

Desert Rodents in Disturbed Shrub Communities and Their Effects on Plant Recruitment

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Abstract—Nocturnal, seed-eating rodents of the family Heteromyidae are the most widespread and abundant mammals in North American deserts. In contrast to other desert rodent taxa, heteromyid densities and species diversity are generally maintained or increased when shrub cover is reduced or removed by disturbance; this pattern is particularly true of the kangaroo rats, a diverse group of bipedal heteromyid species, but quadrupedal heteromyids (pocket mice) may also maintain relatively high densities in disturbed habitats. I illustrate these patterns with rodent population data from a desert shrub habitat following disturbance by wildfire. Based on observational and experimental studies of heteromyid interactions with Indian ricegrass (*Oryzopsis hymenoides*), I also present several lines of evidence indicating that heteromyid activities can have profound effects on the distribution and abundance of particular plant species during successional recovery of disturbed sites. The apparent importance of these animals' interactions with many native plant species suggests close coevolutionary ties between heteromyids and desert plants, and further suggests that these animals may act as natural "engineers" for restoration of disturbed desert environments.

In North American desert environments a diverse array of animals, including various taxa of rodents, birds, and ants, have diets consisting largely of seeds. Seed-eating (or "granivory") is common among these desert herbivores because, compared with the ephemeral availability of plant foliage in deserts, seeds are relatively non-perishable. Thus, they remain available year-round in soil seedbanks and they retain their nutritional properties when properly stored. Because of this latter attribute two groups of desert granivores, rodents and ants, cache large quantities of seeds for later consumption.

The family Heteromyidae is a New World family of nocturnal, granivorous rodents. The vast majority of species representing four of six extant heteromyid genera (*Dipodomys*—kangaroo rats, *Microdipodops*—kangaroo mice, and *Chaetodipus* and *Perognathus*—pocket mice) are restricted to deserts where they often coexist in remarkably diverse assemblages of four to six species (Brown and Harney 1993). It is well known that heteromyids, especially bipedal kangaroo rats and kangaroo mice, often utilize very open desert

habitats rather devoid of vegetation, such as exposed, unstable sand dunes. Even in shrub-dominated habitats, bipedal heteromyids tend to concentrate their activities in the open spaces between shrub canopies (Price and Brown 1983, Reichman and Price 1993). Thus, bipedal heteromyids often increase in abundance and/or species diversity when disturbances such as wildfire remove the shrub component of desert habitats (Price and Waser 1984, Simons 1991, Stangl et al. 1992, Whitford and Steinberger 1989). Populations of quadrupedal pocket mice, which tend to prefer more structurally complex habitats than bipeds, may also persist or increase following disturbance if sufficient vegetation or rock cover is available (Bock and Bock 1978, Quinn 1979). By contrast, non-heteromyid rodents are generally absent from disturbed desert environments until substantial vegetation cover is re-established (Simons 1991).

These taxonomic differences in responses of desert rodent populations to disturbance can be explained on the basis of habitat- and taxon-specific risk of predation. Desert rodents in general are more vulnerable to capture by a primary predator—owls—in open habitats than in vegetated ones. However, heteromyid species, being superior to other desert rodents at detecting and evading attacking predators, are less constrained by this risk differential, and within the heteromyids, bipeds are superior to quadrupeds at avoiding predators (Longland and Price 1991, Webster and Webster 1984). Thus, the tendency of these different desert rodent taxa to utilize disturbed, open habitats is inversely correlated with their relative vulnerability to predators. Although numerous studies have documented the above response patterns of desert rodents to disturbance, potentially profound impacts of early-colonizing desert heteromyids on post-disturbance successional patterns are much less appreciated.

With one notable exception (the Great Basin kangaroo rat—*Dipodomys microps*—which eats the foliage of *Atriplex confertifolia*), desert heteromyid species are obligate granivores. Heteromyids locate seeds, even in small quantities buried greater than 10 cm in soil (Johnson and Jorgensen 1981, Lockard and Lockard 1971), using olfaction. These rodents are also very efficient at harvesting seeds after they are located (Nikolai and Bramble 1983, Price and Podolsky 1989); seeds are rapidly separated from the soil matrix with the forepaws and placed in external cheek pouches outside the mouth, which can hold hundreds to thousands of seeds depending on sizes of particular rodent species and seed types. I have measured rates at which desert kangaroo rats (*D. deserti*) harvest and "pouch" Indian ricegrass (*Oryzopsis hymenoides*) seeds at greater than 40 seeds per second using pure piles of seed and greater than 5 seeds per second when seeds were thoroughly mixed with fine sand.

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Harvested seeds are transported in the cheek pouches either to the rodent's burrow, where seeds are either consumed or cached in an underground granary, or they are cached in scattered shallow holes dug by the rodent around its home range and covered by soil to conceal evidence of cache locations. Seeds cached in the latter manner ("scatterhoards") that are not later recovered and consumed by rodents may germinate and establish, but seeds cached in burrows ("larderhoards") are generally too deep to permit seedling emergence. A single kangaroo rat may have hundreds of scatterhoards each containing tens to hundreds of seeds around its home range (Hawbecker 1940, Reynolds 1958, Shaw 1934), and its larder may contain several kilograms of seed (Shaw 1934, Vorhies and Taylor 1922).

The above discussion of the large quantities of seeds which are harvested, transported, consumed, and cached by a single heteromyid rodent serves to illustrate the potentially tremendous impact that dense heteromyid populations and diverse heteromyid species assemblages may have on desert plant communities. Indeed, in several studies heteromyids and other arid-land rodents have been found to harvest a large majority of the annual seed production of a particular plant species (Table 1). Numerous plant species' seeds have also been found to germinate from heteromyid scatterhoards (Table 2). Because heteromyids cache multiple seeds in scatterhoards, their locations are revealed by clumps of germinating seedlings, although solitary seedlings may also result from scatterhoarded seeds that remain after a rodent partially recovers a cache. If seed harvest by rodents limits recruitment for certain plant species, or if rodents selectively scatterhoard particular seeds and this has a significant effect on plant recruitment, then the activities of these rodents could be said to "cascade" to community-level effects at the producer trophic level.

While the studies listed in Tables 1 and 2 elucidate mechanisms such as seed predation, seed caching, and germination from seed caches by which heteromyids may affect plant populations, an experimental field study by Brown and Heske (1990; see also Heske and others 1993) directly demonstrates dramatic community-level effects of heteromyid activities on desert plant assemblages. Using long-term exclosures in the Chihuahuan Desert that are

Table 1—Studies documenting percentages of plant seed production harvested by rodents

Plant type (Site)	Seeds harvested (%)	Source
Annual grasses (California Central Valley)	93	Pearson 1964
Annual grasses (Southern California)	30-65	Borchert & Jain 1978
<i>Erodium cicutarium</i> (Mojave Desert)	95	Soholt 1973
<i>Larrea tridentata</i> (Chihuahuan Desert)	87	Chew & Chew 1970
<i>Oryzopsis hymenoides</i> (Great Basin Desert)	46	McAdoo & others 1983
Desert plants (Mojave Desert, NV)	30-80	Nelson & Chew 1977

Table 2—Studies documenting germination of desert plant seeds from rodent scatterhoards

Plant species	Location	Source
Velvet mesquite	Arizona	Reynolds & Glendening 1949
Indian ricegrass	Nevada	McAdoo and others 1983
Antelope bitterbrush	California	Hormay 1943
	Oregon	West 1968
	Nevada	Vander Wall 1990
Palo Verde	Arizona	McAuliffe 1990
Cheatgrass	Nevada	La Tourrette and others 1971

selectively permeable to specific taxa of desert rodents, Brown and Heske (1990) found that exclusion of medium-sized kangaroo rat species (*D. merriami* and *D. ordii*) resulted in a shift from a shrub- to a grass-dominated desert plant community. Although this study indicates a key-stone effect of kangaroo rats in maintaining Chihuahuan Desert shrub environments, some evidence suggests that these animals may also play a keystone role in maintaining the grass component of salt desert plant assemblages in the Great Basin Desert. Here, I illustrate with empirical data the responses of heteromyid communities to the large-scale removal of a desert shrub community and present initial data from a study of mechanisms by which these rodents affect plant successional patterns during recovery from the disturbance.

Methods

Field studies were initiated near Flanigan, NV (Washoe Co., Flanigan Quad. T27N.R18E.S2) three years after a 1985 wildfire removed shrubs from one side of a road bisecting the site. The study area has a fine sand (xeric Torripsament) substrate. Unburned vegetation is dominated by desert shrub species, especially big sagebrush (*Artemisia tridentata tridentata*), which comprises more than 80% of the plant community. The burned area is dominated by Indian ricegrass (*Oryzopsis hymenoides*) and the introduced annual barbwire Russian thistle (*Sal-sola paulsenii*). In late April 1991, after Indian ricegrass seed germination had occurred, I estimated densities of seedlings and mature clumps of ricegrass in the burned and unburned habitat types using 80 randomly placed 1.0-m² sampling frames per habitat.

Rodent populations in the burned and unburned habitats were censused monthly beginning in September 1988 by livetrapping with wild bird seed as bait. Captured rodents were identified by species, given a uniquely numbered metal eartag, and released immediately at the site of capture.

From April 1989 to November 1990 I conducted 27 trials of an experiment to quantify harvest rates of Indian rice-grass seeds as a function of seed density and depth in the sand substrate. Seeds were planted in 20-cm-long PVC plastic tubes with a 15-cm diameter and 2-mm mesh screening covering the bottom opening. Two replicate linear transects of 20 tubes each were placed in both the burned and unburned habitats for a total of 80 tubes during each trial

of the experiment. Each transect included one tube with seeds planted at a unique combination of four densities (either 1, 2, 10, or 100 seeds) and five planting depths (either 0, 1, 2, 4, or 6 cm); the position of tubes representing different seed density and depth combinations was randomized within transects. Each tube along a transect was buried flush with the ground surface, supplied with seeds at the specified density and depth, and left out for 7 nights before being checked for seed removal by rodents.

I used Indian ricegrass seeds labeled with powdered fluorescent pigments to estimate the proportion of seeds harvested by heteromyids which are scatterhoarded. Longland and Clements (in press) provide a detailed description of this technique. Before dusk on each of nine dates between 4 August and 3 November 1989, I placed three square (9.0 x 9.0 cm) petri dishes each containing 40 g of seeds mixed with 3 g of pigment in both the burned and unburned habitats at Flanigan. Seed dishes were separated from one another by at least 30 m. Rodents had access to these seeds during the night until I began searching for seed caches with a UV lantern at 0300 h the following morning. Seed cache locations were revealed by large pigment marks on the sand surface. I marked locations of scatterhoards found in the dark and returned shortly after daylight to recover them. The number and mass of seeds within each scatterhoard was determined later.

In early June 1993, after Indian ricegrass seed germination was complete, I determined germination success for seeds within rodent scatterhoards by digging up 100 clumps of seedlings emerging from caches and counting numbers of seedlings and ungerminated seeds. It is impractical to do the same for single seedlings that are unassociated with caching, because locations of ungerminated seeds are not revealed by germinated seedlings as they are in caches. Therefore, I compared field germination of seeds within rodent caches to laboratory germination success of mature Indian ricegrass seeds collected by hand at Flanigan. I also compared the depth of emergence from the sand between single seedlings and the above-mentioned seedling clumps that were taken from rodent caches. I measured emergence depth for five randomly chosen seedlings from each of the 100 dug up scatterhoards and for the five single seedlings nearest to each scatterhoard. I calculated the mean and standard deviation of emergence depths for each group of five seedlings, and compared the grand mean and the mean standard deviation between the 100 groups of seedlings emerging singly versus the groups emerging from caches.

After above-average precipitation from January through March, the Indian ricegrass population at Flanigan exhibited exceptional seedling emergence in spring 1993. I monitored the number of living Indian ricegrass seedlings in four 5 x 5-m plots that were fenced to exclude medium and large herbivores (jackrabbits, pronghorn antelope, cattle) weekly from 20 April through 2 November 1993. I resumed monitoring in late March to early April 1994 to determine numbers of 1993 seedlings in these plots which survived through their first winter. Small gates at the bottom of each fence permitted access by desert rodents. Each week I counted clumps of seedlings representing heteromyid scatterhoards and the number of individual seedlings per clump within each 25-m² enclosure plot. In each enclosure I also counted single seedlings within 8 randomly located 0.25-m² frames

Table 3—Relative abundances (percent) of rodent species occurring in a burned and unburned (control) habitat at Flanigan, NV, study site based on 1988 to 1990 live trapping data. Heteromyid rodents, the primary scatterhoarding species at this site, include species in the genera *Dipodomys* and *Perognathus*

Rodent species	Percentage of captures	
	Burned habitat (Indian ricegrass)	Unburned habitat (Sagebrush)
<i>Dipodomys merriami</i>	54	89
<i>Dipodomys ordii</i>	27	2
<i>Dipodomys panamintinus</i>	12	1
<i>Dipodomys deserti</i>	3	0
<i>Perognathus longimembris</i>	3	1
<i>Ammospermophilus leucurus</i>	1	7

and used these counts to estimate total numbers of single seedlings per 25 m² for comparing relative numbers of seedlings presumably unassociated with caching with numbers emerging from scatterhoards.

Results and Discussion

Five species of heteromyid rodents and one non-heteromyid (*Ammospermophilus leucurus*, white-tailed antelope ground squirrel) were found at Flanigan based on 1988 to 1990 live trapping data. The rodent community in the unburned sagebrush habitat consisted primarily of one heteromyid species (*Dipodomys merriami*, Merriam's kangaroo rat) and a few ground squirrels, while the burned habitat had a rodent community with considerably greater heteromyid diversity (four kangaroo rat species and *Perognathus longimembris*, the little pocket mouse) and ground squirrels were almost completely absent (Table 3). This is consistent with previous reports that heteromyid abundance and diversity are maintained or enhanced following major disturbances, but that other desert rodents are uncommon in disturbed areas (Bock and Bock 1978, Price and Waser 1984, Whitford and Steinberger 1989).

In 1991, nearly six years after the Flanigan fire, densities of both established clumps and seedlings of Indian ricegrass were significantly greater in the burned than in the unburned habitat; seedling densities differed by more than an order of magnitude (Table 4). The vast majority of established clumps were quite robust considering that most were no more than six years old. By uprooting several established clumps I found that most were composed of multiple individual plants of similar stature, suggesting that

Table 4—Densities of established plants and seedlings of Indian ricegrass in burned and unburned habitats at Flanigan, NV (1991)

Habitat	Density (#/m ² ± sd)	
	Established plants	Seedlings
Burned	1.5 ± 1.3	8.8 ± 6.5
Unburned	0.3 ± 0.2	0.8 ± 1.4

these clumped individuals emerged at roughly the same times. This constitutes indirect evidence that much of the Indian ricegrass recruitment following the Flanigan fire resulted from rodent scatterhoarding.

Seed Harvest Rate

The 1989-90 seed harvest rate experiment indicated that the probability of Indian ricegrass seeds being harvested by a rodent differed significantly as a direct function of seed density and as an inverse function of planting depth (Table 5). Seeds planted 6 cm deep in small numbers (1, 2, or 10 seeds) were seldom harvested, but clumps of 100 seeds at this depth were found and at least partially removed by rodents within seven days approximately 10% of the time. By contrast, harvest rates for unburied seeds on the surface ranged from approximately 30% to more than 80% depending on seed density (Table 5). These effects also yielded a significant seed density x depth interaction in a contingency test of numbers of seed clumps harvested versus unharvested ($X^2 = 87.35, df = 12, P < 0.001$). In addition to these depth and density effects, seed harvest rates were significantly greater in the unburned than in the burned habitat ($X^2 = 38.02, df = 1, P < 0.001$), probably reflecting the lower availability of seeds in the former habitat where Indian ricegrass occurred in significantly lower densities. Indian ricegrass seed is a highly preferred food for desert heteromyids (McAdoo et al. 1983, Kelrick et al. 1986, Henderson 1990), so higher harvest rates in the unburned habitat may be due to a greater demand for a valuable, preferred resource where it is rare.

This argument may also apply to comparisons of scatterhoarding rates between the burned and unburned habitats. Specifically, one might expect rodents to consume relatively more and cache less of a valuable seed resource where that resource is less abundant. Indeed, I found that both the mean and maximum numbers of seeds per scatterhoard were greater in the burned ($\bar{x} = 275$ seeds/cache, max. = 1,427 seeds, $n = 25$ caches) than in the unburned habitat

Table 5—Proportion of experimental seed clumps harvested by heteromyid rodents either partially or completely over 7-day periods as a function of seed density and planting depth. Experiment was conducted in both burned and unburned habitats at Flanigan, NV during 1989-90

Habitat*	Planting depth (cm)*	Number of seeds per clump (density)*			
		1	2	10	100
Unburned	surface (0)	.291	.463	.727	.836
	1	.164	.200	.400	.436
	2	.200	.127	.291	.600
	4	.055	.036	.164	.255
	6	.018	.019	0	.109
Burned	surface (0)	.352	.352	.556	.778
	1	.111	.130	.111	.241
	2	.204	.111	.074	.222
	4	.037	.019	.037	.130
	6	.019	0	0	.074

*Effect of variable on seed harvest rate significant ($P < 0.001$) based on contingency analysis of numbers of seed clumps harvested versus unharvested by heteromyid rodents.

($\bar{x} = 240$, max. = 730, $n = 25$) using Indian ricegrass seeds labeled with fluorescent pigments. I also located greater proportions of the initial 40 g of labeled Indian ricegrass seeds in rodent caches in the burned habitat (up to 14.1 g or 35.2%) than in the unburned habitat (up to 9.1 g or 22.7%).

The latter figures represent maximum proportions of experimental seeds recovered, and are probably more reflective of true scatterhoarding rates than mean proportions among all seed caching trials, because it is unlikely that I often located the majority of the seeds which were cached (Longland and Clements, in press). These maximum caching rates also compare favorably with rates at which heteromyids scatterhoard harvested Indian ricegrass seeds in laboratory experiments; about 25% of harvested seeds are cached in this manner (McAdoo et al. 1983, Longland 1994a). Because scatterhoarding is an efficient mechanism of seed burial and buried seeds of many plant species, including Indian ricegrass (Kinsinger 1962), have enhanced germination and establishment rates relative to unburied seeds, scatterhoarded seeds that are not later recovered by a granivore for consumption may often benefit from burial. In the case of Indian ricegrass, however, benefits of rodent scatterhoarding extend beyond simple seed burial, because seeds harvested by heteromyids have enhanced germinabilities relative to seeds which are not handled by these rodents (McAdoo et al. 1983).

Field Germination

Enhanced germinability due to seed handling by heteromyids may have contributed to the dramatically higher field germination rates of seeds I found in heteromyid scatterhoards ($\bar{x}$ % germination $\pm$ $sd = 90.4 \pm 10.8\%$) relative to laboratory germination of hand collected Indian ricegrass seed (less than 2.0% for all trials with native seeds from Flanigan). It is also possible that this resulted from heteromyids selectively harvesting and caching the most viable seeds available, which may also be the most nutritious. Laboratory tests have shown that these rodents avoid aborted Indian ricegrass seeds or those with low viability (McAdoo et al. 1983; Longland, unpublished data).

Another potential mechanism by which germinability may be enhanced for Indian ricegrass seeds in heteromyid scatterhoards concerns the management of caches by rodents in such a manner that germination is favored. In contrast to my initial expectations, seedlings in rodent scatterhoards at Flanigan emerged from significantly shallower depths ($\bar{x} = 4.2$ cm) than nearest-neighbor single seedlings ($\bar{x} = 4.4$ cm) (paired t -test: $t = 1.99, df = 99, P < 0.05$). Although greenhouse experiments have shown that Indian ricegrass seedling emergence is inversely related to planting depth, the 2 mm difference found in this study between emergence depth of rodent-cached and single Indian ricegrass seeds is probably insufficient to account for much of a difference in germination rates (Young and others 1994).

A relatively greater effect of cache management by heteromyids may be due to the significantly greater variation in depths from which single seedlings emerged (sd of emergence depth for 100 groups of 5 single seedlings = 1.4 cm) at Flanigan relative to seedlings in scatterhoards ($sd = 0.3$ mm) (paired t -test = 18.69, $df = 99, P < 0.001$). Both

the greater mean and variation in emergence depth found for single seedlings in this study may be unique to areas with unstable substrates such as the sands at Flanigan; blowing sands may accumulate to varying levels over uncached seeds while they lie dormant for varying periods of time, but rodents may recache scatterhoarded seeds frequently at a relatively constant depth.

If the rather constant emergence depth of clumped seedlings represents a similarly constant scatterhoarding depth that approximates an optimum for establishment of Indian ricegrass seedlings, this could contribute to the high germination and emergence found among scatterhoarded seeds at Flanigan. Field observations by Kinsinger (1962) suggest that the mean emergence depth of scatterhoarded seeds found in this study (4.2 cm) is indeed within the optimal germination depth range for Indian ricegrass. However, because controlled greenhouse experiments imply that Indian ricegrass seedling emergence is optimized at depths of less than 4.0 cm, a more likely explanation is that the emergence depth of scatterhoarded seeds represents a tradeoff between reduced seedling emergence at greater depths and increased levels of seed detection and predation by rodents at shallower depths (Young and others 1994). The latter possibility is supported by data in Table 5 indicating greatly reduced harvest rates of Indian ricegrass seeds planted 4 cm versus 2 cm deep at all seed densities.

While it is certainly true that the above difference between field germination of rodent-cached Indian ricegrass seeds and laboratory germination of uncached seeds could be due to a variety of factors, field monitoring of the survival of single seedlings versus seedlings in scatterhoards during 1993-94 directly demonstrates a greater establishment rate for the latter seedlings. Initial seedling counts shortly after emergence in April 1993 showed that numbers of single seedlings ($\bar{x} = 740/\text{exclosure}$) exceeded seedlings in scatterhoards ($\bar{x} = 274/\text{exclosure}$) by a factor of approximately three. The final counts in fall 1993 showed that this discrepancy had considerably narrowed ($\bar{x} = 190$ single seedlings and 112 scatterhoard seedlings/25-m² exclosure). Counts in spring 1994 were virtually identical to these fall counts indicating minimal overwinter mortality. Based on the numbers given above, survival rates of clumped seedlings in scatterhoards (40.9%) were significantly greater than those of single seedlings (25.7%) (G -test of independence on initial numbers of single vs. scatterhoard seedlings that were alive vs. dead at last 1993 count: $G = 21.34$, $df = 1$, $P < 0.001$). Although attrition was not negligible for seedlings within caches, the density of seedling clumps ($\bar{x} = 11.5$ caches/25-m² exclosure), while small, remained constant over time because at least some seedlings survived in virtually all clumps.

Seedlings Attributed to Caches

The seedling survival data can be compared with rough estimates of expected proportions of seedlings attributable to rodent seed caches based on data from the seed harvest rate and caching rate experiments described above. Assuming that the majority of Indian ricegrass seeds harvested by heteromyids are taken from the soil surface shortly after being shattered from a seed head, the harvest rate data for surface seeds (Table 5) can be used to estimate harvest

rates of native Flanigan seeds. During a foraging bout it is unlikely for a rodent to find large clumps of fallen seeds that have accumulated at a single foraging point, because seed maturation is not strongly synchronized. Therefore, the harvest rate data for clumps of 100 seeds on the soil surface (Table 5) probably overestimate natural harvest rates. Based on the remaining data, it seems reasonable to estimate that not more than 50% of shattered Indian ricegrass seeds are harvested by heteromyids. This also seems reasonable as an upper estimate of harvest rates in view of the fact that data in Table 5 represent proportions of seed clumps that were harvested either completely or partially. Many of the partially harvested clumps had substantial numbers of seeds remaining; there were no combinations of seed density and planting depth that had complete harvest rates as high as 50%.

If up to 50% of Indian ricegrass seeds are harvested by heteromyids and approximately 25% of harvested seeds are scatterhoarded (see above), then the proportion of the seedling population which is attributable to scatterhoarding should not exceed 20% ($[(.25(.5) \times 100) / (.5 + .25(.5))]$) assuming that cached and uncached seeds have similar germination and establishment rates. Actual proportions of seedlings due to scatterhoarding should be substantially less than this estimate, because heteromyids eventually recover and consume the vast majority of their caches (Jacobs 1992). The seedling count data summarized above show that actual proportions of seedlings coming from heteromyid scatterhoards at Flanigan were initially greater than this hypothetical maximum of 20%, and that this proportion increases temporally as seedling attrition progresses. Moreover, these counts probably underestimate the fraction of seedlings arising from scatterhoards, because some of the single seedlings probably resulted from caches that were partially recovered (partial harvest of seed clumps was not uncommon in the seed harvest rate experiment).

Taken together, the combination of experimental and observational data reported here supports the assertion that activities of desert heteromyid rodents enhance the germination of Indian ricegrass seeds and/or the establishment of seedlings. Table 2 indicates that potential benefits of germination from heteromyid seed caches are not limited to Indian ricegrass or even to native plants of the North American deserts. However, while some evidence suggests that scatterhoarding may benefit other native plant species (McAuliffe 1990, Reynolds and Glendening 1949), I have observed that seedlings of three introduced annual weed species (cheatgrass—*Bromus tectorum*, Russian thistle—*Salsola australis*, and barbwire Russian thistle—*Salsola paulsenii*) usually die before producing viable seeds under the clumped conditions associated with emergence from caches. Coevolutionary interactions between desert rodents and the native plant species whose seeds are commonly cached may have selected for greater tolerance for crowding in the seedling stage, but introduced plants certainly lack any coevolutionary ties with local desert granivores. Such coevolutionary rodent/seed relationships may be unique to North American deserts, since the diversity and ecological importance of granivorous rodents here is greater than in other desert regions of the world (Mares 1993). If coevolved rodent/seed interactions affect the species composition of either herbaceous plant or rodent assemblages

in Great Basin Desert communities, this may explain the relative lack of seed-caching rodents in disturbed shrublands of the western Great Basin which have been dominated by introduced weeds (Longland 1994b). Additionally, if a cause-and-effect relationship could be assigned to this pattern (if rodents are absent because important plant species are absent or vice versa), then it may be possible to influence successional recovery of disturbed areas through interventive management of either rodent communities or their seed resources.

Results of this study imply that activities of desert heteromyid rodents are of utmost importance for recruitment in Indian ricegrass populations. Heteromyids have been shown to have keystone effects in maintaining the diversity of winter annuals (Samson et al. 1992) and the shrub component (Brown and Heske 1990) of Chihuahuan Desert plant assemblages. Other studies indicate that heteromyids affect recruitment of mesquite (*Prosopis glandulosa*) (Reynolds and Glendening 1949) and paloverde (*Cercidium microphyllum*) (McAuliffe 1990) in the Arizona Sonoran Desert, of blackbrush (*Coleogyne ramosissima*) in the eastern Mojave Desert (B. Pendleton, personal communication), and of various shrub and grass species in the Great Basin Desert (Everett and Kulla 1977; J. Young, personal communication). Thus, while specific responses of vegetation communities to desert rodent activities may vary geographically, the ubiquitous distributions, seed gathering, and seed harvesting activities of heteromyid rodents within the North American deserts may generally have keystone effects on associated desert plant communities.

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