

SEEDLING RECRUITMENT IN *ORYZOPSIS HYMENOIDES*: ARE DESERT GRANIVORES MUTUALISTS OR PREDATORS?

WILLIAM S. LONGLAND,^{1,2,3} STEPHEN H. JENKINS,² STEPHEN B. VANDER WALL,² JOSEPH A. VEECH,²
AND SANJAY PYARE²

¹USDA, Agricultural Research Service, University of Nevada, 920 Valley Road, Reno, Nevada 89512 USA

²Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Nevada 89557 USA

Abstract. Granivorous animals that cache as well as consume seeds may actually serve as mutualists to their plant resources. Seeds of Indian ricegrass (*Oryzopsis hymenoides*), a perennial bunchgrass in North American deserts, are consumed by various desert granivores and dispersed by seed-caching heteromyid rodents. We used a three-way factorial design at a western Nevada site to selectively exclude or allow access to experimental plots by granivorous rodents and seed harvester ants, and to subsequently follow the fate of radiolabeled Indian ricegrass seeds introduced to the plots. In addition to the presence or absence of rodents or ants, the third experimental treatment factor was to allow “initial caching” of the radiolabeled seeds by single Merriam’s kangaroo rats (*Dipodomys merriami*), which were confined to certain plots for one night. Both rodents and ants larder-hoarded seeds in their burrows, but seedlings rarely established from larders. Only rodents also placed seeds in scatterhoards: shallowly buried surface caches distributed about an animal’s home range. Following initial caching by a kangaroo rat, the number of seedlings established from scatterhoards was significantly greater (usually by more than an order of magnitude) than those from seeds unharvested by either type of granivore. With no initial caching, rodents reduced seedling recruitment from unharvested seeds but facilitated compensatory seedling recruitment from scatterhoards. Seeds harvested by ants seldom established seedlings. We used a seed fate model to estimate that, on average, rodents and ants harvested 96% and 7%, respectively, of seeds to which they had exclusive access, and that the probability of seedling establishment for a seed harvested by a rodent was an order of magnitude greater than from a seed harvested by an ant and slightly greater than for an unharvested seed. The predicted rank order of seedling recruitment among nine experimental treatments based on expected effects of rodent seed caching closely matched the observed ranking pattern, indicating that rodents determined seedling recruitment patterns of Indian ricegrass. Because rodents harvested such a large majority of seeds and their caches enhanced seedling establishment, they played a central role in the population dynamics of Indian ricegrass.

Key words: deserts; *Dipodomys merriami*; granivory; harvester ants; heteromyid rodents; Indian ricegrass; Merriam’s kangaroo rats; *Oryzopsis hymenoides*; plant–animal interactions; seed caching; seed dispersal; seeds.

INTRODUCTION

To establish a new plant, a seed must avoid a virtual gauntlet of hazards, including numerous seed-consuming animals and microbes, and find a suitable site for germination. Animals that cache seeds for later consumption may potentially serve as mutualists to their food plants if, by caching, they reduce the chance that seeds are taken by noncaching granivores, or they transport seeds to favorable microsites, and some portion of their cached seeds remain to potentially establish new seedlings. Gray squirrels (*Sciurus carolinensis*) caching acorns of oak trees (*Quercus* spp.) provide a classic example that may even help explain current range distributions of oaks in eastern North America (Vander Wall 1990).

In North American deserts, seeds are available all year and retain their nutritional quality during long periods separating production events. Consequently, granivory has evolved in a diverse array of desert animals and granivores are abundant in these deserts. Based on quantity of seeds used, rodents, birds, and harvester ants are the most important granivores in North American deserts (Brown et al. 1979, Parmenter et al. 1984).

The abundance of desert granivores has important implications for the biology of desert plants due to the large number of seeds consumed by these animals. For example, a single rodent species was estimated to consume 95% of *Erodium cicutarium* seeds produced at a Mojave Desert site (Soholt 1973). Because desert rodents and ants cache seeds as well as consuming them, these granivores may also act as seed dispersal agents.

Granivorous rodents of the family Heteromyidae, found throughout arid western North America, are the

Manuscript received 2 September 1999; revised 27 June 2000; accepted 30 July 2000; final version received 18 November 2000.

³ E-mail: longland@scs.unr.edu

most abundant group of rodents in most desert localities. Kangaroo rats (*Dipodomys* spp.) and other desert heteromyids are highly specialized granivores that can exist on a diet of seeds alone without free water (Frank 1988). They locate seeds buried several centimeters deep in the soil by olfaction (Reichman 1981, Pyare and Longland 2000). They have external cheek pouches, which they fill with large quantities of seeds during foraging (Vander Wall et al. 1998). They cache seeds in numerous locations distributed around their home ranges, and use spatial memory to later relocate these caches (Jacobs 1992). Two genera of harvester ants (*Pogonomyrmex* and *Veromessor*) forage for seeds in North American deserts. Larks (F. Alaudidae) and sparrow species (F. Emberizidae) are the most common granivorous desert birds. Birds use smaller numbers of seeds than either rodents or ants (Mares and Rosenzweig 1978, Brown et al. 1979, Parmenter et al. 1984), due partly to seasonal differences in the intensity of granivory by birds. Although ant activity is also seasonal, they are very active at times that plants produce and shed seeds. Except for hibernating species, granivorous rodents harvest and utilize seeds year-round. Granivorous desert birds consume seeds upon harvest, but rodents and ants store substantial quantities of seeds (Janzen 1971, Brown et al. 1979).

Regarding potential effects of granivory on desert plants, two behavioral differences set rodents apart from birds and ants. First, rodents dig for buried seeds. Harvester ants and birds only take seeds directly from plants or from the soil surface. Second, many rodents, such as heteromyids, bury seeds in scattered shallow depressions they dig throughout their home ranges (scatterhoards), as well as caching in larders deep within their burrows (larderhoards). Seeds in scattered caches that are not recovered for later consumption may germinate and thereby contribute to recruitment in plant populations (Price and Jenkins 1986). By contrast, ants typically cache deep in underground granaries (Tevis 1958, Lavigne 1969, Clark and Comanor 1973), where seeds have little chance to germinate and establish. Seedling establishment from rodent scatterhoards has been noted for several desert plant species (Reynolds and Glendening 1949, Reynolds 1950, West 1968, La Tourrette et al. 1971, McAdoo et al. 1983, McAuliffe 1990, Vander Wall 1990, 1994), and may sometimes be the primary means of recruitment. For example, Vander Wall (1994) found that >99% of seedling recruitment in an antelope bitterbrush (*Purshia tridentata*) population resulted from caches made by yellow pine chipmunks (*Tamias amoenus*). Indeed, many plants have evolved strategies to utilize animal dispersers, such as enclosing seeds within conspicuous fruits or producing large attractive seeds (Janzen 1971, Vander Wall 1990). In some desert plant species, seed germination rates may even be enhanced by rodent caching activities (Reynolds and Glendening 1949, La Tourrette et al. 1971, McAdoo et al. 1983).

Indian ricegrass (*Oryzopsis hymenoides*), a perennial bunchgrass native to North American deserts, is the most common grass species over vast areas of low-elevation deserts. The morphology of Indian ricegrass seeds suggests that they are dispersed by animals. Its smooth, round seeds are large for a desert grass (1–3 mm in diameter, 2–5 mm in length) and lack awns or barbs to facilitate dispersal by wind or by adhesion. Indian ricegrass seeds are a highly preferred food for heteromyid rodents (McAdoo et al. 1983, Kelrick et al. 1986, Henderson 1990), so they are harvested and cached in abundance when available (McAdoo et al. 1983). Indian ricegrass seedlings often germinate and emerge from rodent seed caches in clumps of several dozen to several hundred (McAdoo et al. 1983; W. S. Longland, S. H. Jenkins, S. B. Vander Wall, J. A. Veech, and S. Pyare, *personal observations*). Caching may benefit germination in two major ways: (1) scatterhoarding results in shallow burial of seeds, where they are more likely to germinate than on the surface (Kinsinger 1962, Vander Wall 1990, 1993, Young et al. 1994); (2) cached seeds are less vulnerable to predation by other granivores and may also be less vulnerable to rodents other than the cacher itself (Vander Wall 1990).

If seedling recruitment comes largely from rodent caches, as in Vander Wall's (1994) bitterbrush–chipmunk system, then Indian ricegrass and desert rodents may be involved in a mutualistic interaction. Certainly rodents benefit from the food resource provided by Indian ricegrass seeds, but whether the grass benefits depends on how seed caching affects seedling establishment and on the abundance of unrecovered caches.

We conducted a field experiment in the Great Basin Desert of western Nevada using exclosures that were selectively permeable to granivorous ants, birds, and rodents to investigate the degree to which each of these granivore groups impact Indian ricegrass seedling recruitment. For two years we followed the fates of radiolabeled Indian ricegrass seeds in these exclosures from late summer or early autumn until the following spring or summer to test effects of different types of granivores on Indian ricegrass seedling recruitment. Our experiment was designed to answer three main questions:

- 1) What are the effects of seed predation by birds and ants and both seed predation and caching by rodents on seedling recruitment of Indian ricegrass?
- 2) Does seed caching by rodents reduce rates of seed predation by other granivores and enhance seedling recruitment of Indian ricegrass?
- 3) Is seedling recruitment from caches more affected by the probability of recovery by the individual animal that actually made the caches or by the probability of recovery by other animals that pilfer caches?

Based on our observations and on limited literature involving effects of seed-caching rodents on Indian ricegrass and other plants, we predicted the following results:

1) Seed caches (scatterhoards) made by rodents yield more seedlings than seeds not harvested by any granivores, because Indian ricegrass seeds benefit from burial by rodents. However, unharvested seeds yield more seedlings than seeds harvested by birds or ants, because birds consume seeds upon harvest and ants cache seeds at depths that rarely permit seedling emergence.

2) Seedling establishment is enhanced when rodents scatter-hoard seeds before nondigging granivores (i.e., birds and ants) can harvest them.

3) Cache-making rodents recover and consume their own scatterhoards, and thus reduce seedling recruitment from caches more than do cache pilferers. This is because rodents use both memory and olfaction to recover their own caches, but rely on olfaction alone when pilfering caches (Jacobs 1992, Vander Wall 1991).

STUDY AREA

The study was conducted on the western escarpment of the Hot Springs Mountains, ~14 km east of Fernley, Nevada (44°00' N, 119°05' W; Churchill County, Nevada, USA). The lower slopes of this basaltic mountain range are covered to varying depths by a veneer of fine sand, driven by wind from a large playa surface to the west. The sands support a dense population of Indian ricegrass and sparse growth of various desert shrub species, including *Sarcobatus baileyi*, *Atriplex confertifolia*, *A. canescens*, *Kochia americana*, *Psoralea polydenius*, *Tetradymia spinosa*, and *T. tetrameres*. Elevation of study plots ranged from 1280 to 1340 m.

The study area has a diverse assemblage of heteromyid rodent species and one sciurid rodent species (*Ammospermophilus leucurus*). Seed harvester ants are represented by *Pogonomyrmex salinas*. Granivorous bird species vary seasonally, but mainly include Black-throated Sparrows (*Amphispiza bilineata*), Sage Sparrows (*A. belli*), and Horned Larks (*Eremophila alpestris*). Although we included birds in our experimental design, they were quite uncommon at our site.

METHODS

Exclosures

We used 36 plots, arranged in three blocks of 12 with >200 m between plots within blocks and >500 m between plots on different blocks. Plots were systematically located in areas with relatively high Indian ricegrass densities to ensure that local soils were conducive to establishment of ricegrass seedlings. Each 5 × 5 m plot was used for seed dispersal, for long-term granivore exclusion, or for short-term confinement of rodents. We constructed exclosures during late winter and spring 1994. The main ("granivory") experiment used 33 plots (11 plots/block), and an additional experiment designed to test exclosure effects on Indian ricegrass seedling emergence used three plots (1 plot/block).

We simply marked corners of six plots (2 plots/block) with steel posts, but otherwise left them as unmanipulated controls. We fenced the remaining 30 plots (10 plots/block) with reinforced 0.6-cm mesh hardware cloth to control access by particular granivores. Fences extended 0.75 m aboveground and 0.5 m belowground. For 24 plots intended to exclude or contain rodents, we attached 30 cm wide strips of sheet aluminum horizontally around the top to deter rodent climbing. For exclosures designed to contain rodents temporarily (see *Methods: Experimental design*), we buried a wooden nestbox (30 × 30 × 20 cm height) just outside the plot. A 50 cm length of 5 cm diameter PVC tubing extended from an opening in the nestbox to just above the soil surface inside the exclosure. Four 7.5 × 7.5-cm holes (1 hole/side) were cut near ground level in each exclosure that allowed free access by rodents, and a 25 cm long tunnel fashioned out of sheet aluminum was fixed in each hole. From our experience with live traps of the same dimensions as these rodent-entry tunnels, we knew they would deter birds from entering. We covered 12 bird-exclusion plots with 5-cm mesh nylon netting. Ants could move freely through exclosure fences. To exclude ants, 30 cm wide strips of sheet aluminum were buried in the sand 40 cm outside the perimeters of 12 exclosures with 10 cm extending aboveground. We also used commercial ant traps and insecticides in these exclosures to prevent ant intrusion.

Experimental design

For the granivory experiment, we randomly assigned 11 plots per block to one of nine experimental treatments or to one of two unfenced control plots. Treatments fell into two categories. In one set of treatments, Indian ricegrass seeds were distributed in exclosures which, immediately following seeding, were either: (1) closed to all granivores ("no granivores" treatment), (2) accessible to "all granivores," (3) accessible to birds and ants but not rodents ("bird and ant"), or (4) accessible to "rodents" but not birds and ants. In the second set, we allowed a brief initial caching period after seeding during which a single Merriam's kangaroo rat (*Dipodomys merriami*) held within each exclosure could cache seeds. Initial caching treatments essentially forced a single animal to cache within each plot for a night, which could not be assured in rodent access plots without initial caching, and thus enabled us to measure effects of granivory subsequent to a relatively controlled level of caching. The exclosures certainly restricted rodents to caching in an area that was a small fraction of their typical home range size. However, we have noted that kangaroo rats often aggregate caches spatially, so confinement of cachers for a night should not have yielded unnaturally high cache densities. Moreover, caching behavior was apparently uninhibited inside exclosures, as confined animals generally cached avidly.

Following initial caching, the confined animal was

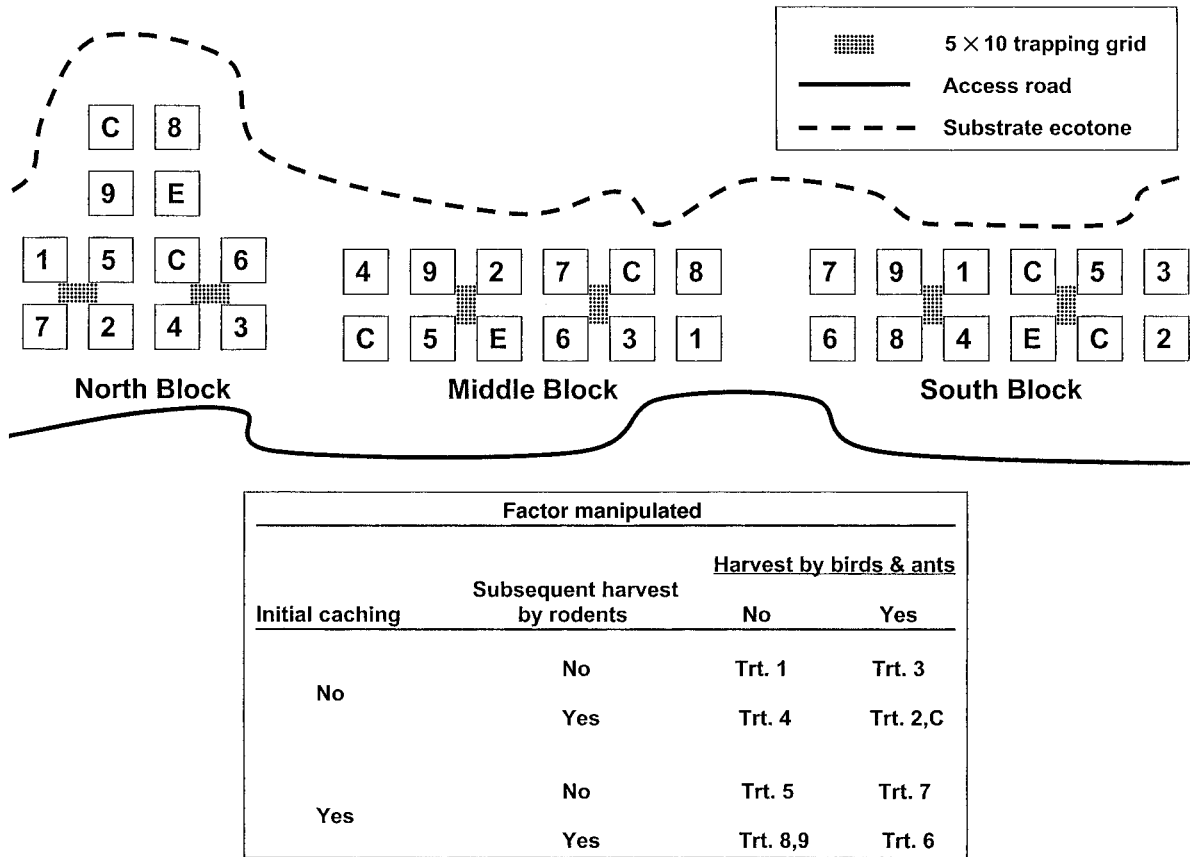


FIG. 1. Factorial structure of experimental treatments and schematic diagram of Hot Springs Mountains study site showing positions of control (C) plots, treatment (1–9) plots, and plots used to test for enclosure effects on seedling recruitment (E). The study plots were on a sand substrate (below substrate ecotone line; the substrate above the line was basalt). The figure is not drawn to scale. Plots were 5 × 5 m. Adjacent plots within each of the three blocks of 12 plots were separated by ≥200 m, while blocks of plots were separated by ≥500 m. The study plots extended an entire distance of ~3.5 km.

released and granivore classes were selectively permitted into or excluded from the plots in treatments 5–8 using the scheme outlined above for treatments 1–4, respectively. Thus, treatments 1–8 represented factorial combinations of three dichotomous factors: initial caching by a kangaroo rat, free access by rodents, and free access by birds and ants. Treatment 9 was identical to treatment 8 (initial caching, subsequent free access to rodents, no ant or bird access) except that the individual rodent used for initial caching in treatment 9 enclosures was removed from the study site and released elsewhere (“cache-maker exclusion” treatment). It was important to separate treatments 8 and 9 because a cache would likely have a greater probability of being recovered by the cache-maker than by a naive rodent. In treatments 6 (all granivores) and 7 (bird and ant), plots were accessible to birds and ants during the initial caching period, and in treatments 6, 8, and 9, rodents other than the single confined animal only gained access to plots following initial caching. Fig. 1 indicates the nature of the experimental treatments, including the factorial structure of treatments 1–8, and

shows a schematic diagram of assignment of plots to treatments.

We labeled commercial “Nezpar” Indian ricegrass seeds (Granite Seed, Lehi, Utah, USA), which are morphologically distinct from native ricegrass seeds at the study site, with radioactive scandium-46 for use in experiments. Scandium-46 is a gamma-emitting radionuclide that has been used as a tracer in other seed-fate studies (e.g., Abbott and Quink 1970, Vander Wall 1992, 1994). It is suitable for this application because the gamma rays that it emits penetrate ≥10 cm of soil, it has a sufficient half-life (84.5 d) to follow seeds up to a year but short enough that it persists in the environment <3 yr, and it is biologically inert. We adsorbed scandium-46 onto the coats of seeds by soaking 1.0 kg of seeds (~250 000 seeds) in a solution of 3.7 × 10⁵ kBq of scandium-46 and ~50 mL distilled water for 4–5 h and then drying the seeds. Laboratory seed-choice tests have shown that desert rodents do not prefer or avoid seeds labeled this way with scandium compared to unlabeled seeds (S. B. Vander Wall, unpublished data).

We conducted the granivory experiment twice between late summer/autumn 1994 and summer 1996, assigning treatments to the same plots both times due to the logistical difficulty of customizing exclosures to admit or exclude particular granivores. Each plot was supplied with 25 g (= 1.0 g/m²) of radiolabeled Indian ricegrass seeds, which is similar to the mean density of viable ricegrass seeds produced at a nearby site at the time of seed shed (McAdoo et al. 1983). Experimental seeds were spread evenly over a 1-m² area inside each plot once between 9 September and 28 October 1994 and again between 15 September and 2 November 1995. Seeds were placed in plots in the afternoon (between the hours of 1500 and 1700), which potentially exposed them to diurnal birds and ants for a few hours on plots that permitted all granivores before they were exposed to nocturnal rodents.

Experimental treatments that either admitted or restricted granivore access to plots were put into effect immediately upon seeding of control and treatment 1–4 plots. However, for treatments 5–9, we released a single *D. merriami* individual, captured within 25 m of the exclosure, in each plot near the opening to the artificial nestbox several hours before seeds were added. We chose similar numbers of male and female adult kangaroo rats for these initial caching treatments. Animals used for initial caching were generally confined for only one night, but were left a second night if >50% of the initial 25 g of radiolabeled seeds appeared to remain unharvested. Following initial caching, confined animals were released either immediately outside exclosures (treatments 5–8) or >5 km from their capture sites (treatment 9). Treatment 6, 8, and 9 exclosures were then opened to permit free access by rodents.

Relocating seeds

One day after seeding (2 d for plots with initial cachers confined for two nights), we searched plots for caches using portable Geiger counters (Eberline Model SPA-3 detector with ASP-1 recorder; Eberline Instruments, Santa Fe, New Mexico, USA), mapped all cache locations, and noted whether large numbers of labeled seeds remained unharvested. We also thoroughly searched for and mapped caches within a 15 m radius outside plots that were accessible to birds and ants only (treatments 3, 6, and 7) and within a 30 m radius of plots that were initially accessible to rodents (treatments 2, 4, and controls). Search distances were based on direct observations of ant foraging distances (generally <12 m for *Pogonomyrmex salinas* at our study site) and (using a night vision scope) of rodents making caches. For cases in which we located rodent caches 25–30 m outside a plot, we extended the search radius in 5-m increments until we no longer located additional caches. Rodents confined as cache-makers made larderhoards in both artificial nestboxes and previously existing burrows within exclosures. It was straightforward to identify caches as representing either an ant

larder, rodent larder, or rodent scatterhoard based on strength and diffusion of the Geiger counter signal and on presence of rodent burrows or ant colonies. We recorded maximum signal strength at ground level of each cache.

From 25 April to 10 August 1995 and from 10 May to 20 June 1996, we again used Geiger counters to systematically search inside all plots and within a 30 m radius around plots with granivore access. We mapped all rodent and ant larders and rodent scatterhoards and counted seedlings that had emerged from cached seeds or from seeds that remained unharvested by granivores within plots. While caches and small groups of unharvested seeds were still easily detectable during the spring/summer surveys, it was sometimes difficult to detect the label on a single seedling. Therefore, we carefully excavated all seedlings inside plots that may have emerged from unharvested seeds and examined the morphology of the seed coat adhering to each seedling to determine if it had emerged from an experimental “Nezpar” Indian ricegrass seed or from an indigenous seed. “Nezpar” was selected for reduced seed dormancy. We saw no evidence of extended dormancy in our tests for effects of scandium-46 or exclosures (see *Results: Isotope and exclosure effects on seedling establishment*) on seedling establishment, so dormancy should not have affected seedling counts. Some rodent seed caches still existed in their original positions from the previous year, but most had been recovered. New caches were often found, resulting from redistribution of seeds. Ant and rodent larders were generally buried too deeply to make excavation practical, so we usually just examined seedlings near larders to determine if they came from our experimental seeds.

Systematic plot searches and cache excavation took considerable time. To determine fate of rodent caches within a narrower time period, we used quick searches between 7 and 11 April 1995 and 5 and 23 April 1996 to check mapped locations of caches from the previous autumn’s trials and count seedlings emerging from original caches.

Exclosure and isotope effects on seedling recruitment

We used the second exclosure experiment to test for effects of exclosures on Indian ricegrass seed germination and seedling establishment. On 2 December 1994, we cached single Indian ricegrass seeds and clumps of 5, 25, 50, or 100 seeds both inside and outside three exclosures (1 exclosure/block) designed to exclude all granivores. We planted seeds in 5 × 10 Latin rectangle arrays in which each of 10 rows had the five seed densities represented in a unique order. To fit arrays inside exclosures, rows were separated by 0.5 m and planting locations within rows by 1.0 m. Arrays outside exclosures had 2.0-m spacing between and within all rows, with each cache covered by a 40 × 40-cm section of hardware cloth to protect them from

digging granivores. Seeds were planted precisely 3.0 cm deep by pushing a planting device consisting of a small metal pipe with a solid wooden dowel fitted snugly inside into the sand, removing the dowel, dropping the seeds down the pipe, removing the pipe, and back-filling the hole with sand. Seedling emergence from artificial caches began in mid-February 1995. We counted seedlings that established from each cache on 4 April 1995.

We tested for an effect of scandium-46 on seed viability during autumn 1995 by using the planting device to cache 10 paired clusters of 10 labeled and 10 unlabeled Indian ricegrass seeds 3 cm deep in three different locations (i.e., 10 such pairs/block). We covered each pair of caches with hardware cloth to protect them from rodents, and counted seedlings resulting from labeled vs. unlabeled seeds the following spring.

Censusing granivore populations

Rodents were censused using mark-and-release live-trapping during June, July, and August 1994; April, June, and November 1995; and April and June 1996. Two 5×10 station grids with 15 m separating all adjacent stations were established on each block of plots (Fig. 1). A single Sherman trap (H. B. Sherman, Tallahassee, Florida, USA) was opened and baited with bird seed mix at each station in evening and checked the following morning for three consecutive nights each trapping session. Captured animals were identified to species and sex, weighed, marked with uniquely numbered ear tags, and released at the point of capture.

We censused birds for three consecutive mornings on the south block of plots using line transects (Emlen 1971) at the same times that we conducted rodent trapping. Beginning at dawn, an observer slowly walked two parallel 1500-m transects separated by >200 m and recorded species, number, and locations of all birds seen or heard.

Attempts to quantify intensity of ant foraging by measuring seed removal by ants and ant visitation to dishes of Indian ricegrass seeds placed just outside each plot yielded variable results that probably depended on such factors as time of year and air and soil temperatures. It was clear, however, both from these trials and from our observations that each plot had at least one harvester ant colony within foraging distance.

Statistical analysis

Seedling recruitment.—Seedling-recruitment data were first analyzed with a three-way repeated measures analysis of variance (rmANOVA) excluding treatment 9 and control plots, because they involved additional differences not reflected in the factorial structure of treatments 1–8. The three treatment factors (initial caching, bird and ant access, and rodent access) were predictor variables and number of emerged seedlings was the response variable, which was repeated with respect to two additional factors: year (1995 or 1996)

and seedling source (unharvested seeds or rodent seed caches; all seedlings emerged from either unharvested seeds within plots, scattered rodent seed caches, or ant larders, but so few emerged from the latter that this category was excluded from analysis). The initial caching term in the three-way rmANOVA was included in several complex interactions that seemed to be due to just one of our treatments. Therefore, we also did separate rmANOVAs for plots with no initial caching and for those that included initial caching (dropping the initial caching factor for these two analyses), and we focused on these for interpreting effects of treatment factors on seedling recruitment. To further explore potential effects of individual treatments, in addition to rmANOVAs on treatment factors, we ran one-way rmANOVAs on “treatment”: a 10-level predictor variable that included all nine experimental treatments and control plots. Seedling count distributions were skewed to the left due to numerous zero values. Therefore, for seedling recruitment analyses we added 0.5 to the number of established seedlings (to remove zeros) and used the square-root transformation of the result as the response variable to meet assumptions of normality and homoscedasticity (Sokal and Rohlf 1981). Data from two plots were excluded from seedling recruitment analyses. The cache-making animal confined to a 1994 treatment 6 plot for initial caching died during the trial, and a treatment 1 plot (no granivores) was breached by a rodent during winter 1995–1996. Because the three-way ANOVA on treatment factors required balanced data, we imputed these two missing values, and reduced the error df by one in the analyses of both treatments 1–4 and 5–8 accordingly. We initially ran all of the above rmANOVAs using block as an additional predictor variable, but it had no significant effect in any analysis, so it was dropped.

For the rmANOVA using treatment as the predictor variable, we used planned comparisons to test five specific hypotheses. These addressed potential mechanisms of granivore–Indian ricegrass interactions by comparing selected pairs of treatments. The hypotheses, and the paired treatment comparisons used to test them, are as follows:

Hypothesis 1: Rodent seed caching benefits Indian ricegrass by placing seeds in a microenvironment where germination and establishment are more likely (treatment 5 vs. 1: no granivores, with and without initial caching).

Hypothesis 2: Seed caching benefits Indian ricegrass by removing seeds from possible predation by birds or ants (treatment 7 vs. 3: seeds available for harvesting by birds and ants, but differed in whether they had initial caching by a rodent).

Hypothesis 3: The net effect of seed harvesting by rodents benefits Indian ricegrass, because seeds are placed in a microenvironment where germination and emergence are more likely, and some seeds escape subsequent recovery and consumption by rodents (treat-

ment 1 vs. 4: both had no initial caching by rodents and no seed harvesting by birds and ants, but differed in whether harvesting by rodents was permitted).

Hypothesis 4: The net effect of seed harvesting by rodents benefits Indian ricegrass germination, because seeds are protected from predation by birds and ants (treatment 2 vs. 3: both had seed harvesting by birds and ants and no initial caching by rodents, but differed in subsequent accessibility to rodents).

Hypothesis 5: Caching benefits Indian ricegrass by making seeds less likely to be discovered and consumed by individual rodents other than the original cache-maker (treatment 8 vs. 9: both had initial caching by a rodent and subsequent harvest by rodents only, but differed in whether the original cache-maker had access).

Additionally, we used another planned contrast to test an hypothesis concerning effects of enclosure fences.

Hypothesis 6: Fences had no effect on seedling recruitment (control vs. treatment 2: all factors the same except whether the plot was fenced).

Predicted patterns of seedling recruitment.—We predicted a priori how experimental treatments would rank with regard to numbers of seedlings established from rodent scatterhoards, and used isotonic regression (Gaines and Rice 1990) to compare expected and observed ranking patterns. We expected to find more seedling recruitment from caches in initial caching treatments (treatments 5–9) than in treatments without initial caching, because confining a kangaroo rat inside plots should ensure that most experimental seeds in these plots were scatter-hoarded. Among the five treatments with initial caching, we expected the following descending order of seedling recruitment from scatterhoards: (1) Treatment 5 (no granivores): the cache-making animal had no competition for labeled seeds and caches could not be recovered later. (2) Treatment 7 (bird and ant): ants and birds could reduce numbers of seeds available to the cache-maker, but caches should not be recovered later, because only nondigging granivores had subsequent access to plots. (3) Treatment 9 (cache-maker exclusion): only rodents naive to seed cache locations could recover them after initial caching. (4) Treatment 8 (rodents only after initial caching): caches could be recovered by any rodents, including the cache-maker. (5) Treatment 6 (all granivores): ants could harvest some seeds during the initial caching period and all rodents had subsequent access to plots. Among treatments with no initial caching, rodents had access to only treatments 4 and 2, so these should rank highest for seedling recruitment from caches, or sixth and seventh overall. (6) Treatment 4 (rodents only) should rank higher than (7) treatment 2 (all granivores) for the same reasons that treatment 8 should outrank treatment 6. Finally, treatments 1 and 3, respectively, should rank lowest, because these plots were never accessible to rodents. (8) Treatment 3 (bird

and ant): rodents could pilfer some seeds removed by ants and cache them outside plots, yielding a small number of scatterhoards. (9) Treatment 1 (no granivores): complete inaccessibility of seeds prevented caching. To summarize, our predicted ranking pattern for seedling recruitment from seed caches in treatments was: $5 > 7 > 9 > 8 > 6 > 4 > 2 > 3 > 1$. In addition to comparing this predicted ranking to the observed ordering of seedling recruitment from caches, we compared it to the observed order of recruitment from unharvested seeds and from all seeds (cached and unharvested) to test whether any agreement between observed and expected ranks was a general phenomenon or was unique to seedlings from seed caches.

Seed caching.—We used rmANOVA models on the late summer/autumn seed-caching data with treatment as a predictor variable and either number of rodent caches (scattered caches and larders) or number of ant larders (both repeated over the two years of the study) as the response variables to test for treatment effects on caching rates of these two granivore classes. Data from the 1994 treatment 6 plot in which the cache-maker died were excluded. We used planned comparisons to test for enclosure effects on rodent caching behavior by comparing treatment 2 with control plots. This addressed the null hypothesis that rodents were equally likely to harvest or cache seeds in enclosures with access holes as in plots of the same size without fences. We also tested for competitive effects of ants on caching by rodents by comparing treatments 2 and 4, both of which allowed access by rodents, but differed in that the latter excluded ants and birds. For the rmANOVA on numbers of ant larders, we tested for enclosure effects as above (treatment 2 vs. controls) and for competitive effects of rodents on seed-caching by ants (treatments 2 vs. 3: all granivores vs. bird and ant treatments, respectively; and treatments 7 vs. 3: bird and ant treatments with and without initial caching, respectively).

As an additional test for competitive effects of ants on rodents and vice versa, we used Mann-Whitney *U* tests on the combined 1994 and 1995 late summer/autumn data to compare seed storage by ants and rodents on plots that were used by both of these granivores vs. those that were used exclusively by one or the other. In two analyses, we used data from plots that allowed caching by both rodents and ants to compare total numbers of rodent caches (scatterhoards and larderhoards), and sum of Geiger counter activity readings from these caches on plots where ants stored no seeds vs. plots where ants stored seeds before they were exhausted by rodents. There were no plots accessible to both ants and rodents that were used only by ants. Therefore, as a similar test for competitive effects of rodents on ant foraging, we compared sum of activity readings from ant larders on plots with vs. without rodent access.

As an indication of cache dynamics and recovery

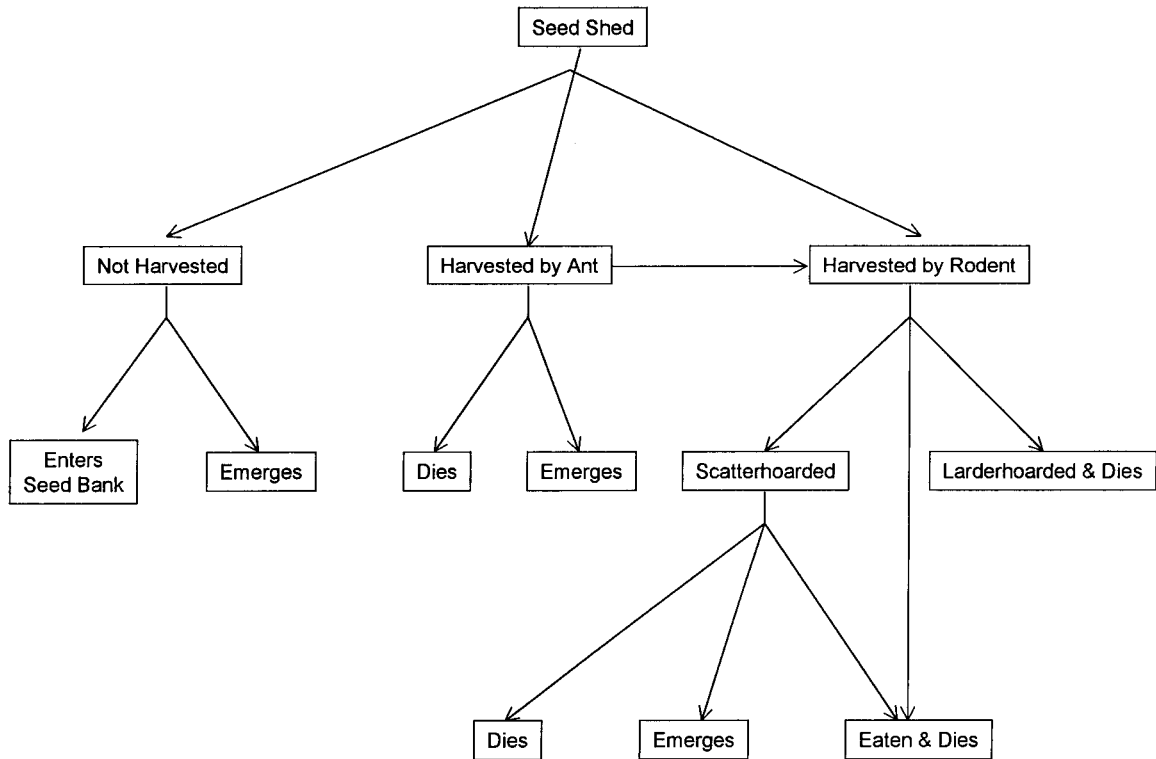


FIG. 2. Fate diagram for Indian ricegrass seeds subject to harvest by rodents and ants. The pathway from seeds initially harvested by ants to subsequent harvest by rodents was based on our own observations and those of Clark and Comanor (1973).

rates by rodents, we used paired *t* tests on all plots that permitted free access by rodents (i.e., controls and treatments 2, 4, 6, 8, and 9) to compare numbers of rodent scatterhoards made during autumn seed-caching trials vs. numbers of these original caches that remained intact during quick searches the following spring, and also vs. total numbers of scatterhoards (original and redistributed caches) found during spring/summer systematic searches. We also compared numbers of original autumn scatterhoards remaining during spring quick searches to numbers of scatterhoards found during spring/summer systematic searches.

Exclosure effects.—We ran a three-way ANOVA on seedling establishment data from treatment 2 to test the null hypothesis that exclosures had no effect on the net probability of Indian ricegrass seed germination and seedling establishment. Predictor variables were block, number of seeds per cache, and exclosure (inside vs. outside), and the dependent variable was number of established seedlings per cache.

Seed fate model

We developed a fate diagram (Price and Jenkins 1986, Vander Wall 1994) to evaluate the net effects of rodents and ants on establishment of Indian ricegrass (Fig. 2). Because our experimental design precluded separation of the probability of a seed being scatter-

hoarded if harvested by a rodent from the probability of a seedling emerging if scatter-hoarded, we used simplified fate diagrams (Fig. 3) to estimate probabilities of seedling emergence for unharvested seeds, seeds harvested by ants, and seeds harvested by rodents. We used three sets of treatments for these calculations: those with no access by granivores (treatment 1), those with access by rodents but not ants (treatments 4, 8, and 9), and those with access by ants but not rodents (treatment 3). For treatment 1, we modeled emergence as a simple binomial process with probability q_0 . For treatments 4, 8, and 9, we modeled emergence as a two-stage multinomial process. At the first stage, seeds were harvested by rodents with probability p_r . If harvested, they were scatter-hoarded and emerged from a scatterhoard with probability q_r . If unharvested, they emerged with probability q_0 , as in treatment 1. We modeled the results of treatment 3 similarly, with p_a = the probability of a seed being harvested by an ant and q_a = the probability of a seedling emerging from an ant larder. Due to the rarity of granivorous birds and lack of Indian ricegrass seed consumption by birds at our study site, we did not consider them in the seed fate model.

We estimated the probability of emergence of an unharvested seed, q_0 , as $\sum X_{0,i} / \sum N_i$ (Fig. 3a), where $X_{0,i}$ = the number of seedlings emerging from unharvested

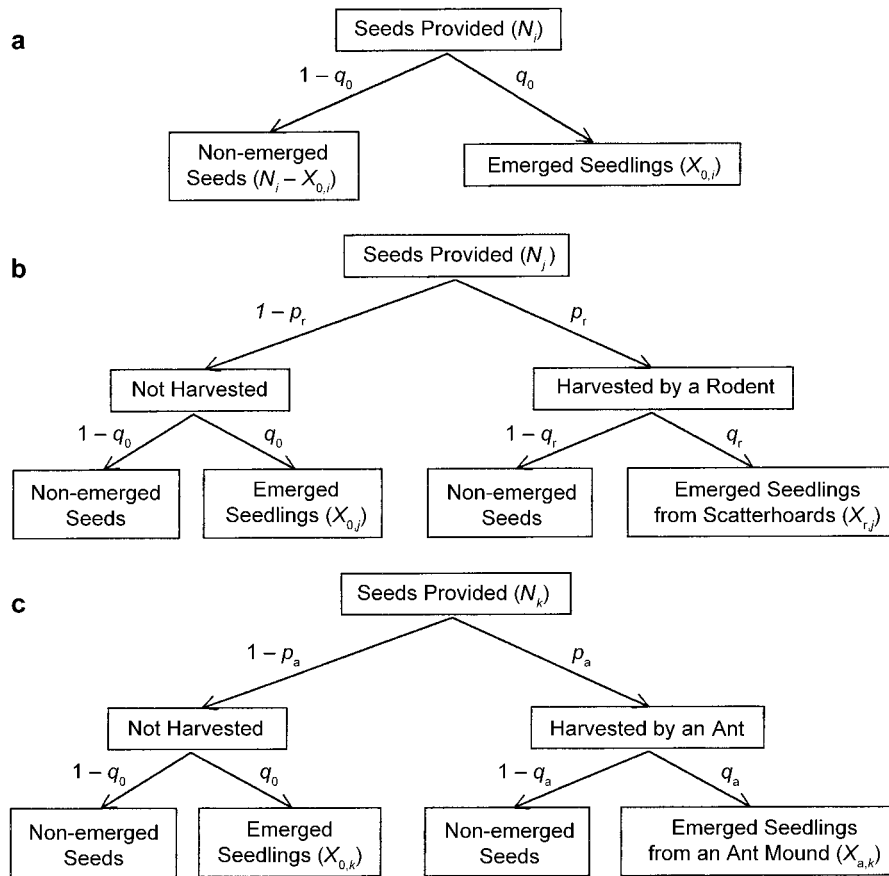


FIG. 3. Simplified seed-fate diagrams used for maximum-likelihood estimation of probabilities of harvest and emergence of Indian ricegrass seeds. Model parameters include probabilities of seed harvest by rodents (p_r) and ants (p_a) and probabilities of seedling emergence from unharvested seeds (q_0), seeds harvested by rodents (q_r), and seeds harvested by ants (q_a). Treatments accessible to neither ants nor rodents provided data for estimating the parameters in (a), treatments accessible to rodents only provided data for (b), and treatments accessible to ants only provided data for (c). In (b), the sum of the two boxes labeled non-emerged seeds was $N_j - X_{0,j} - X_{r,j}$; in (c), this sum was $N_k - X_{0,k} - X_{a,k}$.

seeds and N_i = the number of seeds provided in replicate i of treatment 1. We estimated p_r , probability of harvest by a rodent, as $1 - (\sum X_{0,j} / \sum N_j) / q_0$ (Fig. 3b), where $X_{0,j}$ = the number of seedlings emerging from unharvested seeds and N_j = the number of seeds provided in replicate j of treatment 4, 8, or 9. We estimated q_r , probability of emergence from a rodent scatterhoard, as $\sum X_{r,j} p_r / \sum N_j$ (Fig. 3b), where $X_{r,j}$ = the number of seedlings emerging from scatterhoards in replicate j of treatment 4, 8, or 9. Probability of harvest by an ant and probability of emergence from an ant larder were estimated similarly using Fig. 3c. These are maximum-likelihood estimates of the parameters.

We used a bootstrap method to calculate 95% confidence intervals for these parameters. For each of 1000 trials, we selected plots randomly but with replacement from among those for each type of treatment (no granivore access [treatment 1], access by rodents but not ants [treatments 4, 8, and 9], and access by ants but not rodents [treatment 3]). We used data on numbers

of seeds supplied (N_i , N_j , or N_k), numbers of unharvested seeds emerging as seedlings ($X_{0,i}$, $X_{0,j}$, or $X_{0,k}$), numbers of seedlings emerging from rodent scatterhoards ($X_{r,j}$), and numbers of seedlings emerging from ant larders ($X_{a,k}$) to calculate the sums in the above equations, and thus to estimate the parameters of the model. For each parameter, the 2.5th and 97.5th percentiles defined the 95% confidence interval.

RESULTS

Granivore populations

Four heteromyid rodent species and one sciurid species (*Ammospermophilus leucurus*) were live trapped routinely during the course of the study; *Dipodomys merriami* was the most common species on all six trapping grids (Table 1). Recapture rates of individual *D. merriami* suggested a much higher mortality rate during the first than the second winter of the study. The mean proportion (± 1 SD) of *D. merriami* individuals captured

TABLE 1. Number (and relative percentage) of trap captures per year of four common heteromyid rodent species and one sciurid species (*Ammospermophilus leucurus*) at the study site, 1994–1996.

Species	Year (number of trap-nights)					
	1994 (2700)		1995 (2100)		1996 (1800)	
	No. captures (percentage of captures)	Capture rate (%)	No. captures (percentage of captures)	Capture rate (%)	No. captures (percentage of captures)	Capture rate (%)
<i>Ammospermophilus leucurus</i>	35 (4.4)	1.3	87 (28.7)	4.1	64 (11.9)	3.6
<i>Dipodomys deserti</i>	98 (12.2)	3.6	43 (14.2)	2.0	37 (6.9)	2.1
<i>Dipodomys merriami</i>	492 (61.3)	18.2	95 (31.4)	4.5	270 (50.1)	15.0
<i>Microdipodops pallidus</i>	71 (8.8)	2.6	51 (16.8)	2.4	78 (14.5)	4.3
<i>Perognathus longinervis</i>	107 (13.3)	3.9	27 (8.9)	1.3	90 (16.7)	5.0

Notes: Numbers, which are based on six 50-trap grids and variable trapping effort per year, are also given as capture rates standardized across years by the number of trap-nights. Capture rate = (number of captures/number of trap-nights) × 100.

per trap grid in 1995 that had been previously captured in 1994 was 0.046 (± 0.217), whereas the same proportion for 1995–1996 was 0.297 (± 0.217).

Granivorous birds were uncommon throughout the study area. From 1994 to 1996, mean numbers of granivorous birds seen or heard per km walked on bird transects were 0.9–2.2 for *Amphispiza bilineata*, 0.6–1.5 for *A. belli*, and 0.2–0.8 for *Eremophila alpestris*. All other species combined amounted to only 0.1–0.4 individuals/km. Birds were so rare at the site that they had little or no effect on our bird and ant treatments, which could therefore effectively be considered as just ant treatments. When we seeded plots, we found only one case (a bird and ant plot in 1995) of tracks indicating probable ground foraging by birds. During our ant-foraging trials, all plots were within range of at least one or two ant colonies, but three colonies foraged in the vicinity of at least two of the 33 plots.

Treatment effects on seedling establishment

In all treatments with either initial caching or continuous access by rodents, the greatest number of established seedlings came from rodent scatterhoards; this usually exceeded the number of seedlings from unharvested seeds by more than an order of magnitude

(Table 2). Seldom did any seedlings establish from ant larders, and we only found one seedling emerging from a rodent larder during the entire experiment (Table 2).

The rmANOVA on treatment factors for initial caching plots (treatments 5–8) revealed a significant effect of seedling source ($F = 46.25$, $df = 1,7$, $P < 0.001$). Seed caches yielded more seedlings (usually far more) than unharvested seeds in all of these treatments. The year × rodent × bird and ant interaction was significant ($F = 5.99$, $df = 1,7$, $P < 0.05$), because the greatest number of total seedlings established on plots that restricted access to both ants and rodents (treatment 5), and access by both (treatment 6) reduced the number of seedling recruits much more dramatically in 1996 than in 1995. However, several other significant terms in this analysis were due solely to the much greater number of seedlings in treatment 5 (initial caching, no subsequent granivore access) than in others (Table 2). For example, the rodent ($F = 10.31$, $df = 1,7$, $P < 0.025$) and bird and ant ($F = 12.41$, $df = 1,7$, $P < 0.01$) terms and their interaction ($F = 15.65$, $df = 1,7$, $P < 0.01$) were all significant, because treatment 5 was not accessible to either rodents or ants and treatments with any other combination of rodent and ant accessibility had many fewer seedlings.

TABLE 2. Mean number (± 1 SE) of Indian ricegrass seedlings recruited per plot from rodent scatterhoards, unharvested seeds, ant larders, and rodent larders at Hot Springs Mountains study area, 1995–1996.

Initial caching	Rodents	Ants	Treatment	Mean number (\pm SE) of seedlings				
				Scatterhoards	Unharvested seeds	Ant larders	Rodent larders	Larderhoards
No	Yes	Yes	Control	21.1 (17.7)	1.4 (1.2)	0	0	0
No	No	No	1	0	29.2 (12.3)	0	0	0
No	Yes	Yes	2	12.3 (6.9)	2.5 (2.5)	0.5 (0.5)	0	0
No	No	Yes	3	14.0 (12.5)	26.7 (12.7)	1.3 (1.2)	0	0
No	Yes	No	4	54.2 (30.0)	2.0 (0.8)	0	0	0.2 (0.2)
Yes	No	No	5	589.3 (147.5)	1.7 (1.0)	0	0	0
Yes	Yes	Yes	6	51.0 (33.1)	2.2 (2.2)	0.2 (0.2)	0	0
Yes	No	Yes	7	9.3 (4.0)	4.2 (2.2)	0	0	0
Yes	Yes	No	8	27.8 (14.0)	0.8 (0.8)	0	0	0
Yes†	Yes†	No	9	34.5 (16.2)	0.2 (0.2)	0	0	0

† Cache-maker exclusion. Treatments 8 and 9 differed only in that the kangaroo rats that made caches in treatment 9 plots were removed from the area subsequent to confinement within plots.

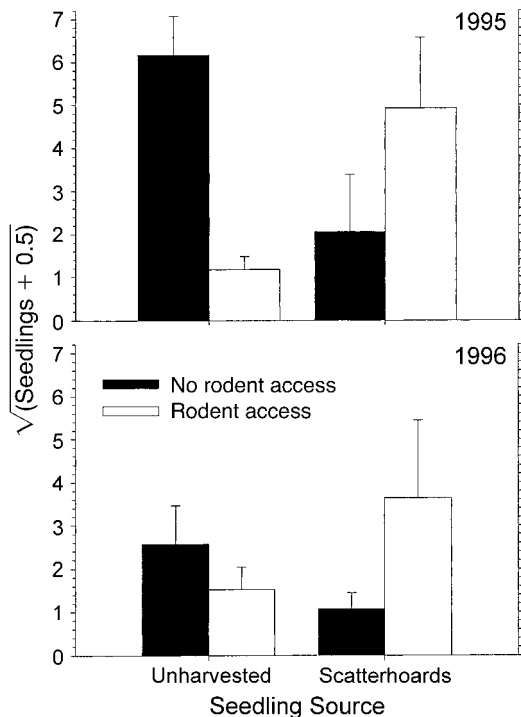


FIG. 4. Emergence of Indian ricegrass seedlings from seeds in rodent scatterhoards and from unharvested seeds in plots with vs. without rodent access. Data have been square-root ($x + 0.5$) transformed. Emergence of seedlings from scatterhoards around plots that excluded rodents was due to rodents stealing seeds from ant larders outside plots accessible exclusively to ants. Error bars represent $+ 1$ SE.

Results of rmANOVA on treatments 1–4, with no initial caching, were quite different: seedling source \times rodent was the only significant term ($F = 16.59$, $df = 1,7$, $P = 0.005$). This was because, in both years of the study, rodent access to plots without initial caching reduced seedling recruitment from unharvested seeds, but yielded a concomitant and roughly equivalent increase in recruitment from scatterhoards (Fig. 4).

As expected, rmANOVA with treatment as the single class variable indicated significant variation among the nine experimental treatments and control plots ($F = 11.95$, $df = 9,21$, $P = 0.0001$). One repeated factor, year, had no significant effect on seedling recruitment ($F = 3.33$, $df = 1,21$, $P = 0.08$), nor did any interaction terms that included year ($P > 0.30$). However, seedling source ($F = 42.63$, $df = 1,21$, $P < 0.0001$) and seedling source \times treatment ($F = 15.29$, $df = 9,21$, $P < 0.0001$) were significant, because scatterhoards generally yielded many more seedlings than unharvested seeds, yet treatments differed in relative numbers of seedlings from these two sources.

Of the five planned comparisons used to test specific hypotheses concerning seedling recruitment, only the treatment 1 vs. 5 contrast was significant ($F = 43.34$, $df = 1,21$, $P = 0.0001$). Thus, we cannot reject Hypothesis 1; that scatter-hoarding enhances seedling re-

cruitment by placing seeds in a favorable microenvironment for germination and establishment. No other planned comparisons approached statistical significance (all $P > 0.28$); perhaps most importantly, rejection of Hypothesis 6 ($F = 0.06$, $df = 1,21$, $P = 0.81$) implies that fences surrounding exclosures had no effect on seedling recruitment. An insignificant interaction between the latter contrast and seedling source ($F = 0.003$, $df = 1,21$, $P = 0.95$) further implies that fenced plots did not affect seed caching by rodents nor burial of unharvested seeds by wind-blown sand. Rejection of Hypothesis 3 ($F = 0.29$, $df = 1,21$, $P = 0.38$) indicates that rodent access to treatment 4 plots did not significantly affect overall seedling recruitment relative to treatment 1 (both lacked initial caching, but the latter also prohibited all granivores). This contrast did, however, interact significantly with seedling source ($F = 10.12$, $df = 1,21$, $P = 0.005$), because all treatment 1 seedlings came from unharvested seeds, while 96% of treatment 4 seedlings came from scatterhoards (Table 2). The latter results, together with the seedling source \times rodent interaction in the analysis of treatment factors for treatments without initial caching, indicate that the apparent trade-off in recruitment from scatterhoards vs. unharvested seeds in Fig. 4 is compensatory.

Predicted patterns of seedling recruitment.—For both years of the experiment isotonic regressions indicated significant concordance between expected and observed treatment ranking patterns of seedling emergence from rodent scatterhoards (Fig. 5; one-tailed $P = 0.001$ for both years). Because seedlings from scatterhoards constituted the vast majority of all seedlings, our expected ordering for scatterhoards also successfully predicted total seedling recruitment with results that were qualitatively (and nearly quantitatively) identical to the previous analysis. The expected order from scatterhoards did not, however, successfully predict the observed order of seedling establishment from unharvested seeds in either year (Fig. 5; 1995, one-tailed $P = 0.92$; 1996, one-tailed $P = 0.84$).

Isotope and exclosure effects on seedling establishment

Number of established seedlings from seeds planted inside and outside exclosures differed significantly among cache sizes ($F = 756.0$, $df = 4,270$, $P < 0.001$), as expected, but percentage of seeds that established seedlings was similar for all cache sizes (Table 3). Seedling establishment did not differ among blocks ($F = 0.94$, $df = 2,270$, $P = 0.39$) or inside vs. outside exclosures ($F = 0.18$, $df = 1,270$, $P = 0.68$), so fencing of plots should not have affected levels of seedling recruitment (Table 3).

ANOVA on effects of scandium-46 and blocks on seedling establishment in our artificial Indian ricegrass caches indicated no significant block effect ($F = 1.06$, $df = 2,54$, $P = 0.36$), so we pooled all 30 pairs of labeled and unlabeled seeds and used a paired com-

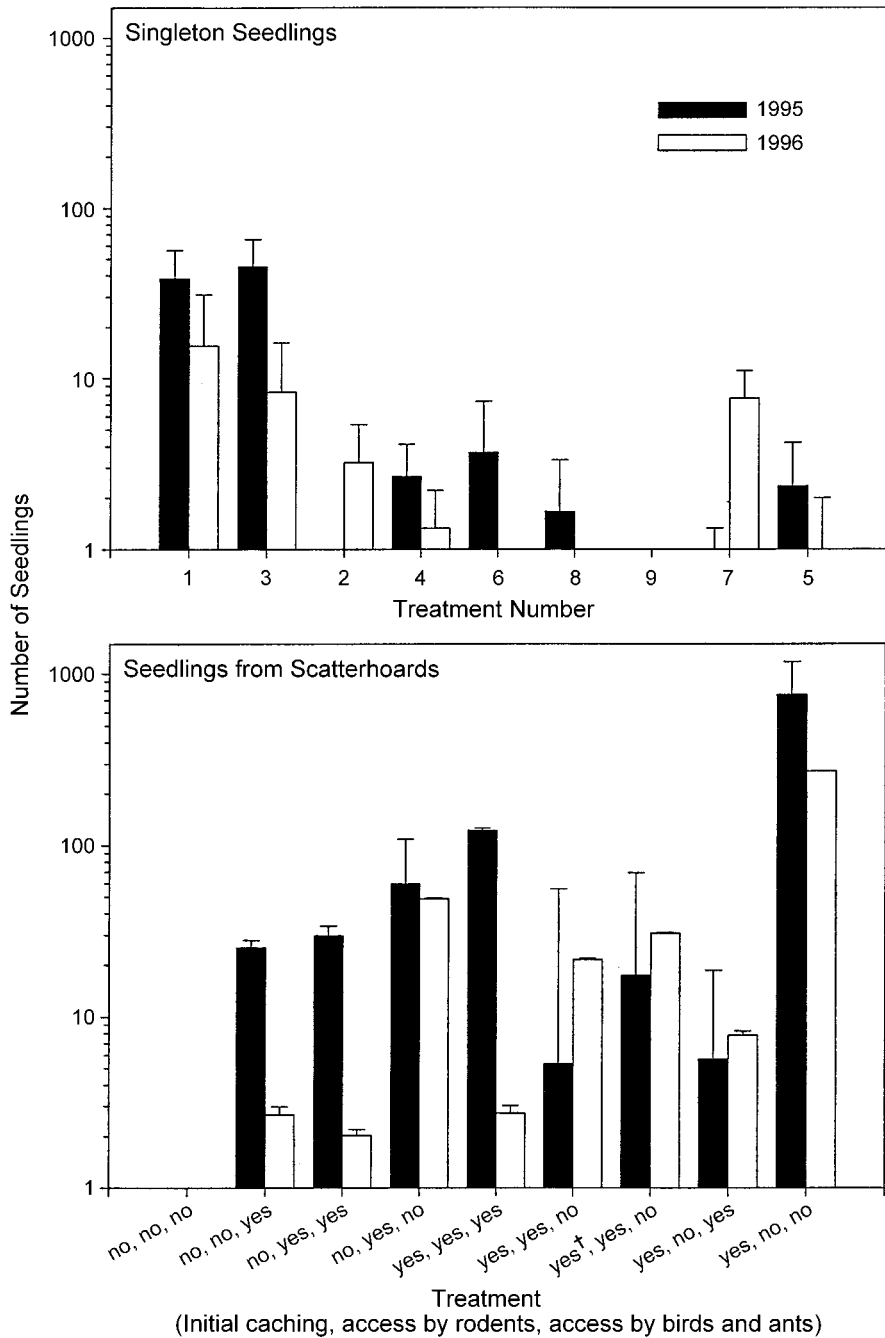


FIG. 5. Emergence of Indian ricegrass seedlings from experimental plots ordered along x-axis by a priori expectation of rank order of emergence from rodent scatterboards (x-axis labeled as treatment numbers in upper panel and as combinations of treatment factors corresponding to treatment numbers in lower panel). Isotonic regression indicated that the expected and observed rankings matched significantly for seedlings from scatterboards (lower panel) and for overall seedling recruitment (not shown) but did not match for singleton seedlings from unharvested seeds (upper panel). The dagger symbol indicates the cache-maker exclusion treatment. Error bars represent + 1 SE.

parisons *t* test to test for an isotope effect. Mean emergence rates of Indian ricegrass seedlings did not differ between paired clumps of 10 radiolabeled seeds (62.7% of seeds germinated and emerged) and 10 unlabeled seeds (63.3%; *t* = 0.15, *df* = 29, *P* = 0.88).

Treatment effects on seed caching, seed dispersal, and cache recovery

Rodent scatterboards so vastly outnumbered larderboards (Table 4) that the following results of rm-

TABLE 3. Mean number of Indian ricegrass seedlings established (\pm SD) and percentage of seeds that emerged as seedlings at five seed planting densities inside versus outside exclosures.

Seed density	Inside exclosures		Outside exclosures	
	Number of seedlings	Seedling emergence (%)	Number of seedlings	Seedling emergence (%)
1	0.83 (0.38)	83.3	0.73 (0.45)	73.3
5	3.73 (1.26)	74.7	3.80 (1.37)	76.0
25	19.30 (4.97)	77.2	18.77 (3.51)	75.1
50	36.93 (9.02)	73.9	36.33 (8.12)	72.7
100	67.20 (15.82)	67.2	70.27 (12.52)	70.3

Notes: Seeds were planted 3 cm deep in December 1994, and seedlings were counted in April 1995. $N = 30$ replicate plantings both inside and outside exclosures for all seed densities.

ANOVA using total number of rodent caches as the response variable were qualitatively identical to those obtained using number of scatterhoards. As expected, numbers of both rodent caches and ant larders varied widely among treatments (Table 4). Number of caches per plot differed significantly among treatments (rodent caches, $F = 3.25$, $df = 9,22$, $P = 0.01$; ant larders, $F = 8.08$, $df = 9,22$, $P = 0.0001$), but not between years (rodents, $F = 0.56$, $df = 1,22$, $P = 0.46$; ants, $F = 0.59$, $df = 1,22$, $P = 0.45$). Planned comparisons contrasting controls vs. treatment 2 exclosures, which admitted all granivores, indicated that caching rates were unaffected by exclosure fences (rodent caches, $F = 2.59$, $df = 1,22$, $P = 0.12$; ant larders, $F = 0.0$, $df = 1,22$, $P = 1.0$). Planned comparisons indicated that there were significantly more ant larders associated with plots that excluded rodents than on plots that either had initial caching (Treatments 3 vs. 7: $F = 7.75$, $df = 1,22$, $P = 0.01$) or continuous rodent access (Treatments 2 vs. 3: $F = 15.18$, $df = 1,22$, $P = 0.0008$). Comparisons of Geiger counter activity readings associated with ant larders on plots with and without rodent access also indicated competitive effects of ro-

dent in reducing seed caching by ants (Fig. 6; U test, $P = 0.001$).

Comparison of treatments 2 and 4 (no initial caching with access to all granivores vs. only rodents) suggested that ants did not significantly reduce numbers of caches made by rodents ($F = 1.43$, $df = 1,22$, $P = 0.25$), perhaps because ants did not store seeds on all plots to which they had access. In some plots, virtually all seeds were removed by rodents before being discovered by ants, while in others the small number of caches made during initial caching suggested that ants rapidly removed the majority of seeds during daylight before the nocturnal rodent in the plot became active (cf. number of caches made in treatments 7 vs. 5: Table 4). In contrast to these rmANOVA results, comparisons of plots where ants stored seeds vs. those where they did not implied that ants competitively reduced seed caching by rodents (Fig. 6); rodents made significantly more caches where ants failed to store seeds ($P = 0.014$), and, to a lesser extent, Geiger counter readings from rodent caches were reduced where ants stored seeds ($P = 0.056$).

Paired t test results for separate years on numbers of scatterhoards found during plot searches were qualitatively identical to those based on data pooled over the two years, so we present only the pooled results. Number of original scatterhoards made during autumn trials had declined significantly during quick searches the following spring ($t = 4.70$, $df = 36$, $P = 0.0001$), indicating that rodents recovered the majority of caches. However, rodents also made many new scatterhoards by redistributing caches. The number of scatterhoards (original plus new) found during spring/summer systematic searches significantly exceeded original autumn scatterhoards that remained during spring quick searches ($t = 2.38$, $df = 36$, $P = 0.023$). New scatterhoards made through cache redistribution did not, however, compensate for removal of original scatterhoards, as significantly more scatterhoards were made during autumn seed caching trials than numbers found during spring/summer systematic searches ($t = 3.83$, $df = 36$, $P = 0.0005$).

TABLE 4. Mean number (± 1 SE) of Indian ricegrass seed caches per plot placed in scatterhoards and larders by rodents and in larders by ants at the Hot Springs Mountains study area, 1994–1995.

Initial caching	Rodents	Ants	Treatment	Mean number (\pm SE) of seed caches		
				Scatterhoards	Larderhoards	Ant larders
No	Yes	Yes	Control	15.5 (4.2)	1.0 (0.3)	0.7 (0.2)
No	No	No	1	0 (0)	0 (0)	0 (0)
No	Yes	Yes	2	22.8 (6.4)	1.0 (0.4)	0.7 (0.3)
No	No	Yes	3	0 (0)	0 (0)	1.8 (0.3)
No	Yes	No	4	15.7 (7.7)	0.7 (0.4)	0 (0)
Yes	No	No	5	16.7 (1.9)	1.2 (0.2)	0 (0)
Yes	Yes	Yes	6	10.2 (2.4)	0.6 (0.4)	0.8 (0.4)
Yes	No	Yes	7	2.0 (0.6)	1.2 (0.4)	1.0 (0.3)
Yes	Yes	No	8	8.8 (3.2)	1.7 (0.3)	0 (0)
Yes†	Yes†	No	9	10.2 (2.6)	1.3 (0.3)	0 (0)

† Cache-maker exclusion. Treatments 8 and 9 differed only in that the kangaroo rats that made caches in treatment 9 plots were removed from the area subsequent to confinement within plots.

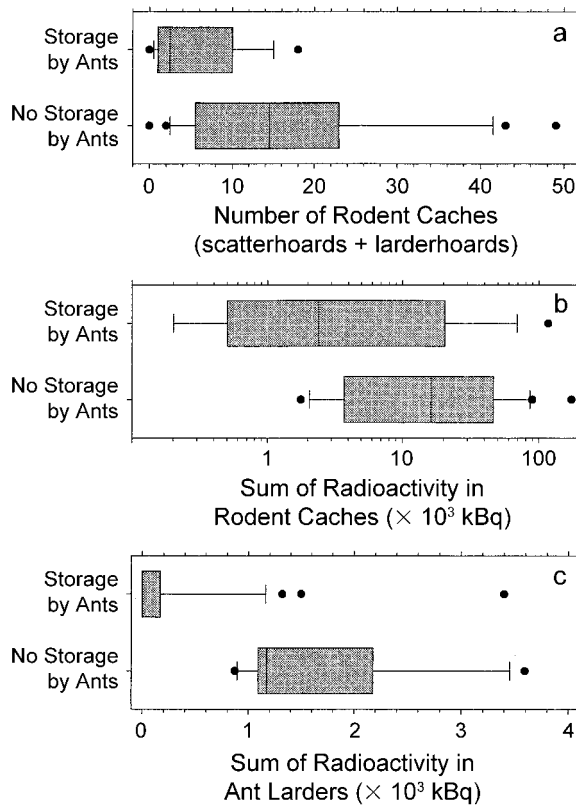


FIG. 6. Seed caching levels by rodents, in terms of (a) number of caches made and (b) radioactivity of caches, in the presence vs. absence of seed storage by ants; and (c) radioactivity of ant larders in plots with vs. without rodent access. Caching levels were lower for rodents in the presence of ants and lower for ants in the presence of rodents. The interior line in each box is the median, ends of boxes are 25th and 75th percentiles, whiskers are 10th and 95th percentiles, and points are outliers. The scale in (b) is logarithmic.

Seed fate

Although Fig. 2 provides a conceptual model of the various possible fates of an Indian ricegrass seed shed by a parent plant, our experiments were not designed to yield estimates of the probabilities of each of the transitions in this fate diagram. However, we were able to use our experimental results to estimate five key parameters: probability of seed harvest by rodents in the absence of ants and by ants in the absence of rodents, probability of seed emergence if unharvested,

and probability of emergence if harvested by a rodent and if harvested by an ant. Probability of emergence if harvested by a rodent is the product of the probability of a seed being scatter-hoarded and the probability of surviving and emerging if it is scatter-hoarded. Even though we cannot separate these two components, the probability of emergence if harvested by a rodent represents the net effect of rodent harvesting on Indian ricegrass establishment.

From analysis of simplified fate diagrams (Fig. 3), we estimated that rodents harvested ~96% of seeds from plots to which they had exclusive access and ants harvested ~7% of seeds from plots to which they had exclusive access (Table 5). For the six plots on which the estimate for seed harvesting by ants was based, the numbers of seedlings emerging from ant larders were 0, 0, 0, 0, 1, and 7. Because of the small sample size and skewed distribution of these data, the 95% confidence interval for probability of harvest by ants was very large. Our estimate of probability of harvest by rodents was more reliable because more data were available (18 replicates instead of 6) and a smaller proportion of the values were zeros.

The probability of a seed emerging from an ant larder was no greater than the probability of an unharvested seed emerging, and may have been much smaller than this (Table 5). For seeds harvested by rodents, however, our best estimate of probability of emergence from a scatterhoard was 1.5 times the probability of emergence for unharvested seeds. This discrepancy together with the fact that rodents harvested ~96% of seeds provided explains why almost all of the Indian ricegrass seedlings that became established at our study site did so from scatterhoards made by rodents.

We estimated probabilities of harvest by each type of granivore in the presence of the other using a model similar to those illustrated in Fig. 3 but with three pathways at the first stage of the process: harvest by rodents, harvest by ants, and no harvest. It was not possible to get independent estimates of the parameters based on the data for treatments which allowed access by both classes of granivores, but maximum-likelihood estimation yielded the following relationships:

$$p_{r,b} + p_{a,b} = 0.935$$

$$p_{r,b}q_r = 0.0041$$

$$p_{a,b}q_a = 0.000029$$

TABLE 5. Estimates of probabilities of seed harvest by rodents and ants and of emergence of seedlings from seeds.

Parameter	Description	Exact estimate	Median of bootstrap estimates	95% confidence interval
P_r	probability of harvest by a rodent	0.965	0.964	0.883–0.991
P_a	probability of harvest by an ant	0.044	0.072	0–0.787
q_o	probability of emergence if unharvested	0.0048	0.0046	0.0018–0.0088
q_r	probability of emergence if harvested by a rodent	0.0067	0.0068	0.0032–0.0109
q_a	probability of emergence if harvested by an ant	0.0052	0	0.005–0.0054

where $p_{r,b}$ represents probability of harvest by a rodent with both granivores present, $p_{a,b}$, probability of harvest by an ant with both granivores present, q_r , probability of emergence if harvested by a rodent, and q_a , probability of emergence if harvested by an ant. These relationships imply that the maximum probability of harvest by a rodent in the presence of ants was 0.935 and the minimum probability of emergence if harvested by a rodent was 0.0041. These results are consistent with the analysis of treatments accessible to rodents alone (Table 5). Furthermore, analysis of treatments accessible to both classes of granivores suggested that probability of emergence if harvested by an ant was an order of magnitude less than probability of emergence if harvested by a rodent.

DISCUSSION

Granivorous heteromyid rodents at our study site acted as both predators and dispersers of Indian ricegrass seeds, while harvester ants acted largely as seed predators, and birds had negligible effects on the seed pool. The vast majority of Indian ricegrass seedlings that established from our radiolabeled seeds emerged from rodent seed caches, suggesting a beneficial effect of heteromyids on fitness of Indian ricegrass plants. For all treatments that permitted either initial caching or continuous access by rodents, the number of seedlings from caches exceeded those from the only other non-negligible source of seedlings, seeds that were unharvested by any granivores, often by more than an order of magnitude. The contribution of rodents to seedling recruitment may have been even greater than measured because: (1) diurnal ants could harvest seeds in many plots before rodents became active, (2) some rodent caches may have been beyond our 30-m search distance from plots, and (3) some seedlings attributed to unharvested seeds inside plots could have actually come from relocated rodent scatterhoards that were subsequently but incompletely recovered.

Treatments varied greatly in the relative contribution of rodent seed caches to seedling recruitment, but perhaps plots that did not restrict granivore access (treatment 2 and unfenced control plots) best reflect natural seedling recruitment regimes. Rodent caches yielded a mean of 83.1% and 93.7% of experimental Indian ricegrass seedlings recruited on treatment 2 and control plots, respectively. This figure was even greater in many treatments. Scatterhoards even accounted for 34.4% of seedlings recruited from treatment 3 plots, where rodents only had access to seeds pilfered from ant larders outside plots. Considering numbers of seedlings recruited on most initial caching plots, it seems surprising that a mean of only 9.3 seedlings (68.9% of total seedling recruitment) resulted from rodent caches on plots with initial caching and free access to ants only (treatment 7); this occurred because initial cachers in treatment 7 plots made very few (≤ 4) scatterhoards (Table 4). Taken together, seedling-recruitment results

confirmed our initial expectation that scatterhoards would yield more seedlings than unharvested seeds, which would, in turn, yield more than seeds placed in rodent or ant larders, where seedling recruitment was negligible.

Mechanisms producing seedling recruitment patterns were quite complex. The major contributing factor to high levels of recruitment from rodent caches was that rodents harvested the vast majority of seeds we supplied: $\sim 96\%$ based on our seed fate model. Moreover, greater seedling recruitment on treatment 5 than on treatment 1 plots (no granivores, with and without initial caching, respectively) implied that burial of seeds by rodents enhanced recruitment. Our seed fate model suggested that probability of seedling emergence from seeds buried by rodents was 1.5 times that from unharvested seeds. Indian ricegrass seeds do not germinate unless they are buried (Kinsinger 1962, Young et al. 1994), and we even noted the importance of burial for seedling recruitment from seeds that were not harvested by granivores. One of our treatment 1 plots, which completely restricted all granivory, was in an area of particularly unstable sand. Wind-blown sand in this plot buried unharvested seeds, yielding many more Indian ricegrass seedlings (74 and 31 in 1995 and 1996, respectively) than other treatment 1 plots (0–24 seedlings/plot). Seedling recruitment from unharvested seeds was highest in treatment 1 (mean 29.2 seedlings/plot), but this was $< 5\%$ of seedling recruitment from rodent caches in treatment 5 (589.3 seedlings/plot), where initial caching occurred but granivores were otherwise prohibited.

The lack of significant bird and ant effects, and the seed fate model estimate that ants only harvested $\sim 7\%$ of available seeds in the absence of rodents, imply that ants had little effect on seedling recruitment. However, rodents made fewer caches on plots where ants stored seeds than where they did not. Such competition for seeds could result in reduced seedling recruitment from rodent caches, the primary source of recruits in this study.

There was stronger evidence of a competitive effect of rodents in suppressing seed harvest by ants than vice versa. There were significantly more ant larders from plots that excluded rodents (treatment 3) than from plots with either initial caching (treatment 7) or free access by rodents (treatment 2). Furthermore, lower Geiger counter activity associated with ant larders on plots that allowed rodents than on those that excluded them implies that ants cached fewer seeds in the presence of rodents. Because seeds cached by ants seldom produced seedlings, reduced seed storage by ants due to competition with rodents could indirectly benefit Indian ricegrass seedling recruitment. The lack of any clear effects of ants on seedling recruitment probably occurred because rodents recovered a sufficient majority of their own caches to overwhelm potential effects of competition for the smaller number of seeds

that were harvested by ants. Indeed, the vast majority of seed caches made by rodents during late summer/autumn seed dispersal trials had been removed by early spring of the following year. At least some of these may have been recached, because kangaroo rats commonly redistribute caches over time (Jenkins and Peters 1992, Jenkins et al. 1995). We found evidence of such cache management, as numbers of rodent seed caches found during spring/summer surveys significantly outnumbered original caches that remained. However, there were still significantly more caches made during autumn seed-caching trials than numbers found the following year. Because the vast majority of seeds were harvested and cached by rodents, and the vast majority of these caches were recovered, presumably to be consumed by a rodent, competition for seeds between ants and rodents may have been unimportant for seedling recruitment.

Our seed fate model suggested that an individual Indian ricegrass seed that remains in a rodent cache enjoys a slight advantage in probability of seedling emergence over seeds that remain unharvested and an advantage of up to an order of magnitude over seeds harvested by ants (Table 5). Based on model estimates, the combined effect of the much higher proportions of seeds harvested by rodents and the greater probability of seedling emergence from their caches as compared to ant larders yielded more than two orders of magnitude more seedlings than from seeds dispersed by ants.

Because rodents did such a thorough job of harvesting our experimental seeds, they did, however, reduce the number of seedlings recruited from unharvested seeds, while ants did not. In treatments 1–4, with no initial caching, effects of rodents in enhancing seedling recruitment from caches vs. reducing recruitment from unharvested seeds were compensatory (Fig. 4). The overall effect of rodents on seedling recruitment thus depends on how we view our data. Rodents may simply substitute clumped seedlings from caches for unclustered seedlings from unharvested seeds, or they may account for a large majority of all seedling recruitment, suggesting a plant–granivore mutualism. At the very least, our results demonstrate that heteromyid rodents can harvest a huge proportion of Indian ricegrass seeds without affecting the plant negatively. Net effects of rodents on seedling recruitment may depend partly on population sizes when seeds are being cached vs. being recovered. For example, an interaction involving year in our analyses of seedling recruitment in initial caching treatments may have occurred because of greater overwinter mortality of rodents in the first year of the study. Even if seedling recruitment from seed caches and unharvested seeds are often only compensatory, caching may result in greater survival of Indian ricegrass recruits to reproductive age, because survivorship of aggregated Indian ricegrass seedlings (as in seed caches) is, counterintuitively, greater than

that of single seedlings (Longland 1995, McMurray et al. 1997).

Perhaps the strongest evidence that seedling recruitment dynamics in the Indian ricegrass population we studied are determined largely by rodent seed caching comes from isotonic regression analyses. We predicted recruitment rankings from rodent caches among our experimental treatments based on expected effects of rodent caching on seed burial, on protection of seeds from ants and birds, and on expected levels of cache recovery by rodents in our different treatments. The predicted ranking patterns did not apply to seedlings in general, because they did not agree with observed seedling recruitment patterns from unharvested seeds. However, expected rankings for seedlings from scatterhoards did successfully predict total seedling recruitment rankings among treatments, because seedlings from scatterhoards outnumbered those from unharvested seeds sufficiently to drive overall patterns of recruitment. Taken together, our findings that caches yielded significantly more recruits than other dispersal pathways and that recruitment patterns from caches could be predicted based on the nature of experimental treatments imply that seed-caching rodents can play a dominating and beneficial role in the dynamics of Indian ricegrass seedling recruitment. Although a previous study has documented that seed caching by chipmunks is essential to recruitment of antelope bitterbrush seedlings (Vander Wall 1994), and seedling emergence from scatterhoards made by heteromyids has been noted for various desert plants (Reynolds 1950, LaTourrette et al. 1971, McAdoo et al. 1983, McAuliffe 1990), the potential importance of heteromyids on seedling recruitment has not previously been demonstrated quantitatively.

We found no evidence that removing the cache-making animal in a given area reduces the cache recovery rate and thereby enhances seedling recruitment. Recruitment was similar in treatments 8 and 9, which both had initial caching and subsequent rodent access, but differed in that the cache-making kangaroo rat was excluded from recovering caches in treatment 9. Perhaps the apparent high mortality rate of kangaroo rats during the first winter of the study obscured a potential difference between recovery of caches in treatments 8 vs. 9, or perhaps pilferage of caches made by other animals was common. Pilferage may be reduced when the initial cache-making animal is present, because kangaroo rats repeatedly shuffle cache positions, perhaps to reduce pilferage by intraspecific or interspecific competitors (Jenkins and Peters 1992, Jenkins et al. 1995). Indeed, the adaptive significance of scatter-hoarding among heteromyids and other rodents has been addressed by various hypotheses, many of which invoke amelioration of competition (Smith and Reichman 1984, Vander Wall 1990, Jenkins et al. 1995). The role of individual animals and of interspecific and intraspecific variation in seed caching and cache recovery patterns (Jenkins

1997, Jenkins and Breck 1998) deserves further attention regarding implications for both adaptive behavioral strategies and seedling recruitment.

Seedling recruitment of Indian ricegrass appears to represent a system in which the plant pays a proportion of its seed production as food in return for the seed dispersal and burial services of heteromyid rodents (Janzen 1986). This is analogous to frugivory systems in which trees invest in and package their seeds in fleshy fruits that provide food to frugivorous animals in return for their dispersal services. For such a system to evolve and persist, it should not matter that only a small proportion of seeds actually reap the benefits offered by the dispersers to eventually establish a seedling. Instead, it is the relative probability of establishing a seedling through a seed-dispersing animal vs. alternate paths that is important, and we have shown that this probability is enhanced when Indian ricegrass seeds are harvested by heteromyids.

While granivory is ubiquitous in nature, plant-granivore mutualisms may be more frequent in arid areas, such as deserts, than in mesic environments. Seeds are relatively less perishable than other plant tissues and are produced in annual pulses. Seed caching thus offers animals a solution for overcoming the general paucity of food resources in harsh desert environments. For plants, seed burial by caching granivores may be particularly advantageous in arid environments, where desiccation on the soil surface likely deters seed germination and seedling establishment.

Brown and Heske (1990) demonstrated that long-term removal of kangaroo rats from a Chihuahuan Desert site had profound effects on the local plant community; when kangaroo rats were absent, numerically dominant shrub species were replaced by perennial grasses. No such effects on the plant community occurred where ants, but not rodents, were excluded. In the western Great Basin Desert, disturbed sites lacking heteromyid populations are often dominated by annual weeds, while native perennial grasses re-establish better in disturbed sites with heteromyids (Longland 1994). Our present results also suggest that populations of Indian ricegrass, a native perennial grass, can benefit from seed-dispersing heteromyids. Perhaps there are regional differences among the North American deserts in the extent to which these animals influence populations of woody vs. herbaceous plant species. Heteromyids may have site-specific, yet pervasive, effects on the physiognomy of desert communities. Their patterns of seed predation, seed caching, and their interactions with other desert granivores contribute to these effects.

ACKNOWLEDGMENTS

We thank J. Armstrong, S. Chudd, C. Clements, E. Harrison, S. Hem, A. Jones, A. Long, J. Stiver, P. Torneo, and K. Vanderbeek for assistance in the field. Reviews by Joel Brown, Mary Price, Jim Young, and an anonymous reviewer improved the manuscript considerably. This study is a con-

tribution of the USDA, ARS, Exotic and Invasive Weeds Research Unit, Reno, Nevada, USA. This material is based upon work supported by the Cooperative State Research, Education, and Extension Service, USDA, under Agreement No. 93-37101-8995.

LITERATURE CITED

- Abbott, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. *Ecology* **51**:271–278.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**:1705–1707.
- Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* **10**:210–227.
- Clark, W. H., and P. L. Comanor. 1973. The use of western harvester ant, *Pogonomyrmex occidentalis* (Cresson), seed stores by heteromyid rodents. *Occasional Papers of the Biological Society of Nevada* **34**:1–6.
- Emlen, J. T. 1971. Population estimates of birds derived from transect counts. *Auk* **88**:323–342.
- Frank, C. L. 1988. The influence of moisture content on seed selection by kangaroo rats. *Journal of Mammalogy* **69**:353–357.
- Gaines, S. D., and W. R. Rice. 1990. Analysis of biological data when there are ordered expectations. *American Naturalist* **135**:310–317.
- Henderson, C. B. 1990. The influence of seed apparency, nutrient content and chemical defenses on dietary preference in *Dipodomys ordii*. *Oecologia* (Berlin) **82**:333–341.
- Jacobs, L. F. 1992. Memory for cache locations in Merriam's kangaroo rats. *Animal Behaviour* **43**:585–593.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* **2**:465–492.
- Janzen, D. H. 1986. Seeds as products. *Oikos* **46**:1–2.
- Jenkins, S. H. 1997. Perspectives on individual variation in mammals. *Journal of Mammalogy* **78**:271–273.
- Jenkins, S. H., and S. W. Breck. 1998. Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy* **79**:1221–1233.
- Jenkins, S. H., and R. A. Peters. 1992. Spatial patterns of food storage by Merriam's kangaroo rats. *Behavioral Ecology* **3**:60–65.
- Jenkins, S. H., A. Rothstein, and W. C. H. Green. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. *Ecology* **76**:2470–2481.
- Kelrick, M. I., J. A. MacMahon, R. R. Parmenter, and D. V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds, and ants: the relationship of seed attributes and seed use. *Oecologia* **68**:327–337.
- Kinsinger, F. E. 1962. The relationship between depth of planting and maximum foliage height of seedlings of Indian ricegrass. *Journal of Range Management* **15**:10–13.
- La Tourrette, J. E., J. A. Young, and R. A. Evans. 1971. Seed dispersal in relation to rodent activities in seral big sagebrush communities. *Journal of Range Management* **24**:118–120.
- Lavigne, R. J. 1969. Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **62**:1166–1175.
- Longland, W. S. 1994. Seed use by desert granivores. Pages 233–237 in S. B. Monsen and S. G. Kitchen, editors. *Proceedings of the symposium on ecology, management, and restoration of intermountain annual rangelands*. USDA Forest Service **INT-GTR-313**.
- Longland, W. S. 1995. Desert rodent communities in disturbed shrub communities and their effects on plant recruitment. Pages 209–215 in B. A. Roundy, E. D. McArthur, J. S. Haley, and D. K. Mann, editors. *Proceedings*

- of the symposium on wildland shrubs and arid land restoration. USDA Forest Service **INT-GTR-315**.
- Mares, M. A., and M. L. Rosenzweig. 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* **59**:235–241.
- McAdoo, J. K., C. C. Evans, B. A. Roundy, J. A. Young, and R. A. Evans. 1983. Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. *Journal of Range Management* **36**:61–64.
- McAuliffe, J. R. 1990. Paloverdes, pocket mice, and bruchid beetles: interrelationships of seeds, dispersers, and seed predators. *Southwestern Naturalist* **35**:329–337.
- McMurray, M. H., S. H. Jenkins, and W. S. Longland. 1997. Effects of seed density on germination and establishment of a native and an introduced grass species dispersed by granivorous rodents. *American Midland Naturalist* **138**:322–330.
- Parmenter, R. R., J. A. MacMahon, and S. B. Vander Wall. 1984. The measurement of granivory by desert rodents, birds, and ants: a comparison of an energetics approach and a seed dish technique. *Journal of Arid Environments* **7**:75–92.
- Price, M. V., and S. H. Jenkins. 1986. Rodents as seed consumers and dispersers. Pages 191–235 in D. R. Murray, editor. *Seed dispersal*. Academic Press, Sydney, Australia.
- Pyare, S., and W. S. Longland. 2000. Seedling-aided cache detection by heteromyid rodents. *Oecologia* **122**:66–71.
- Reichman, O. J. 1981. Factors influencing foraging in desert rodents. Pages 195–213 in A. C. Kamil and T. D. Sargent, editors. *Foraging behavior; ecological, ethological, and psychological approaches*. Garland STPM Press, New York, New York, USA.
- Reynolds, H. G. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. *Ecology* **31**:456–463.
- Reynolds, H. G., and G. E. Glendening. 1949. Merriam kangaroo rat, a factor in mesquite propagation on southern Arizona rangelands. *Journal of Range Management* **2**:193–197.
- Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics* **15**:329–351.
- Soholt, L. F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecological Monographs* **43**:357–376.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Tevis, L., Jr. 1958. Interrelations between the harvester ant *Veromessor pergandei* (Mayr) and some desert ephemerals. *Ecology* **39**:695–704.
- Vander Wall, S. B. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago, Illinois, USA.
- Vander Wall, S. B. 1991. Mechanisms of cache recovery by yellow pine chipmunks. *Animal Behaviour* **41**:851–863.
- Vander Wall, S. B. 1992. The role of animals in dispersing a “wind-dispersed” pine. *Ecology* **73**:614–621.
- Vander Wall, S. B. 1993. A model of caching depth: implications for scatterhoarders and plant dispersion. *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., W. S. Longland, S. Pyare, and J. A. Veech. 1998. Cheek pouch capacities and loading rates of heteromyid rodents. *Oecologia (Berlin)* **113**:21–28.
- West, N. E. 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* **49**:1009–1011.
- Young, J. A., R. R. Blank, W. S. Longland, and D. E. Palmquist. 1994. Seeding Indian ricegrass in an arid environment in the western Great Basin. *Journal of Range Management* **47**:2–7.