within 30m of the central point. The correction factor was used to account for any quadrats with missing data, i.e. those in which no tree was found within the 30 m boundary (Warde and Petranka 1981). This method assumes random spatial distribution of individuals but is fairly robust to departures from that assumption (Warde and Petranka 1981).

Density of single Jeffrey pine seedlings or saplings (less than 1.5 m tall) and clumps of seedlings or saplings were measured in the same way but within a radius of 10m from the central point. In addition, all single seedlings and clumps of seedlings in 2 x 2 m 'mini-plots' around the central point were counted, and their heights were measured. Maximum and minimum ages were estimated for each seedling by counting the number of branching rings and bud scars on the stem. Clumps were defined as described above (Study 3a). Mean annual growth rates were estimated by dividing a sapling's height (in cm) by the maximum and minimum age estimates.

Analyses. I compared the density of single and clumped seedlings in the three different zones of the fire using MANCOVA with zone (burned, unburned and edge) as the factor and mean overstory tree density, mean understory tree density, shrub density and mean size as covariates. The unit of replication was the transect. I performed a second MANCOVA, with the same covariates, with seedling and cache growth rates as the response variables. For this analysis, I included all seedlings and caches measured in the miniplots, as well as those counted in the density analyses.

RESULTS

Rodent communities

At the prescribed burn sites burned in 1999 at Incline Village, rodent communities changed significantly over time (F (8,32) = 8.64, $p < 0.0001$). However, the repeated-measures analysis showed that the effect of treatment (fire) was not significant (F (1,8) = 0.16, p = 0. 70) and there was no significant interaction between time and treatment (F (4,32) = 1.28, p = 0.30). Despite this lack of significance, the data reflect a trend of declines in captures 8 mo and 1 yr after burns on treatment plots only (Fig. 1 c). Before the prescribed burns, similar numbers of individuals were captured on pairs of treatment and control plots (9.80 ± 3.03 and 8.4 ± 3.05, respectively; Fig 2). Mean numbers of captures were similar on control plots in the trapping sessions conducted 8 mo, 1 yr and 2 yr after the burns. Three years after the fire, mean numbers of captures on both treatment and control plots combined (20.1± 4.75) were higher than at any other time ($p < 0.02$ for all post-hoc comparisons between time periods).

The species composition of the rodent communities did not change substantially on control plots over time until 3 yr post fire (Fig 2a and b). Chipmunks (*T. specious* and *T. amoenus*) accounted for most of all captures on control plots until three years after the fire, when the mean abundance of deer mice increased to 31 % of captures (Fig 2 b). Larger sciurids such as Douglas' squirrels, flying squirrels, California ground squirrels, and golden-mantled ground squirrels were captured at low frequencies (5- 20%) on most plots except for treatment plots L and S, which had 30- 40% golden-mantled ground squirrels at every session after the fire. On treatment plots, chipmunks represented the majority of captures (90 %) at all time periods. Chipmunk numbers also declined 8 mo after the fire, whereas deer mice numbers rose slightly (Fig 2 b).

The rodent communities on the 2 plots burned in 2000, and their controls, showed a different pattern of changes in abundance over time. Thus, these plots were not combined with the 1999 series for analysis. The data were not analyzed statistically as the sample size (2 plots) was so low. Mean numbers of captures were higher on control than on treatment plots at the preburn trapping sessions as well as the 8 mo and 1 yr post burn trapping session (Fig. 2). At 2 yr post fire, numbers on the burned plots increased and were comparable to numbers on the control plots. This season, fall 2002, was the same time period at which high numbers of animals were trapped on 1999 treatment and control plots: a general increase in rodent populations was apparent at this and other long-term research sites in the area (Vander Wall, pers. comm., Klieforth, pers. comm.) For example, on one treatment plot (SU), which had previously contained only one animal when I trapped both before and after the burn in Fall 2001, I caught 16 individuals in Fall 2002.

At the Floriston wildfire site, I captured few animals (2-5) on the unburned trapping grid in the first three trapping sessions after the fire occurred , and even fewer (0-2) on the edge and burned areas (Fig. 3c). At 25 mo post fire, I captured 10 animals on the unburned grid, and captures there remained higher for the rest of the study. In general, higher proportions of chipmunks relative to deer mice were captured on this grid (Figs 3a versus 3b). Both lodgepole and yellow-pine chipmunks were present, in roughly equal proportions. On the edge plot, numbers of chipmunks tracked the numbers caught on the unburned plot fairly closely over time, but higher numbers of deer mice were trapped on the edge. The burn plot had the fewest captures in the first two sessions after the burn, but beginning at 25 months post fire, I trapped the highest numbers of animals (20) there; these were almost all deer mice until 40 mo after the fire. At 40 mo, approximately half of the captures in the center of the burn were chipmunks and half were deer mice (10 versus 11).

Seed removal transects

At Floriston 5 mo after the fire, seeds in burned and edge transects had a half-life of 51 days (Fig. 3d). (Half-lives were calculated using the exponential decay equation, and represent the time taken for half the seeds to be removed from a transect). On the unburned plot, seeds had a half-life of 4.9 days, which represented a removal rate 20.6 times faster than on the burn and the edge ($p < 0.0001$; d.f. = 1). However, 3 yr later (40 mo after the fire), seeds on the burn were removed 2.4 times faster than seeds in the unburned area ($p < 0.001$) and 2.9 times faster than seeds on the edge of the burn ($p < 0.001$). All seeds on all transects were removed significantly faster 40 mo after the fire compared to 5 mo after fire (Fig 2d); the greatest difference was 225.1 times faster removal of seeds on the burned transect at 40 mo versus 5 mo ($p < 0.0001$).

Similar patterns were apparent at the prescribed burn sites at Incline Village, where seed removal rates were examined before as well as after the burns. In spite of considerable variation among replicate plots, the survival analysis did detect some significant patterns, not always reflected in the means shown in Fig. 3, when the times till removal of each individual seed were compared between treatment and control plots, and among time periods, in post-hoc contrasts. For seeds on both the series of plots burned in

1999 and the series burned in 2000, times until removal were similar on treatment and control plots before the burns (1.25 times greater on treatment plots versus controls in 1999, $p = 0.41$; 1.07 times greater in 2000, $p = 0.94$). After the 1999 burns, seeds on the treatment plots had longer half-lives than those on control plots at both 1 mo (13.0 times slower rate of removal on treatment plots, $p < 0.0001$) and 2 yr post fire, although this latter comparison was not statistically significant (1.67 times slower, $p > 0.3$).

Removal was 9.45 times slower on the 1999 treatment plots at 1 mo post fire than on the treatment plots before the burns ($p < 0.0001$). For the 2000 plots, seeds on both treatment and control plots were actually removed somewhat faster at 1 yr after the burn than before the burn (Fig 3b), but this trend was not statistically significant due to variation between sites. In Fall 2002, which was 3 yr after the 1999 burns and 2 yr after the 2000 burns, seeds on all treatment plots were removed significantly faster than before the burn (9.2 times faster for 1999 plots, $p < 0.0001$; 118.7 times faster for 2000 plots, $p < 0.0001$). However, relative to the control plots at this time, seeds on the 1999 treatment plots and the 2000 treatment plots were all still removed significantly more slowly (1.8 times slower for 1999 plots, $p = 0.007$; 2.22 times slower for 2000 treatment plots, $p = 0.0005$).

Natural seedling emergence and survival

Very few seedlings emerged on burned and unburned sampling plots during the three years of this study (Table 2). In annual surveys of 5-8 burned plots, each 1600 m^2 in area, and smaller subplots on control sites (125 m^2 per plot), I found only 13 single seedlings and 12 clumps of seedlings in 2000, 1 clump in 2001, and 23 single seedlings and 28 clumps of seedlings in 2002. For the 79 seedlings and caches that emerged in 2000- 2002, survival was low (Table 2). The low levels of annual and summer precipitation at the sites before and during this study are shown in Table 3. Twenty two percent of all single seedlings and clumps survived until the end of their first growing season (i.e. October- November), but all of them were dead at the time of the first check the following June. Fifty percent emerged in mineral soil and 50% in plant litter (Table 2). Thirteen percent were underneath shrubs and 87 % in shrub interspaces. Sample sizes were too low in all categories to permit valid statistical comparisons of seedling density, survival or microsite characteristics, either among burned plots or between burned and control plots. Only 2 newly emerging single seedlings and 2 clumps were found on unburned plots, which were 87 % smaller in size than burned sampling plots. However, on the same sized subplots within the burned plots, a total of 4 single seedlings and 4 clumps were found over the course of 3 yr.

Fates of artificial caches made before burns

Of the 4410 seeds planted in different microsites, a total of 638 (15%) emerged after the fires. Emergence was similar on treatment and control plots (45 % versus 55 %, odds ratio = 0.89, $p > 0.05$). Table 4 shows the emergence of seedlings (as a percentage of the seeds planted in each category) among all different combinations of treatment, cover, substrate and depth. Within treatment plots, similar proportions of seedlings emerged in both burned and unburned patches (treatment x burn, odds ratio 1.03, $p = 0.86$). Seedlings under the two different types of shrub did not show significant differences in emergence when all depths were summed (odds ratio 0.84, $p > 0.12$), but a lower percentage of seedlings emerged under the flammable shrub at the medium depth. The reverse was true for the 25 mm depth (Table 4). Emergence was 3.5 times higher in soil than in litter ($p < 0.001$). The emergence of seeds planted at 5 mm and 25 mm was 5.5 and 8.5 times greater, respectively, than that of seeds placed on the surface ($p < 0.0001$ for both odds ratios).

The microsite in which the highest proportion of seedlings emerged - in mineral soil in the open on control plots at a depth of 5 mm (Table 4) - was more favorable than the next category by a factor of 1.45, but this difference was not quite statistically significant ($p > 0.05$). The second most favorable condition for emergence was mineral soil under non-flammable shrubs on treatment plots at a depth of 5 mm. Sites in the open, in litter at depths of 0 or 5 mm had much lower emergence on the treatment plots than on the controls (Table 4).

Although sites in the open, in litter, or both often had relatively high levels of emergence, very few seedlings (only 3) survived until the end of their first growing season in those sites (Tables 4 and 5). 57 other seedlings in this study survived one or more growing seasons, and all were in mineral soil. Approximately half were in the treatment plots, and all of these were in burned patches (burn increased survival time by 87 %, $p < 0.05$). The survival analysis showed that survival in mineral soil was 2.75 times longer than in litter ($p < 0.05$).

Fates of artificial caches made after the burns

Of the 1272 seeds placed in caches <1 mo after prescribed fires at Incline Village, 187 (14.75%) produced seedlings the following spring. Most (82 %) of these seedlings were on the treatment plots in burned substrate rather than on the unburned control plots, a highly significant difference (odds ratio 14.82; $p = 0.002$). Emergence was thus higher on treatment plots than controls in all comparisons between categories of cover and depth; for example more seedlings emerged from the depth of 0 mm in the open on ash plots versus at 0 mm in soil in the open on control plots (odds ratio 1.84, $p < 0.02$). The most favorable microsite for emergence in ash was under shrubs at the 5 mm depth; this was 6.15 times more favorable than the same depth (5 mm) in mineral soil on control plots ($p < 0.02$) and 1.33 times more favorable than the most successful site on control plots: 25 mm deep in mineral soil under shrubs ($0.02 < p > 0.29$). (The significance of this comparison could not be estimated directly from that of other parameter estimates).

The survival analysis on the seedling fates showed that, over the longer term, survival of seedlings in ash substrates remained higher under shrubs at 25 mm than in any other category (Wald Chi-square for 3-way interaction = 4.701, df = 1, $p < 0.03$). However, survival in this category was similar to survival on control plots in mineral soil under shrubs at 25 mm (odds ratio = 1.01, $p > 0.25$).

Sapling densities and growth rates at the 1981 wildfire site

The mean densities of both single and clumped seedlings were highest on edge transects at the Little Valley wildfire site (Table 6), although not significantly so ($F = 1.66$, df = 2,12; $p = 0.23$ for single seedlings; $F = 2.03$, df = 2,12, $p = 0.17$ for clumps). There was considerable variation among transects within each zone. Overall, I encountered similar total numbers of saplings in edge transects and burn transects (115 and 117, respectively) when measuring density, but fewer saplings (79) were present on unburned transects. A different pattern was apparent for clumps of seedlings: almost twice as many clumps (72) were recorded on edge transects compared to burned and unburned transects (42 and 37, respectively).

The first MANCOVA did not identify any significant differences in the densities of single (F (2,9) = 1.88, p = 0.21) and clumped seedlings among zones (F (2,9) = 0.11, p = 0.74), or any significant relationships between these densities and the covariates (shrub, understory and overstory tree density). The second MANCOVA, on seedling and clump growth rates, was also not significant. However, a one-way analysis of variance on growth rates of saplings (< 1.5 m tall) among zones showed that in burned zones, growth rates of saplings (4.06 ± 0.96 cm/yr) were significantly higher than those of saplings on either the edge or the unburned transects (Table 6). Saplings in the edge and unburned transects did not have significantly different growth rates (Tukey's comparisons, p > 0.02). I ran another analysis that included the 56 taller saplings that had established since the burn in this comparison. These were so tall, e.g. 2-3 m, that they were recorded as understory trees in the density measurements, but they were all less than 22 yr old, i.e. had established since the burn. This combined set of saplings on the burn showed even faster mean growth than the edge and unburned saplings in this comparison (7.85 ± 2.72 cm/yr; F = 20.55; df = 2,12; p = < 0.0001).

DISCUSSION

Prescribed burns had a short-lived effect (less than one year) on the abundances of small mammals and on several aspects of the interactions between animals and pine seeds. A decline in mean numbers of captures on the plots burned in 1999 was apparent, although not statistically significant, the spring and fall following the fires. Variation among pre-burn animal populations on the 5 plots in this study may have masked a significant response to the burn; or the burns may not have been severe enough on all plots to cause a significant change in animal distribution and abundance. Burns varied in intensity and patchiness with the weather, topography, fuels present at a site, etc. After the burns, numbers of captures on burned plots rose steadily and were not significantly different from the controls at any time. At 3 yr after the fire, numbers of animals on treatment plots were significantly higher than before the burn. This was also the case for control plots and plots burned in 2000, and reflects a local-scale increase in populations rather than an effect of the fires. Several other studies (Halvorson 1982, Sullivan and Boateng 1997, Bock and Bock 1983) also emphasize that certain species can respond very rapidly to burns (the deer mouse is the usual early colonist) but that population dynamics vary among sites and the effects of the fires interact with local availability of food sources (Halvorson 1982).

Rates of seed removal generally increased as the abundances of rodents increased. However, this was not the case on the 1999 plots at 3 yr post burn, compared to before the burns. After 3 yr, the rodent populations on the control plots were significantly greater (19.4 ± 6.0 versus 12.0 ± 1.7, $p < 0.02$), and seed removal rates were 2.3 times higher, than in 1999 ($p = 0.0003$). In contrast, rodent populations on the treatment plots were also significantly greater, but rates of seed removal were only 1.3 times faster than before the burn, a non-significant increase ($p < 0.24$). This suggests that animals were not foraging as actively on the forest floor on burned plots as they were on the unburned controls, even though they were present in higher numbers.

Some aspect of the burned environment may have limited animals' frequency or success rate of foraging there. In a previous study (Briggs and Vander Wall, submitted; Chapter 2) I found that chipmunks' ability to detect seeds buried in ashy substrate whose location in unknown to them is low, so they may focus their foraging efforts in (unburned) portions of the habitat where they are better able to detect buried seeds as well as those on the forest floor, or where they are able to cache seeds in sites that will be easier to relocate using olfaction. Alternatively, natural seed availability may have been lower on burned plots, deterring rodents from foraging there. Although I did not quantify and compare seed availability in burned and unburned areas, this explanation is less likely because most mature trees throughout the study area (including those on the burns) produced large cone crops in 2002, and masting appears to stimulate high levels of foraging by rodents (Vander Wall 2002). Seeds removed by animals may have been consumed, stored in below-ground larders, or cached (Vander Wall 1994).

The natural seedling establishment study produced inconclusive results due to the very low recruitment during the time of this 3 yr study (68 seedlings or clumps were found on burned plots, 4 on controls). In future studies, a larger-scale transect surveying method that covered a much wider area may be more effective to identify trends. It was difficult to tell from my results if animals just did not cache many seeds to start with, or if conditions were unfavorable for emergence and survival of both wind- and animal-dispersed seeds. At my sites, the cone crop was high in fall 1999, almost zero in fall 2000, and moderately high in fall 2001. As there was no seed crop in fall 2000, it is not surprising that 2001 was such a low year for seedling establishment. The low survival from seeds planted in my artificial cache studies reinforced the importance of constraints of abiotic conditions on the frequency and success of establishment during this time period.

Frequencies of emergence of single seedlings and clumps of seedlings in different microsites at the prescribed burn sites were dissimilar to those observed during animal caching trials I conducted in unburned forest in Little Valley (Chapter 1). There appeared to be more frequent establishment of both clumps and single seedlings in the open on burned plots at Incline, compared to animals' frequent use of under-shrub sites in Little Valley. Also, on burned plots I observed approximately equal emergence in litter and mineral soil instead of the higher proportion of emergence in mineral soil that would have reflected the cache site selections observed in Little Valley. Again, environmental conditions and small sampling areas may have affected my ability to detect patterns of animal caching on burns. In future studies, animals could be presented with labeled seeds on the edge of burned areas and their movements and caching activities tracked directly to identify whether and how seeds are dispersed into burned areas. The results of previous studies (Chapter 1 and 2) suggested that animals would make caches in burned areas in the field, and this prediction was supported by the 38 caches that I did locate during surveys. The range of clump sizes (2-22 seeds) observed on burns were consistent with the range of cache sizes I observed for deer mice (1-8 seeds) and both species of chipmunks (1-25 seeds). Throughout the study area, I observed clumping in trees of all age classes, including mature trees growing with trunks very close together. Although it becomes more difficult to infer that two or more trees emerged from a cache as they grow older and larger, many seedlings, saplings and trees that are growing singly originated from single seeds cached by animals (Vander Wall 1992). Thus, signs of clumping at some level indicate the contribution of seedhoarding animals.

Results of the artificial cache study confirmed that burial of seeds below the surface and in certain microsites, notably in mineral soil and/or under shrubs, does significantly enhance survival after burns. As I predicted, no seedlings emerged from sites typical of abiotic dispersal (surface or 5 mm depths in litter microsites in the open) in burned patches of the treatment plots, although 4 seedlings did emerge from the 25 mm depth in that condition. It was striking that emergence was relatively high from 25 mm caches in litter in the open and under shrubs, but survival of those seedlings was very low-- only 3 seedlings in litter survived longer than one growing season but 57 out of 60 seedlings emerging from soil did so. tThis may be an example of seed-seedling conflict (Schupp 1998) where the conditions that favor emergence are not the same as those that favor survival. High levels of light may stimulate emergence of seedlings in the litter in the open (e.g. Ibanez and Schupp 2001, Chambers 2001) but as seedlings develop, litter acts as a barrier to their roots and limits access to the nutrients and moisture contained in mineral soil below (Facelli and Pickett 1991).

Another striking difference in emergence success occurred between seeds planted in burned versus unburned patches of treatment plots. I anticipated that if cache sites did not get directly burned, proportional emergence in those unburned patches would be similar to those in the control sites, but this was not the case, especially for litter microsites. For seeds buried in unburned soil and litter sites on treatment plots, emergence was significantly lower than on unburned control plots. This suggests that even the low-intensity prescribed burns studied here may heat the soil during and after a fire to an extent that reduces a seed's chance of surviving, as found by Tingey et al. (1996) and Vallette et al (1994) in controlled lab experiements. Pyne et al. (1999) demonstrate that the fine fuels found on the forest floor (e.g. in litter) undergo sustained smoldering and transmit heat for considerable periods of time. However, emergence of seedlings in patches that had been burned was higher than that of seedlings in unburned patches. These results are difficult to reconcile without detailed knowledge of abiotic factors such as nutrient availability, soil temperature, soil moisture and the potential interactive effects of all of these on seed germination and establishment probabilities (Izhaki et al 2000).

The lifespans of the seedlings that did establish in burned patches of treatment plots were significantly longer than those of seedlings that established on control plots. Chambers and Linnerooth (2001) found a similar result in burned grass and sedge meadows and suggested that once a seedling has established in this initially harsh environment, survival is enhanced. In our study, all of the seedlings (n=5) that survived from May 2000 to November 2002 were in mineral soil under shrubs in burned patches. Sample sizes are too small, and knowledge of the abiotic variables in this system is too incomplete, to draw any significant conclusions from this result, but it suggests that burial of seeds at these relatively shallow depths in favorable microsites before fires may, even in very dry years, contribute to pine regeneration shortly after the fire.

The study of density and growth rates of saplings and clumps at the Little Valley 1981 wildfire site support the idea that fires may create favorable conditions for conifer growth, and that instead of competing unsuccessfully with shrub species in the early stages of succession, young pines may effectively colonize portions of a burned area.

Although Shainsky and Radesovitch (1986) found that ponderosa pine saplings' growth rates were significantly limited when grown in proximity to greenleaf manzanita (one of the dominant shrubs on the Little Valley site), I found pine seedlings that had either been growing rapidly since the fire, and may have established before the shrub understory grew very dense, or had established under the canopy of shrubs and apparently benefited from their roles as 'nurse plants' (Callaway and Walker 1997). Even though shrub density was significantly higher in transects through the center of a burn, density of saplings was similar to density of saplings along the edge of the burned area. The mean density of both single and clumped seedlings was higher in edge zones than in burned or unburned zones, but there was too much variation among edge transects for this difference to be significant. Patchy establishment of pines in all areas may reflect small-scale variation in animals' home ranges or the presence and frequency of caching by certain species as well as variation in abiotic conditions like soil moisture, depth of litter and light availability to seeds and seedlings.

Densities of saplings and clumps were both lower (although not statistically so) in burned than in edge areas. If they had established successfully on the burn, however, saplings exhibited significantly higher growth rates than saplings in edge or unburned forest. This result is consistent with those of the short-term study at Incline. Abiotic conditions after this wildfire probably enhanced initial emergence and survival. Most importantly, the 3 years following the 1981 wildfire had above average precipitation (Klieforth, pers. comm.). When soil moisture is not limiting (Peterson et al 1994, Chambers and Linnerooth 2001), disturbed habitat may provide several types of favorable microsites for seedling establishment both in the burned area and, as my results show, around the edges of the burn, where densities of cached seedlings were higher. Previous studies have shown that increased levels of nutrients, reduced competition from other plants, and high levels of light may stimulate both establishment and growth of conifers (McNab and Cromack, 1994, Peterson et al 1994).

My findings at the site of the Floriston wildfire suggest that even sites which have been intensely burned may, as at Floriston, support populations of seed-dispersing rodents just a few years after the fire that are similar or greater than those in adjacent unburned areas. These results are consistent with those of many other studies of the "fire-adapted" deer mouse (Bock and Bock 1983, Ahlgren 1966, Sullivan and Boateng 1997). Although the Floriston wildfire was small in size, differences between the numbers and species trapped on the center of the burn versus in adjacent unburned forest were very striking. Previous studies of the caching behavior of deer mice (Chapter 1, Vander Wall et al 2001, Vander Wall and Hollander, submitted) found that deer mice make many shallow caches, typically of 1-2 seeds each, at a mean depth of 3.2 mm that was close to the depth (5 mm) from which 38 % of all seeds germinated in the artificial cache study at Floriston (8 % of these survived till the end of the first growing season). Thus, although my study was perhaps too short in duration and conducted during too dry a period to observe establishment from natural caches at Floriston, a potentially effective disperser species was present in high numbers and known to make caches, at least in unburned forest, of a size and depth that I found resulted in much greater emergence and survival relative to seeds placed on the forest floor. In the artificial cache study, the ashy substrate in which I planted seeds 3 yr after fire appeared to give the seeds a "boost" in stimulating emergence, although this effect declined (in terms of survival) over the first growing season to be equivalent with survival on the unburned plot.

At the much larger burned site (Little Valley), I found that caching by animals has occurred since the fire, both in the center of the burn and around its edges. In fact, my estimates of caching frequency must be regarded as conservative because a significant proportion of seedlings growing singly may have established from seeds buried by animals, either in single-seed caches originally (Chapter 1;Vander Wall 1997, Vander Wall and Joyner 1998) or in multiple-seed caches in which the other members died. Some seedlings on the Little Valley burn may have established from caches made by animals (rodents or birds such as Clark's nutcrackers or Stellar's jays) because the nearest live tree that could have produced seeds was several hundreds of meters away. However, little is known about maximum abiotic dispersal distances (e.g. via wind) for Jeffrey pine on steep slopes, and this is a possible alternative explanation. No management activities such as planting or seedling have occurred on or immediately adjacent to the sites of my transects since the wildfire (Klieforth, pers. comm.)

In summary, my results suggest that at the sites of small wildfires, prescribed fires, or the edges of large wildfires, conditions exist that allow seed-hoarding animals to continue directed dispersal of pine seeds into the disturbed sites, and abiotic conditions (eg light, nutrients) permit or even enhance the successful establishment and growth of seedlings, thus facilitating succession there. These findings are consistent with those of several other studies that have identified a positive role of mammals or birds in succession (Tomback 1986, Johnson et al 1997, MacClanahan and Wolfe 1993) and confirm that biotic dispersal remains effective after fires of varying intensity.

High frequencies of establishment from abiotic dispersal have been reported at other wildfire sites in the eastern Sierra (e.g. Crystal Peak, pers. obs., Blank and Zamudio 1998) as well as Little Valley. In a study at the site of the Crystal Peak fire, Blank and Zamudio (1998) observed cones opening immediately after the fire, even though it had occurred in early August. The pine seeds were mature enough to germinate and establish in extremely high densities, and a critical factor in sustaining this pulse of emergence was the high precipitation in several of the years immediately following the fire (Vander Wall, pers. obs. and Klieforth, pers. comm.) This combination of fire timing, intensity and favorable precipitation is unlikely to occur frequently or be easy to recreate without high risk; thus more frequent prescribed burning late in the growing season appears to be a strategy more likely to enhance the contribution of animal-made caches to pine regeneration.

Future studies are needed to quantify the changes in availability of favorable microsites for seedlings after patchy, low-intensity prescribed fire,; this was beyond the scope of my study. Several researchers confirm that in Sierra Nevadan conifer forests, this type of fire exposes patches of mineral soil (Kauffmann and Martin 1997), releases nutrients (Johnson et al 1996) and maintains portions of the shrub understory that can serve as possible nurse plants for emerging seedlings (Busse et al 1996). My findings show that emergence of seeds and survival of seedlings from seeds buried in these favorable microsites (in soil under shrubs) both before and after prescribed fires can be as high or higher than in unburned areas.

This suggests that prescribed burns similar in timing, intensity and spatial heterogeneity to those I investigated in this study may represent a management strategy in which the contribution of animals to postfire regeneration is maintained or even enhanced, relative to regeneration processes typical of unburned forests. This type of fire is probably similar to the frequent, patchy, low intensity lightning-caused fires characteristic of pre-settlement yellow pine forests (McKelvey et al 1996). In the context of this fire regime, the “diffuse mutualism” (Wenny 2001) between pines and scatter-hoarding rodents presumably evolved. In contrast, establishment of pine seedlings on severely burned wildfire sites may be more episodic, with pulses of regeneration coming primarily from abiotic dispersal processes if seed availability and precipitation are both high. In general, animals that direct dispersal of seeds to safe sites for establishment after both low- and high-intensity disturbances will have important impacts on the long term ability of plants to maintain a presence in the early stages of succession, colonize new habitat and respond to large-scale environmental or climatic change (Keane et al 1990, Tomback 1986, Johnson et al 1997).

LITERATURE CITED

Ahlgren CE, 1966 Small mammals and reforestation following prescribed burning. J. Forestry 64: 614-619.

Allison PD, 1995. Survival analysis using the SAS system: a practical guide. Cary, NC.: The SAS Institute, Inc.

Andersen DC, Macmahon JA, 1985. Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. The American Midland Naturalist 114:63-69.

Blank RR, Zamudio DC, 1998. The influence of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern front of the Sierra-Nevada range, California. Int. J. Wildland Fire 8:79-85.

Bock CE, Bock JH, 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. Journal of Wildlife Managment 47:836-840.

Burnham KP, Anderson DR, 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer.

Busse MD, Cochran PH, Barret JW, 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Sci. Soc. Am. J. 60:161-1621.

Callaway RM,Walker LR, 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965

Chambers JC, 2001. Pinus monophylla establishment in an expanding Pinus juniperus woodland: environmental conditions, facilitation and interacting factors. Journal of Vegetation Science 12:27-40.

Chambers JC, Linnerooth AR, 2001. Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts- the establishment component. Applied Vegetation Science 4:154-166.

Chambers JC, MacMahon JA, 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Duncan RS, Chapman CA, 2002. Limitations of animal seed dispersal for enhancing forest succession in degraded lands. In: Seed dispersal and frugivory: ecology, evolution and conservation (Wenny DG, Silva WR, Galetti M, eds). New York: CABI.

Facelli JM, Pickett STA, 1991. Plant litter: effects on community structure. Botanical Review 57:1-32.

Halvorson CH, 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. Ecology 63:423-433.

Hardy CC, Arno SF, 1996. The use of fire in ecological restoration. USFS Gen Technical Report INT GTR-341 Ogden Utah.

Hutchins HH, Hutchins SA, Liu B, 1996. The role of birds and mammals in Korean pine (*Pinus koraienis*) regeneration dynamics. Oecologia 107:120-130.

Ibanez I, Schupp EW, 2001. Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. Oecologia 129:543-550.

Izhaki I, Henig-Sever N, Ne'eman G, 2000. Soil seed banks in Mediterranean Aleppo pine forests: the effects of heat, cover and ash on seedling emergence. Journal of Ecology 88:667-675.

Jensen TS, Nielsen OF, 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70:214-221.

Johnson DW, Susfalk RB, Dahlgren R, Klopatek JM, 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. Environmental Science and policy 1:79-86.

Johnson,W. C., C. S. Adkisson, T. R. Crow, and M. D. Dixon. 1997. Nut caching by blue jays (Cyanocitta cristata L.): Implications for tree demography. American Midland Naturalist 138:357-370.

Keane RE, Arno SF, Brown JK, Tomback DF, 1990. Modelling stand dynamics in Whitebark pine (Pinus albicaulis) forests. Ecological Modelling 51:73-95.

Kilgore BM, 1973. The ecological role of fire in Sierran conifer forests. Quaternary Research 3:496-513.

MacMahon JA, 1981. Successional processes among biomes with special reference to the probable influences of animals. In: Forest succession (Shugart,West, eds). New York: Springer.

M'Closkey RM, 1975 Habitat succession and rodent distribution. J. Mamm. 56: 950-955

McGee JM,1982) Small mammal populations in an unburned and early fire successional sagebrush community. J. Range Mgmt 35: 177-179

McClanahan TR, 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology 7:279-289.

McKelvey KS, et al. 1996. An overview of fire in the Sierra Nevada. Sierra Nevada Ecosystem Project: Final report to Congress, vol II.:1033-1040.

McNabb, DH, Cromack D. 1990. Effects of presecribed fire on nutrients and soil productivity. In JD Walstad et al., eds. Natural and prescribed fire in Pacific Northwest Forests. Oregon State University Press, Corvallis OR.

Meffe GK, Carroll CR, 1994. Principles of Conservation Biology. Sunderland, MA: Sinauer Assoc.

Parminter J, 1998. Natural disturbance ecology. In: Conservation biology principles for forested landscapes (Voller J, Harrison S, eds). Vancouver: UBC Press.

Parsons DJ, DeBendetti SH, 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21-33.

Peterson DL, Sackett SS, Robinson LJ, Haase SM, 1994. The effects of repeated prescribed burning on Pinus ponderosa growth. International Journal of Wildland Fire 4:239-247.

Pyne S. Andrews PL, Laven RD, 1999. Introduction to wildland fire. New York: John Wiley and sons.

Saigo BW. 1969. The relationship of non-recovered rodent caches to the natural regeneration of ponderosa pine. Master's Thesis Oregon State University. Corvallis, OR.

Schupp EW, Fuentes M, 1995. Spatial Patterns of Seed Dispersal and the Unification of Plant-Population Ecology. Ecoscience 2:267-275.

Sullivan TP, Lautenschlager RA, Wagner RG, 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. Journal of Applied Ecology 36:327-344.

Vander Wall SB, 1992a. Establishment of Jeffrey pine seedlings from animal caches. Western Journal of Applied Forestry 7:14-20.

Vander Wall SB, 1992b. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73:614-621.

Vander Wall SB. 1994. Removal of wind-dispersed pine seeds by ground-foraging vertebrates. Oikos 69: 125-132

Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck, and J. R. Roth. 2001. Scatter-hoarding behavior of deer mice (Peromyscus maniculatus). Western North American Naturalist 61:109-113.

Warde W, Petranka JW. 1981. A correction factor table for missing point-center data. Ecology, 62(2), pp. 491-494.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences of the United States of America 95:6204-6207.

Wenny DG, 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3:51-74.

Wheelwright NT, Orians GH, 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119:402-413.

Whitmore TC, 1989. Canopy gaps and the two major groups of forest types. Ecology 70:536-538.

Wunderle JM, 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.

TABLE 1. Characteristics of the plots used in studies 1-4: Rodent trapping study (1); seed removal study (2), Natural seedling survey (3a), Artificial cache study, pre-fire (3b), Artificial cache study, post-fire (3c), Seedling density and long-term growth rate study (4). At the wildfire sites, B, E and U represent burned, edge of burn and unburned areas respectively.

Location	Plot	Date burned	Size of burn (ha)	Aspect	Mean elevation (m)	Distance (m) to control plot	Included in studies:
Incline Village (prescribed burns)	G	1999	37.5	ENE	2530	50	1,2,3a
	J	1999	22.5	ENE	2270	30	1,2,3a
	L	1999	17.5	W	2300	150	1,2,3a
	M	1999	20	W	2500	50	1,2,3a
	S	1999	25	ESE	2360	75	1,2,3a
	B1	2000	12.5	ENE	2500	150	1,2,3a,b
	SU	2000	17.5	ESE	2400	30	1,2,3a,c
	SB	2001	17.5	SSW	2410	30	1,3 bc
	B2	2001	7.5	E	2480	N/A	3 b,c
Floriston (wildfire)	B	1999	500	WSW	5300	200	1,2,3a,c
	E	1999		SSE	5310	40	1,2,3 c
	U	n/a		S	5310		1,2,3ac
Little Valley (wildfire)	B	1981	transects	varied			4
	E	1981					4
	U	n/a					4

TABLE 2. Numbers, microsites and survival of newly emerging single seedlings and clumped seedlings on pairs of burned and control plots at Incline Village. 5 pairs of plots were monitored until fall 2002 after burns in 1999, 2 pairs after burns in 2000, and one after a burn in 2001. Sampling plots on burns were 1600 m^2 and control plots were 125 m^2. No seedlings or caches were found on 7 of the 8 control plots. Survival represents the number of single (s) or clumped (c) seedlings alive at the end of their first and second growing seasons.

	2000		2001		2002		Microsite				Survival	
							Substrate		Understory			
Plots	Seedlings	Clumps	Seedlings	Clumps	Seedlings	Clumps	Soil	Litter	Shrub	Open	Yr 1	Yr 2
Burned												
G	0	0	0	0	0	0	0	0	0	0		
J	2	6	0	0	4	6	11	7	3	15	1s	0
L	1	0	0	0	1	0	1	1	2	10	1s	0
M	1	1	0	0	6	17	8	17	0	22	1s, 3c	0
S	7	5	0	0	1	0	13	0	2	11	5s, 4c	0
BI	-	-	0	0	3	2	2	3	2	3		
SU	-	-	0	1	6	0	2	5	2	5		
SB	-	-	-	-	2	3	1	4	0	5	1c	0
Total	9	6	0	1	23	28	38	37	10	66		
Control												
S	2	2	0	0	0	0	0	4	0	4		

TABLE 3. Annual precipitation (mm) at Wood Creek canyon, Incline Village, NV, 1997-2002. Monthly totals are shown for the summer growing season (May –October) every year. All values represent rain and melted snow combined. Data courtesy of John Bugge.

	1997	1998	1999	2000	2001	2002
May	13.6	32.8	10.8	26.7	2.8	5.1
June	34.1	50.8	4.4	8.0	2.1	1.8
July	7.7	0	9.0	0	11.5	7.4
August	1.8	3.3	7.4	1.3	0	0
September	15.4	54.1	2.1	4.6	1.0	0.5
October	16.2	7.2	14.1	11.0	0	0.5
Total (summer)	89	148	48	52	17	15
Total (year)	655	402	301	133	275	*

TABLE 4. Percentage emergence of seedlings from seeds planted at 3 depths (0, 5, and 25 mm) in different microsites on treatment (burned) and control plots. Microsites represent all possible combinations of 2 substrate types (mineral soil and litter) and 3 cover types: flammable (F) shrubs, nonflammable (NF) shrubs, and shrub interspaces (open). On treatment plots, categories are subdivided to show emergence in burned (U) versus unburned (B) patches within the treatment plots. Data represent 3 treatment plots and 3 control plots. The sample sizes in each category were 143-174 seeds at the depths of 5mm and 25mm and 45-57 seeds at 0 mm.

		Treatment						Control					
		Mineral soil			Litter			Mineral soil			Litter		
Depth	Patch	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open
0mm	U	0	0	2	0	0	0	8.8	7.4	7.4	0	0	0
	B	2.0	4.2	4	0	2	0						
5mm	U	3.9	7.6	10.0	5.9	0.7	2.1	20.5	17.5	29.4	0	3.5	5.3
	B	15.0	27.1	14.0	0	0	0.7						
25mm	U	7.8	8.3	11.8	8.1	5.2	4.9	25.1	21.8	21.6	17.6	15.8	17.8
	B	23.5	13.9	5.2	7.4	5.2	2.1						

TABLE 5. Proportional survival of seedlings in the microsite and depth combinations shown in Table 3. Values are percentages of the seedlings that emerged in each category that survived for longer than 1 growing season. The actual numbers of surviving seedlings represented by these values are given in parentheses.

		Treatment						Control					
		Mineral soil			Litter			Mineral soil			Litter		
Depth	Patch	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open	F. Shrub	NF. Shrub	Open
0mm	U	–*	–	0	–	–	–	0	0	0	–	–	–
	B	0	50 (1)	0	–	0	–						
5mm	U	0	0	0	0	0	0	14 (5)	13 (4)	4 (2)	–	0	0
	B	35 (8)	18 (7)	14 (3)	–	–	0						
25mm	U	0	0	0	0	0	0	16 (7)	6 (2)	12 (4)	7 (2)	0	0
	B	25 (9)	25 (5)	0	0	13 (1)	0						

* No seedlings emerged in these categories

TABLE 6. Mean densities (± SD) of pine saplings (growing singly and in clumps), shrubs and trees in transects across different "zones" of a 1981 wildfire site. 5 transects were surveyed in each of 3 areas: burned, unburned and edges of the burn. Growth rates are shown for the single and clumped saplings measured in the density analyses plus a) saplings < 22 yrs old recorded in the understory category on burned transects, and b) any seedlings found within 2 m of each transect point. Mean growth rates were calculated for all of these saplings on each transect.

	Densities (individuals/100 ha)					Growth rates (cm/yr)	
Zone	Single saplings	Clumped saplings	Shrubs	Understory trees	Overstory trees	Saplings	Caches
Burned	1.52 ± 0.5	0.40 ± 0.2	78.6 ± 64.2	0.26 ± 0.31	0	7.85* ± 2.72	2.98 ± 2.01
Edge	2.34 ±1.5	1.72 ±1.8	7.04 ± 3.9	0.70 ± 0.59	0.72 ± 0.23	1.66 ± 0.54	1.46 ± 0.49
Unburned	1.08 ±1.1	0.98 ±0.8	1.9 ± 1.19	1.44 ± 0.48	0.98 ± 0.19	2.56 ± 0.70	1.89 ± 1.75

FIGURE LEGENDS

FIGURE 1. Schematic diagram of a site on which artificial caches were made in Study 3 b). This design was replicated on 3 pairs of treatment and control plots. See text for full details.

FIGURE 2. Mean numbers of rodents on 5 plots burned in Fall 1999 (filled bars) and adjacent control plots (open bars) and 2 plots burned in 2000. Values represent means ±1 SD for number of chipmunks known alive (a,d); number of deer mice known alive (b, e); and numbers of all species known alive (c,f). Pre-burn trapping was done 2 - 6 wks before fires and at up to 4 times after fires: 8 mo, I yr, 2 yr and 3 yr later, until Fall 2002. Asterisks above means indicate significant differences between that mean and other levels of the same treatment (repeated measures ANOVA, $P < 0.05$). Data from the 2000 plots were not analyzed statistically.

FIGURE 3. Numbers of rodents captured on the burned (filled bars), edge (shaded bars) and unburned (open bars) plots at Floriston. Values are minimum numbers of A) Chipmunks B) Deer mice and C) all rodents known alive at different times since burn. Half lives of seeds on transects on the same plots are shown in panel D (hatched bars).

FIGURES

Figure 1

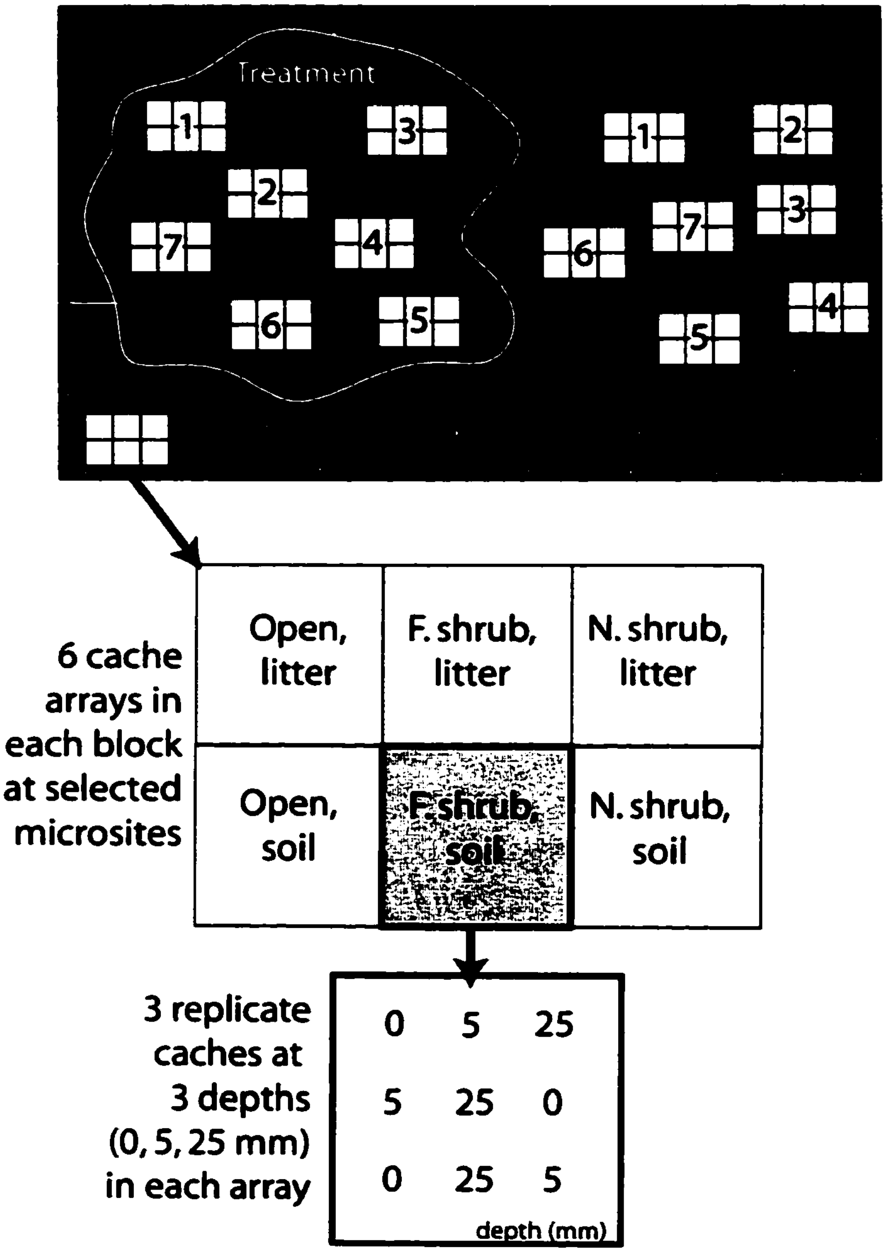


Figure 2

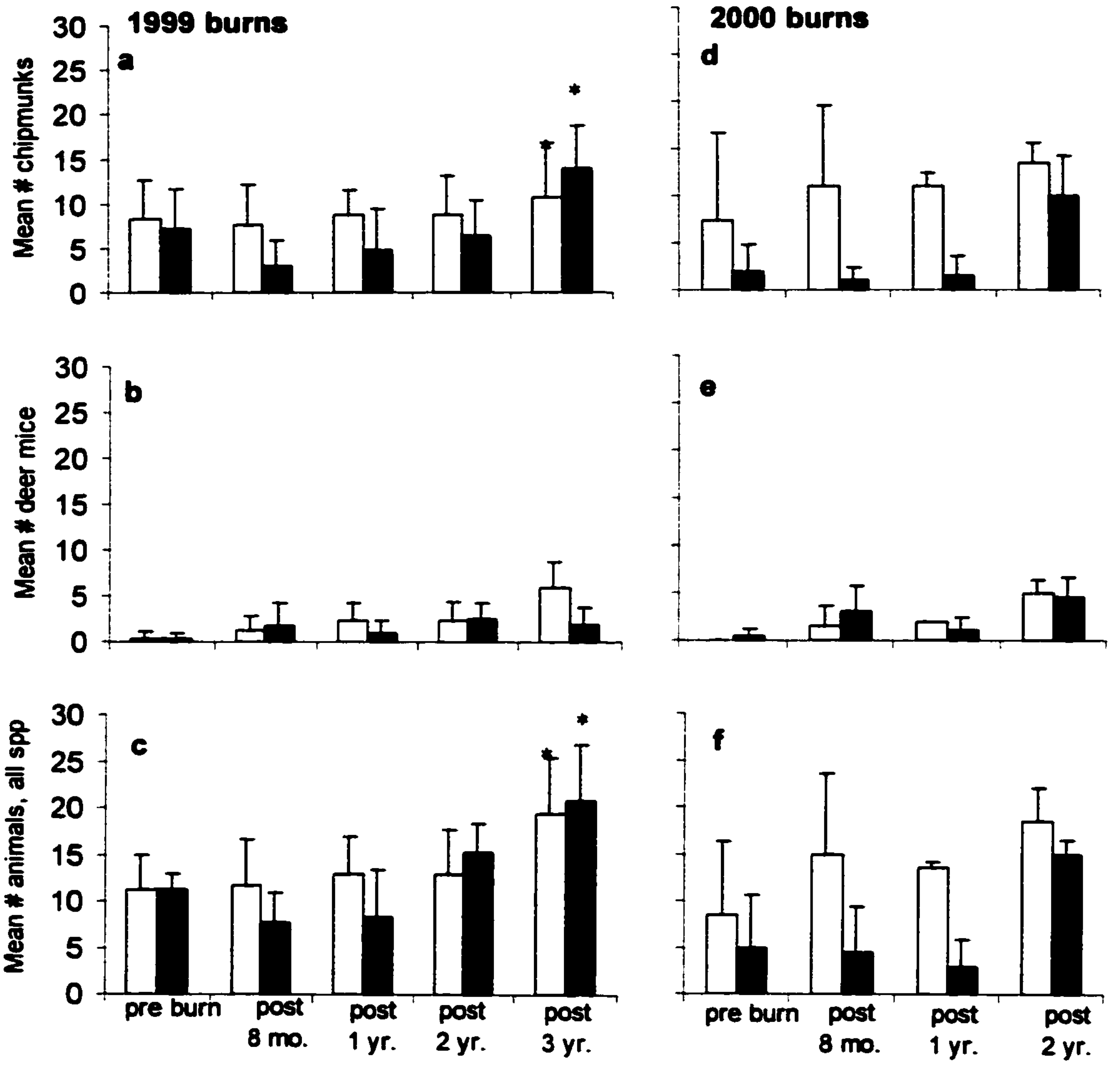
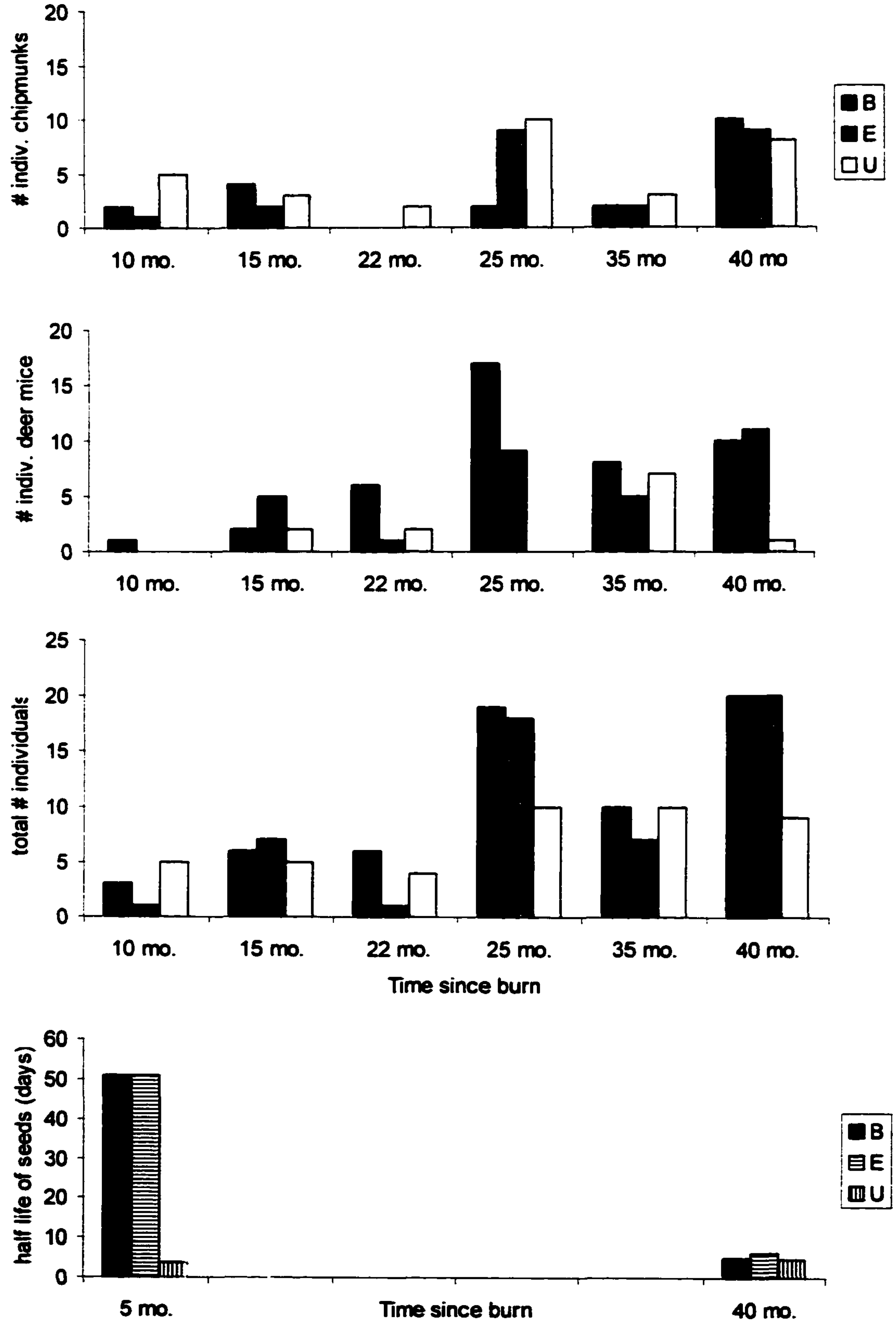

1999 burns
2000 burns
a
b
c
d
e
f
Mean # chipmunks
Mean # deer mice
Mean # animals, all spp
0
5
10
15
20
25
30
*
pre burn
post 8 mo.
post 1 yr.
post 2 yr.
post 3 yr.

Figure 3



indiv. chipmunks
20
15
10
5
0
10 mo.
15 mo.
22 mo.
25 mo.
35 mo
40 mo
B
E
U
indiv. deer mice
20
15
10
5
0
10 mo.
15 mo.
22 mo.
25 mo.
35 mo.
40 mo.
total # individuals
25
20
15
10
5
0
10 mo.
15 mo.
22 mo.
25 mo.
35 mo.
40 mo.
Time since burn
half life of seeds (days)
60
50
40
30
20
10
0
5 mo.
Time since burn
40 mo.
B
E
U

General Summary and Conclusions

My study focused on three aspects of the relative contribution of biotic and abiotic processes to the regeneration of pine after fire. I investigated the effects of animals' caching behavior on establishment and survival of pine seedlings in Chapter 1, and provided evidence that several common rodent species perform directed dispersal of pine seeds to favorable microsites. Chapter 2 examined how changes in the physical environment created by fire influence key behaviors of two important seed dispersing species (*Tamias amoenus* and *T. speciosus*) identified in Chapter 1. Chapter 3 investigated multiple effects of fire on the interaction between animals and pine seeds.

The experiments conducted in Chapter 1 revealed that four species of granivorous rodents (*Tamias amoenus, T. speciosus, P. maniculatus* and *S. lateralis*) made caches of Jeffrey pine seeds that differed in size, depth and microsite characteristics. Cache size (and to some extent, depth) increased with animals' body size, and each species showed slightly different tendencies to make caches in different substrates and locations relative to shrubs and trees. As a community, the animals used microsites in mineral soil and under shrubs significantly more frequently, relative to their availability, than other types of sites. Seeds in artificial caches made in microsites and at depths used by animals emerged and survived significantly better than seeds placed in microsites and at depths typical of wind-dispersal.

Taken together, these results suggest that the four species of rodents may provide directed dispersal of Jeffrey pine (Howe and Smallwood 1982) if the relative abundances and preferences of the animals in the conditions of my study reflect those in unrestricted field conditions. If the species-specific behavior patterns I observed persist regardless of animal community composition, the yellow-pine chipmunk may have the most favorable effect on pine seedling establishment of the four species examined. Both its cache site selection preferences (under shrubs in mineral soil or light litter) and its mean cache depth were associated with high emergence and survival of seedlings.

When a fire burns the forest floor, the mechanisms by which rodents find, cache and retrieve seeds are influenced by changes in substrate type. A laboratory experiment (Chapter 2) quantified and compared the foraging success and caching frequency of chipmunks in ash versus sand substrate. Ash appeared to limit rodents' ability to detect seeds buried in unfamiliar locations, suggesting that olfaction is less effective in this substrate. Surprisingly, chipmunks made greater or equal numbers of caches in ash than in sand. They recovered high proportions of their own caches in both substrates but were significantly less successful in finding caches made by other animals in ash. This finding emphasized the importance of spatial memory in cache retrieval and suggested that animals may use ash substrate as a secure location for storing seeds where they may escape detection and pilferage by competitors.

Chapter 3 identified the importance of dispersal of pine seeds by animals to the successful regeneration of Jeffrey pine after prescribed and wild fires. Rodent communities declined immediately after prescribed, low-intensity burns but rapidly returned to pre-burn levels, with species composition remaining relatively constant. At a single high-intensity wildfire site, the size and species composition of the rodent community was more significantly altered, relative to that in the adjacent unburned forest, immediately after the fire. Numbers of animals on the wildfire site also returned to high levels a few years after the fire, but the species composition was different, with deer mice outnumbering chipmunks over the 3.5 yr period of this study. The rate at which seeds were removed from the forest floor on both types of burn reflected the size of the animal communities, and was significantly slower than on unburned plots only for a few (1-5) months after fires. The frequency of natural caching observed on all burned plots was low and difficult to detect during the drought conditions and low seed availability that prevailed during much of this study.

As the experiments described in Chapters 1 and 2 identified the range of microsites and strategies used by seed caching animals, I used preliminary results from these studies to design the artificial cache study in Chapter 3, which compared the fates of seeds in sites typical of both animal and abiotic dispersal before and after prescribed fires. I found that seeds survived the fires and emerged significantly more frequently if buried in certain substrates, microsites, and depths; notably, the mineral soil/under shrub microsites in which animals had made the highest proportions of their caches in Chapter 1. Very few seeds placed on the forest floor, simulating wind dispersal, emerged after prescribed fires compared to those buried at depths typical of animal caches. Survival of seedlings was also significantly higher in the microsites and at the depths used most frequently by animals when caching.

At the site of a 1981 wildfire, I found that densities of single and clumped seedlings were highest around the edges of the burn (in areas where the forest understory had been burned), but that growth rates of saplings in the center of the burned areas were significantly higher than those in the edge or unburned forest. This suggests that both the edges and the center of wildfires may provide environments that are favorable for pine regeneration and that fires may create conditions in which caching by animals can facilitate recolonization and succession.

As large-scale wildfires are becoming increasingly frequent in semi-arid western forests, ecologists and forest managers alike must increase their knowledge of regeneration dynamics and interactions between biotic and abiotic factors after fire. Awareness and perhaps exploitation of the role of seed-dispersing animals in facilitating succession may be an important component of efforts to maximize the regeneration and recovery of disturbed ecosystems (Chambers and MacMahon 1994). A few studies in temperate ecosystems have investigated the significant effects of seed dispersal by mammals and birds on plant recolonization of areas disturbed by fires (Tomback 1986, Johnson et al 1997) or volcanic eruptions (Andersen and MacMahon 1983) but these were all post-hoc in nature and did not examine the mechanisms shaping regeneration dynamics. Still fewer studies (Longland and Bateman 1998, McClanahan and Wolfe 1991) have explored the possibility of including animal dispersal in post-disturbance restoration efforts in temperate ecosystems.

Duncan and Chapman (2002) review recent attempts to incorporate animal dispersal into restoration programs developed by managers working in degraded tropical forests. In these systems, the primary dispersers of large-seeded tree canopy species are frugivorous birds and mammals whose potential to successfully disperse seeds into disturbed systems is often limited by several factors: lack of food sources in the critical areas, increased risks of predation both on the dispersers and the seeds, and limited availability of favorable sites for seed germination and seedling establishment even if seeds do reach the area (Duncan and Chapman 2002, Wunderle 1997). Although some of these problems apply to granivorous rodents in burned, semi-arid pine forests, many do not. Several of the species that scatter-hoard pine seeds also consume foods such as grass seeds and insects that are available soon after fires (Ahlgren 1966, Bock and Bock 1983), and these resources may attract or maintain animal populations. Predation risks on animals in burned vs. unburned forests have not been directly examined, but one study found that changes in forest structure were correlated with behavior patterns of chipmunks which may reflect vigilance and predation risk (Mahan and Yahner 1999). However, Sullivan et al (1999) captured more chipmunks on both burned and unburned clearcuts in spruce-fir forest than in unburned forest habitat, and population densities of deer mice are almost always found to be high in open, severely burned areas (Sullivan and Boateng 1996, Ahlgren 1966, Bock and Bock 1983; this study), suggesting that if there is an increase in perception of predation risk on burned sites, it does not affect the presence and probability of capture in these areas.

Predation risks for seeds in burned vs. unburned areas in the field were not addressed in this study, but the results of Chapter 2 show that, in laboratory conditions, chipmunks found significantly fewer caches buried in ash by other animals relative to caches they had previously made themselves. Thus, unlike seeds transported to tropical forest gaps (Duncan and Chapman 2002), seeds cached in burned microsites might not suffer disproportionate predation, and if unretrieved by the original cacher they appear to have a higher probability of emergence and an similar probability of survival compared to seeds buried in unburned sites.

Overall, the potential for animals to enhance succession in burned conifer forests may be greater than the potential for animals to do so in the systems reviewed by Duncan and Chapman (2002) in which constraints seemed to outweigh benefits. The timing and spatial heterogeneity of the prescribed fires I studied had important and positive effects on seed dispersal dynamics and seedling survival. My results suggest that burns that are patchy in nature and occur either shortly before or after seeds ripen in the fall are likely to a) maintain habitat for seed-hoarding species; b) have neutral or positive effects on the emergence and survival of seedlings from caches made by animals before the fire after seeds were released from the cones; c) produce favorable sites for seed caching (e.g. exposing patches of mineral soil) by animals after the fire; and d) create favorable conditions (e. g. ashy substrates) for the germination, emergence and rapid growth of pine seedlings from seeds dispersed either by wind or animals after the fire.

Such fires, even if on a much smaller spatial scale, may mimic the frequent, patchy, low-intensity fires thought to characterize pre-settlement conditions (Brown et al 1994). Although historic fires probably occurred in summer (Baker and Ehle 2001), this is currently an impossible time to plan or conduct prescribed burns in semi-arid forests due to the risks to property and human life associated with an escape. However, in spite of the differences in scale and timing, prescribed burns may be a management tool that takes advantage of the potential for rodents to significantly contribute to pine regeneration, and simulates several aspects of disturbance regime with which seed dispersal processes evolved.

Managers are becoming increasingly aware that the biotic integrity of ecosystems depends on the incorporation of natural disturbance regimes and the patchiness they create into the process of ecosystem management (Hardy and Arno 1996, Parminter 1997). In 1973, Kilgore described the negative effects of (and possible solutions to) the problem of fire suppression in National Forests of the western states. Since his assessment, fuel loading in pine and mixed-conifer forests has continued to increase, and each summer brings catastrophic stand-replacing wildfires to many western states. Consequently, many less risky management alternatives to prescribed fires have been proposed. But in addition to the political and financial issues raised by management practices such as mechanical fuels reduction treatments and logging (Covington 2003), forest managers and biologists must address the ecological question of whether logging will affect ecosystem processes, components and succession in the same ways as fire.

In Douglas fir (*Pseudotsuga menziesii*) forests in western Oregon, Dyrness (1973) compared succession of plant communities on plots that had been logged and burned at varying intensities. He found considerable differences in both the species abundance and diversity after 5 yr: invader species dominated burned plots and a mixture of invader and residual species occupied areas than had been logged. Thus, fire produced both a quantitative and qualitatively different community. Johnson et al's study (1998) of the strong effects of fire nutrient cycling dynamics is another example of the unique chemical, ecological and physical processes associated with fire but not with mechanical disturbances like logging. These studies did not examine animal communities, but a national study is currently in progress at 13 sites throughout the U.S. to compare both plant and animal succession, as well as many other processes such as nutrient cycling, in forests that have undergone mechanical fuels reduction treatments, prescribed burns, both, or neither (Riegel, pers. comm.).

Understanding the roles of important species in a community, their effects on each other, and the consequences of changes in their relative abundance allows insight into the mutualistic and possibly co-evolutionary relationships between some species. Howe (1989) suggests that plant species dispersed by scatter-hoarding animals may be extremely vulnerable to the loss of their dispersal agents; the interactions between plants and their animal dispersers or pollinators have long been studied in this light (Regal 1982, Vander Wall 1992). Knowledge of the effects of major natural disturbances on such interactions may clarify the selective forces shaping these relationships. Thoreau's observations of squirrels and oaks in the 1850s led him to conclude that "This wonderful activitiy of the squirrels—in collecting and dispersing and planting nuts and acorns and so forth—every autumn is all the more necessary, since the trees on whose fruit they mainly live are not annual plants...if the forests were to be planted only at intervals equal to the age of the trees, there would be danger, what with fires and blight and insects, of a sudden failure and famine" (Thoreau 1993, p. 132).

Interpreting my results in the context of disturbance ecology and evolutionary history, I suggest that my findings support a modified version of the directed dispersal hypothesis described by Howe and Smallwood (1982) to explain the benefits of seed dispersal. I identified a form of disturbance- related directed dispersal of pine seeds by providing direct evidence that seeds buried in sites typical of animal burial (and especially in certain sites that appear to be preferred by animals for caching) survive in significantly higher proportions than those in sites typical of wind-dispersal both in the presence and the absence of fire. I could not directly assess frequency of use of these preferred sites in the field after a fire, but obtained indirect evidence (clumped seedlings on burns in the field, many caches made in ash in the lab, high numbers and activity levels of animals in burned plots soon after fires, high emergence and survival of seedlings in ash) suggests that directed dispersal may continue after fires. Forest rodents may be especially critical to the long term reproductive success of pines in semi-arid environments in which low-intensity surface or understory fires have been frequent. I found less evidence that would support the colonization hypothesis (Howe and Smallwood 1982), as I observed no natural regeneration on the small 1999 wildfire site for 3 yr after fire, and found higher densities of both clumped and single seedlings on the edges rather than in the center of the 1981 wildfire site. My study did not address the escape hypothesis.

Abiotic dispersal may be very successful when wild fires occur just before or during seed maturation and cone opening, and are followed by years with ample precipitation to sustain the pulse of regeneration, as at the Little Valley and Crystal Peak fire sites (pers. obs.) Patterns of high seedling density on burns have also been observed by Chappell and Agee (1996) in red fir forests and by Ne'eman et al (1997) in *Pinus halapensis* forests in the east-Mediterranean ecosystem on Mt Carmel, Israel.

However, in the arid climates and frequent fire regimes characterizing yellow-pine forests in the western U.S., the processes of pine seed dispersal by animals may maintain a successional cycle that could be slowed or even arrested if wind-dispersed seeds were rarely buried below the soil surface, or remained in the thick and combustible layer of pine litter beneath parent trees. Caching of seeds by animals in mineral soil microsites under shrubs prevents the desiccation of most (although not all) surface seeds in unburned forests as well as buffering the usually fatal effects of even low-intensity fires on these surface seeds. In this study, placement of seeds in microsites typical of animal dispersal also enhanced the probability of seedling emergence and survival even in very dry years directly following prescribed fires. These findings suggest that granivorous rodents may play a “keystone” role in maintaining an ecosystem-level process (Simberloff 1999) in the face of significant disturbance. When they are designing plans to restore severely burned areas or reintroduce prescribed fire into long-unburned forests, managers and ecologists alike should consider these animals’ potential to act as low-cost, effective reseeding agents if seed availability and abiotic conditions are favorable.

LITERATURE CITED

Ahlgren CE, 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry 64:614-617.

Andersen DC, Macmahon JA, 1985. Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, Thomomys talpoides. The American Midland Naturalist 114:63-69.

Baker WL, Ehle D, 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Canadian Journal of Forest Research 31:1205-1226.

Bock CE, Bock JH, 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. Journal of Wildlife Managment 47:836-840.

Chambers JC, MacMahon JA, 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Chappell CB, Agee JK, 1996. Fire severity and tree seedling establishment in Abies magnifica forests, Southern Cascades, Oregon. Ecological Applications 6:628-640.

Duncan RS, Chapman CA, 2002. Limitations of animal seed dispersal for enhancing forest succession in degraded lands. In: Seed dispersal and frugivory: ecology, evolution and conservation (Wenny DG, Silva WR, Galetti M, eds). New York: CABI.

Dyrness CT, 1973. Early stages of plant succession following logging and burning in teh Western Cascades of Oregon. Ecology 54:57-69.

Hardy CC, Arno SF, 1996. The use of fire in ecological restoration. USFS Gen Technical Report INT GTR-341 Ogden Utah.

Howe HF, 1989. Scatter-and clump- dispersal and seedling demography: hypothesis and implications. Oecologia 79:417-426.

Howe HF, Smallwood J, 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Kilgore BM, 1973. The ecological role of fire in Sierran conifer forests. Quaternary Research 3:496-513.

Longland WS, Bateman SL, 1998. Implications of desert rodent seed preferences for range remediation. Journal of Range Management 51:679-684.

MacMahon JA, 1980. Ecosystems over time: succession and other types of change. In: Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th annual Biology colloquium. (Waring RH, ed). Oregon State University, Corvallis, Oregon.; 27-57.

Mahan CG, Yahner RH, 1999. Effects of forest fragmentation on behaviour patterns in the eastern chipmunk (Tamius speciosus). Canadian Journal of Zoology 77:1991-1997.

McClanahan TR, 1993. Accelerating foreat succession in a fragmented landscape: the role of birds and perches. Conservation Biology 7:279-289.

Ne'eman G, 1997. Regeneration of natural pine forest-- review of work done after the 1989 fire in Mount Carmel, Israel. International Journal of Wildland Fire 7:295-306.

Parminter J, 1998. Natural disturbance ecology. In: Conservation biology principles for forested landscapes (Voller J, Harrison S, eds). Vancouver: UBC Press.

Simberloff D, 1999. The role of science in the preservation of forest biodiversity. Forest Ecology and Management 115:101-111.

Sullivan TP, Klenner W, 2000. Response of northwestern chipmunks (Tamias amoenus) to variable habitat structure in young lodgepole pine forest. Canadian Journal of Zoology 78:283-293.

Sullivan TP, Lautenschlager RA, Wagner RG, 1999. Clearcutting and burning of northern spruce-fir forests: implications for small mammal communities. Journal of Applied Ecology 36:327-344.

Tomback DF, 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono 33:100-110.

Vander Wall SB, 1992. The role of animals in dispersing a "wind-dispersed" pine. Ecology 73:614-621.

Wunderle JM, 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.