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Caching propensities and effectiveness of five coexisting heteromyid rodent species as dispersers of Indian ricegrass (*Achnatherum hymenoides*) seeds

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Abstract.—Recruitment of Indian ricegrass (*Achnatherum hymenoides*) seedlings occurs primarily from surface seed caches made by scatter-hoarding desert rodents of the family Heteromyidae. We used radiolabeled Indian ricegrass seeds in field seed-caching experiments with 5 coexisting heteromyid species (*Dipodomys deserti, D. merriami, D. microps, Microdipodops pallidus,* and *Perognathus longimembris*) to compare their potential effectiveness as dispersers. *Dipodomys microps* individuals deposited seeds almost exclusively in larders rather than in scatter hoards, implying that this species is unlikely to be an important seed disperser. Among the other species, individual caches made by larger species had more seeds than those made by smaller species, but smaller species made more caches. At the level of individual animals, *M. pallidus* was the most effective disperser in a quantitative sense; they made more caches than other species tested and placed fewer excess seeds in caches relative to optimal cache sizes for Indian ricegrass seedling establishment. However, because *D. merriami* individuals were considerably more abundant at the study site than other species and were also avid scatter hoarders, *D. merriami* is likely to be the most quantitatively effective disperser of Indian ricegrass seeds at the species level. Ranking species according to qualitative effectiveness (e.g., by considering effects such as the caching microsite on seedling establishment) was more ambiguous. For example, *P. longimembris* made relatively shallow caches that most closely match optimal planting depths for Indian ricegrass seedling emergence, but such shallow caches are probably more likely than deeper caches to be discovered by foraging rodents before they can germinate. With the possible exception of *D. microps,* any of the species we tested may be effective dispersers of Indian ricegrass seeds.

Resumen.—El reclutamiento de plántulas de hierbas de arroz indio (*Achnatherum hymenoides*) ocurre, principalmente a partir de depósitos de semillas en la superficie, realizados por roedores del desierto de la familia Heteromyidae. Utilizamos semillas de hierba de arroz indio radiomarcadas en experimentos de almacenamiento de semillas en el campo, llevada a cabo por medio de 5 especies heteromidas coexistentes (*Dipodomys deserti, D. merriami, D. microps, Microdipodops pallidus* y *Perognathus longimembris*) para comparar su posible eficacia como dispersores. Los individuos de *D. microps* almacenan semillas casi exclusivamente en despensas, por lo que es poco probable que esta especie sea un importante dispersor de semillas. En cuanto a las otras especies, los almacenes individuales realizados por las especies más grandes contaron con más semillas que aquellos hechos por especies más pequeñas, aunque estas últimas generaron más almacenes. A nivel individual, los *M. pallidus* fueron los dispersores más eficaces, en sentido cuantitativo, ya que generaron más almacenes que otras especies evaluadas, y colocaron menos exceso de semillas en relación con el tamaño óptimo del almacén para el establecimiento de plántulas de hierba de arroz indio. Sin embargo, debido a que los *D. merriami* fueron mucho más abundantes en el sitio de estudio que otras especies, y también eficientes acumuladores y dispersores de semillas, es probable que a nivel especie sean los dispersores de semillas de hierba de arroz indio más efectivos cuantitativamente. La clasificación de las especies según su efectividad cualitativa, así como considerar los efectos del micro-sitio de almacenamiento en el establecimiento de las plántulas, fue más ambigua. Por ejemplo, los *P. longimembris* realizaron almacenes relativamente poco profundos que se corresponden más con las profundidades óptimas de siembra para la emergencia de plántulas de hierba de arroz indio, aunque es probable que los almacenes poco profundos sean descubiertos por los roedores forrajeros antes de que puedan germinar. Con la posible excepción de los *D. microps,* cualquiera de las especies que analizamos podrían ser dispersores efectivos de semillas de hierba de arroz indio.

Granivorous rodents that cache seeds for later consumption do so in 2 distinctive fashions: larder hoarding and scatter hoarding. Larder-hoarding rodents typically gather large numbers of seeds and store them in their nests or burrow chambers deep belowground.

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The larder is the product of many foraging excursions, and the contents of a larder change over time as animals add or consume items. Woodrats (*Neotoma* spp.) and pine squirrels (*Tamiasciurus* spp.) are examples of larder-hoarding rodents (Vander Wall 1990). Scatter-hoarding animals make small surface caches usually consisting of one to several items from one foraging bout. These caches are often scattered throughout an animal's home range and can exist for a few hours or for several months, but the contents are usually treated as a unit. Tree squirrels (*Sciurus* spp.) and agoutis (*Dasyprocta* spp.) exclusively scatter-hoard nuts, but there are many species of rodents that use both forms of seed storage (Vander Wall 1990). For example, most chipmunks (*Tamias* spp.) scatter-hoard during the summer and early fall and then larder-hoard seeds in late autumn to provide a winter food source (Kuhn and Vander Wall 2008). Many rodents in the family Heteromyidae also employ a combination of larder hoarding and scatter hoarding. In such species, individuals may differ in their propensities to make surface caches versus larders (Dochtermann and Jenkins 2007, Jenkins 2011).

Seeds of many plant species are dispersed by scatter-hoarding rodents. Seeds that remain in surface caches until environmental conditions favor germination can establish new seedlings, but larder hoarding is not conducive to seedling establishment (Vander Wall 1990). Establishment of seedlings from rodent caches has been found to be an important means of seedling recruitment in numerous and diverse plant species, including trees (Vander Wall 1992, Hollander and Vander Wall 2004), shrubs (Vander Wall 1994), broadleaf herbaceous plants (Barga and Vander Wall 2013), and grasses (Longland et al. 2001).

Because the probability of seedling establishment is much greater for scatter-hoarded seeds than for seeds in larders, the effectiveness of a species as a potential dispersal agent is largely dependent on the relative frequency of scatter hoarding versus larder hoarding (Vander Wall 1990). In addition to the proportions of seeds cached in these alternative manners, variation in the ways seed-caching rodents store seeds may influence the rodents' effectiveness as seed dispersers (Schupp et al. 2010). Depth of seed burial can affect seedling establishment success, and some rodent species may bury seeds at a depth that is optimal for emergence of a particular plant species (Vander Wall 1993). Microsites of cache placement can also influence probability of seedling establishment. For example, seedlings of some plants may have either greater or reduced survival when establishing near other plants. Seedlings that benefit by proximity to "nurse" plants are an example of the former, and seedlings that are harmed by resource competition with established plants are an example of the latter (Howe and Smallwood 1982, Callaway et al. 1996). The number of seeds placed in each cache can influence disperser effectiveness as well. A hypothetical rodent that scatter-hoards a small number of seeds in numerous locations may facilitate greater seedling establishment than one that caches large numbers of seeds in fewer caches (Hollander and Vander Wall 2004). This is the case especially if large caches result in high seedling mortality due to competition. Schupp et al. (2010) provides a theoretical framework that considers 2 variables—the quantity of seeds dispersed and the quality of that dispersal—as contributors to seed disperser effectiveness. Other variables may influence disperser effectiveness beyond cache attributes, such as the probability that cached seeds will be recovered and eaten. This includes the effects of pilferers recovering caches for consumption before seeds can germinate (Vander Wall 1990, Longland et al. 2001).

Various lines of evidence suggest that desert rodents in the family Heteromyidae are involved in a seed dispersal mutualism with a native bunchgrass that occurs widely throughout the desert Southwest—Indian ricegrass (*Achnatherum hymenoides*). Germination of Indian ricegrass seeds is enhanced when the seeds are handled by heteromyid rodents (McAdoo et al. 1983). Using radiolabeled Indian ricegrass seeds to follow seed fates, Longland et al. (2001) demonstrated that nearly all Indian ricegrass seedling recruitment was attributable to seedling emergence from heteromyid caches. Long-term survival of Indian ricegrass following initial seedling establishment is also greater for clumped seedlings that emerge from caches than for solitary seedlings (Longland and Dimitri 2016). Although heteromyids have a keen sense of smell for buried seeds (Johnson and Jorgensen 1981, Vander Wall et al. 2003), the husk of Indian ricegrass seeds masks odors within the seed embryo and reduces the probability that scatter-hoarded seeds will be located and consumed by pilferers naïve to their locations (i.e., individual animals other than the original cache-maker) (Longland and Dimitri 2018). This, in turn, increases the probability that a cached seed will remain in place long enough to germinate.

We conducted field experiments to determine whether coexisting heteromyid species are likely to differ in the effectiveness of dispersing Indian ricegrass seeds through their caching activities. All heteromyids have external fur-lined cheek pouches in which they carry seeds as they forage, but the family includes genera that show conspicuous differences in locomotory morphology; heteromyid fauna in the North American deserts include 2 genera of quadrupedal pocket mice (*Chaetodipus, Perognathus*) and 2 genera of saltatorial bipedal forms, kangaroo rats (*Dipodomys*) and kangaroo mice (*Microdipodops*). These forms also differ behaviorally, with quadrupeds generally being associated with microhabitats beneath shrubs or other cover and bipeds being associated with open microhabitats (see review by Reichman and Price 1993). We thus predicted that bipeds in our studies would cache seeds farther from shrub cover than quadrupeds. Heteromyids also vary dramatically in body size, with individuals of some pocket mouse species weighing <10 g as adults, while adults of a few kangaroo rat species exceed 100 g or even 150 g. Because cheek pouch volume is correlated with body size (Vander Wall et al. 1998), we expected that larger heteromyid species would either make larger caches with more seeds or would subdivide pouch-loads of seeds into more caches than smaller species. Finally, we predicted that because digging ability is correlated with body size (Morgan and Price 1992), depth of buried seeds would be directly correlated with body mass of cache-making animals.

METHODS

We conducted experiments in a sandy environment on the western slope of the Hot Springs Mountains in western Nevada (44°00′ N, 119°05′ W; ~1300 m elevation) intermittently from May to October in 2001–2004. This desert habitat is typified by scattered shrub species, including *Atriplex confertifolia, A. canescens, Kochia americana, Psorothamnus polydenius, Sarcobatus baileyi, Tetradymia spinosa,* and *T. tetrameres.* Indian ricegrass is the only common native grass at the site, but introduced cheatgrass (*Bromus tectorum*) occurs in varying densities during years with sufficient precipitation. Six species of heteromyid rodents occur at the Hot Springs Mountains, namely *Chaetodipus formosus, Dipodomys deserti, D. merriami, D. microps, Microdipodops pallidus,* and *Perognathus longimembris.* The latter 5 species occur in sandy habitat (Longland et al. 2001), while *C. formosus* is restricted to a rocky (basaltic) habitat in the upper elevations of the mountain range (USDA, ARS, unpublished data).

We conducted seed-caching experiments inside a series of 5 × 5-m rodent-proof fenced enclosures, which are described in detail in Longland et al. (2001). We tested a single animal at a time in a given enclosure. We provided an artificial burrow within each enclosure that consisted of a plastic bucket partitioned into 3 levels, buried with the lid just below the surface of the sand. Two PVC tubes that were connected to the bucket at the upper and middle levels extended to the surface to provide access tunnels. Trials were conducted with individuals of the 5 heteromyid species that occur in sandy habitat at the site (i.e., all species except *C. formosus*). For the large species tested (i.e., *Dipodomys* spp.), burrows were constructed with 19-L buckets and 5-cm-diameter PVC tubes; trials with smaller species (i.e., *M. pallidus* and *P. longimembris*) used burrows made from 7.6-L buckets and 3-cm-diameter access tubes. To give access tunnels a more natural surface texture, inner surfaces of the PVC tubes were lined with sand held in place by an adhesive. Most of the individual animals that were tested accepted the artificial burrows, but some excavated new burrows beneath a shrub inside of enclosures.

For trials, we mixed 2.0 L of sieved sand with 25 g of Indian ricegrass seeds labeled with radioactive scandium-46 (see Longland et al. 2001 for details regarding labeled seeds) and spread the seed/sand mixture to a uniform depth in a cafeteria tray near the edge of a shrub within an enclosure. Animals were live-trapped in the immediate vicinity of the enclosures in which they were tested. A single individual of one of the heteromyid species was placed inside the artificial burrow in mid- or late afternoon and left overnight. We recorded the species, sex, and body mass of each animal, and fitted them with uniquely numbered ear tags to prevent testing any individuals more than once. Animals were removed the following morning either by extracting them from the artificial burrow or by herding them into a live trap on the surface. In a small number of trials, no or very few seeds were taken overnight, in which case we left the animal in the enclosure for an additional night before removing it. Because heteromyids are known to reduce aboveground activity and alter microhabitat use under bright moonlight (Kotler 1984, Longland and Price 1991), we did not conduct any trials within a period 3 nights before or after a full moon so that all trials included several hours of darkness lacking lunar illumination.

After removing an animal from an enclosure, we sieved the contents of the cafeteria tray to recover and weigh any labeled seeds, and we determined by subtraction the mass of seeds removed from trays by foraging animals. We weighed seeds cached inside the artificial burrow and recorded these as seeds stored in a larder. The enclosure was thoroughly searched for caches using a portable Geiger counter (Eberline Model SPA-3 detector and ASP-1 recorder; Eberline Instruments, Santa Fe, NM). We marked caches with pin flags and excavated them after the plot search was completed. The distance from each cache to the nearest shrub was measured. Occasionally, we found large caches of seeds inside natural burrow tunnels excavated by animals during a trial; these were recorded as larders. We carefully removed sand at each cache with spoons and brushes, and measured the depth of the top of each cache. Seeds were then removed, and the bottom depth of the cache was measured. We counted the seeds in each cache.

To compare observed cache sizes to cheek pouch capacities of the heteromyid species, we calculated the estimated number of Indian ricegrass seeds that each species can hold in both cheek pouches combined (Table 1). This estimate was based on data given in Vander Wall et al. (1998) for cheek pouch volume of each rodent species, bulk density of Indian ricegrass seeds (1.16 g/mL), and mean number of Indian ricegrass seeds per gram (245 seeds/g). Vander Wall et al. (1998) did not include data for *M. pallidus* but did provide an equation relating body mass of heteromyid species to pouch volume, so we estimated cheek pouch volume for this species using that allometric equation.

Data Analysis

We conducted a series of mixed model analyses of variance (mmANOVAs) using Proc MIXED (SAS Institute 2012) to test for differences among species and sexes of subjects in caching behavior and cache attributes. Dependent variables tested in separate mmANOVAs included mass of seeds removed from trays, number of caches made, number of seeds per cache, distance of caches to shrubs, number of caches placed beneath shrub canopies (as opposed to in the open), the arcsine-transform of proportion of caches placed under shrubs, number of larders made, and number of seeds per larder. In the analysis of number of seeds per cache, we omitted any trials in which animals made no caches. Species and sex of animal subjects were fixed effects in these models, while year was a random factor. A Satterthwaite adjustment was used for degrees of freedom. We used Tukey-adjusted differences of least-squares (L-S) means among species pairs in each analysis to determine which species differed in these variables. We conducted linear regressions (Proc REG, SAS Institute 2012) with the same dependent variables included in mmANOVAs using body mass and sex of animal subjects as independent variables. Sex was coded as a binary dummy variable for regressions. We did not include body mass as a covariate in the first series of analyses because it differs systematically among the species tested and would therefore be confounded with the species variable included in those models. We used Proc GLM (SAS Institute 2012) to conduct a multiple analysis of variance (MANOVA) to compare caching depth among species and between sexes. Species and sex were independent class variables, while top depth and bottom depth of caches were the dependent variables.

RESULTS

The number of individuals tested varied among species depending on availability of live-trapped animals when we set up the trials. We tested ≥5 individual animals of each species in trials (Table 1), but 2 *D. microps* individuals did no caching over 2 nights, leaving only 3 usable trials for that species. Because only 1 *D. microps* individual made any surface caches and because that individual made only a single large cache, we omitted this species from statistical analyses.

All mmANOVAs and the MANOVA that we ran as full models on effects of rodent species and sex on caching variables had nonsignificant sex and species-by-sex interaction terms, so we report results of reduced models testing the main effect of species. Species did not differ significantly in mass of Indian ricegrass seeds harvested from trays during trials ($F_{3,33} = 1.04$, $P = 0.39$; Table 1). Although the 4 species took similar amounts of seeds, species differed significantly in the number of caches made per trial ($F_{3,46} = 12.40$, $P < 0.0001$); the mean number of caches made by *M. pallidus* individuals was approximately twice the number made by *D. merriami* individuals, which made the second most (Table 1). Differences of L-S means indicated that *M. pallidus* individuals made significantly more caches than did *D. merriami* ($t = 3.23$, df = 46, $P = 0.01$), *D. deserti* ($t = 5.93$, df = 46, $P < 0.0001$), or *P. longimembris* individuals ($t = 3.64$, df = 46, $P = 0.004$), and that *D. merriami* individuals made more caches than *D. deserti* individuals ($t = 3.09$, df = 46, $P = 0.02$).

Interspecific differences in numbers of caches made were counterbalanced to some extent by a significant effect of species on number of seeds per cache ($F_{3,36} = 3.89$, $P = 0.02$), because species that made the most caches tended to place fewer seeds per cache than those that made fewer caches (Table 1). However, the only species pair that differed significantly in cache sizes based on differences of L-S means were *D. deserti* and *M. pallidus* ($t = 3.11$, df = 36, $P = 0.02$), which made the largest and smallest caches respectively. Mean cache sizes were considerably smaller than numbers of Indian ricegrass seeds that these rodent species can carry in their cheek pouches (Table 1). Caches were only 10.5% of cheek pouch capacity for *D. deserti*, 19.3% for *D. merriami*, 53.1% for *P. longimembris*, 29.9% for *M. pallidus*, and 28.5% for *D. microps* (but the latter 2 values were based on estimated cheek pouch volume of *M. pallidus* and on a single *D. microps* cache).

Rodent species also differed in mean distances of caches to the nearest shrub ($F_{3,34} =$

TABLE 1. Summary of data gathered on 5 heteromyid rodent species in caching trials at Hot Spring Mountains, Churchill Co., Nevada. All values (other than those for *n* and cheek pouch capacity) are means per individual tested (standard error). Entries with a value for the mean, but none for SE, are based on a single data point.

Variable	*Dipodomys deserti*	*Dipodomys merriami*	*Microdipodops pallidus*	*Perognathus longimembris*	*Dipodomys microps*
n (males, females)	20 (10, 10)	16 (9, 7)	9 (2, 7)	5 (3, 2)	3 (2,1)
Body mass (g)	107.6 (3.2)	38.2 (1.4)	11.5 (0.2)	7.5 (0.9)	41.2 (1.6)
Seeds removed (g)	15.8 (1.6)	15.1 (2.3)	19.0 (2.0)	20.3 (3.4)	15.5 (9.0)
Caches*	2.1 (0.6)	8.3 (1.5)	16.2 (3.6)	4.2 (1.5)	0.3 (0.3)
Seeds/cache*	335.7 (57.2)	203.4 (17.4)	142.1 (25.5)	173.5 (19.3)	764.0 (—)
Cheek pouch capacity (no. of seeds)†	3191	1052	475	327	2683
Cache depth (mm), Top*	16.7 (2.9)	19.8 (2.8)	12.5 (1.6)	3.4 (1.3)	8.0 (—)
Cache depth (mm), Bottom	33.4 (3.9)	33.3 (2.9)	26.0 (2.7)	19.0 (4.3)	25.0 (—)
Distance to shrub (cm)*	139.3 (29.4)	85.8 (10.6)	191.5 (24.3)	123.5 (52.2)	40.0 (—)
Caches beneath shrubs	0.17 (0.09)	0.50 (0.20)	0.89 (0.66)	0.50 (0.29)	0 (—)
Proportion beneath shrubs	0.13 (0.09)	0.05 (0.02)	0.06 (0.04)	0.09 (0.05)	0 (—)
Larders	0.9 (0.1)	0.6 (0.2)	0.8 (0.1)	1.5 (0.3)	1.7 (0.3)
Seeds/larder	703.3 (169.5)	606.7 (246.1)	1360.0 (—)	1789.0 (581.0)	—

*Variable differs significantly among species.

†Cheek pouch capacity is the estimated number of Indian ricegrass seeds that each species can hold in both cheek pouches combined and was calculated from data in Vander Wall et al. (1998) for all species other than *Microdipodops pallidus*. For *M. pallidus*, cheek pouch capacity was estimated based on an allometric equation in Vander Wall et al. (1998).

3.66, $P = 0.02$; Table 1). Differences of L-S means indicated that *M. pallidus* placed seeds significantly farther from shrubs than *D. merriami* ($t = 3.25$, df = 34, $P = 0.01$). However, there were no significant species differences in numbers ($F_{3,33.4} = 1.31$, $P = 0.29$) or proportions of caches placed beneath shrubs ($F_{3,39} = 0.64$, $P = 0.60$; Table 1).

The mean number of larders made per trial was marginally nonsignificant among species ($F_{3,45} = 2.75$, $P > 0.05$; Table 1). However, differences of L-S means indicated that *P. longimembris* made significantly more larders than *D. merriami* ($t = 2.80$, df = 45, $P = 0.04$). Numbers of seeds per larder did not differ among species ($F_{3,13} = 2.53$, $P = 0.10$; Table 1).

Univariate statistics from the MANOVA indicated that differences occurred among species in the mean top depth of caches ($F_{3,34} = 3.26$, $P = 0.03$) but not in bottom depth ($F_{1,34} = 2.01$, $P = 0.13$). The multivariate test indicated that composite depth of seed burial was marginally nonsignificant among species (Wilks' lambda = 0.70, $F_{6,66} = 2.19$, $P = 0.06$).

As with the above analyses, the sex term and its interaction with body mass were nonsignificant in all linear regressions, so we tested reduced models that only included body mass as an independent variable. The only regressions showing significant effects of rodent body mass were those on numbers of caches that animals made per trial ($F_{1,44} = 16.23$, $P = 0.0002$; $R^2 = 0.27$) and numbers of seeds placed in each cache ($F_{1,34} = 8.44$, $P = 0.01$; $R^2 = 0.20$). Smaller animals made more caches with fewer seeds than larger individuals (Fig. 1), reflecting the above results regarding species differences, which showed that smaller species made more, but smaller, caches.

Perhaps the only noteworthy result from *D. microps* trials is that it was the only species for which all individuals made at least one larder among those individuals that did any caching at all. Two *D. microps* individuals made 2 larders and the other individual made one larder, which yielded the largest mean number of larders per trial among the 5 species tested (Table 1). Larders were often placed in natural burrows excavated by the subject, and we could usually not get accurate counts of seeds within these burrows, mainly due to the difficulty of separating whole seeds from large quantities of labeled seed shells and coarse debris.

DISCUSSION

The heteromyid species that we tested differed in seed caching behavior, including their propensities to make caches, the size and depth of those caches, and the distance they placed caches from shrub cover. Other studies have compared caching behavior among sympatric species, including work on heteromyids in the field (Leaver and Daly 2001, Hollander and Vander Wall 2004, Swartz et al. 2010) or in laboratory arenas (Jenkins and Breck 1998, Price et al. 2000, Jenkins 2011, Sivy et al. 2011). Most of this research has involved interspecific comparisons of caching behavior and cache pilferage that may facilitate coexistence of ecologically similar species. Fewer studies have considered how seedling recruitment in plants is likely to be affected by different rodent species within a community (e.g., Hollander and Vander Wall 2004, Cheng et al. 2005), as is our focus here.

We predicted that larger heteromyid species would either make more caches during trials or would make larger caches with more seeds than smaller rodent species. The first prediction was incorrect, as number of caches made was inversely related to body size, but the latter prediction was supported by a direct relationship between body size and numbers of seeds per cache (Fig. 1). This latter result suggests that interspecific differences in numbers and sizes of caches are a function of cheek pouch volume, which is correlated with body size among heteromyid species (Vander Wall et al. 1998). This is relevant to the potential fitness of a plant species dispersed by seed-caching rodents, as opportunities to establish seedlings increase with the number of locations at which an animal caches seeds during foraging activities. Although body mass was inversely correlated with numbers of caches made and directly correlated with cache sizes, the relatively low R^2 values for these relationships (see Fig. 1) and the fact that only one pair of species differed significantly in cache sizes clearly indicate that factors other than species and body mass also influence these aspects of caching behavior. Heteromyids can exhibit significant intraspecific variation in caching behavior (Dochtermann and Jenkins

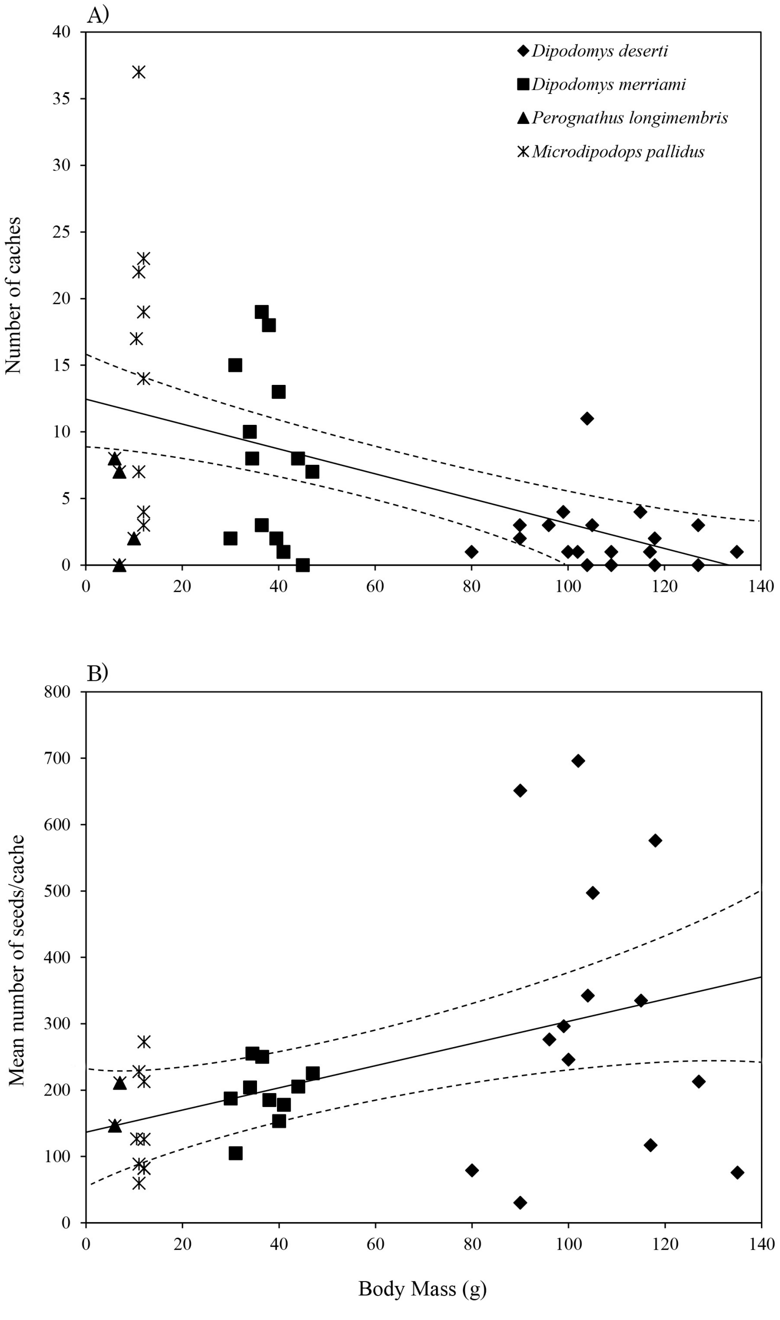

Fig. 1. Relationship between body mass of individual heteromyid rodents of 4 species tested in seed caching trials and (*A*) the number of caches made per trial (Caches/trial = −0.1[Body mass] + 12.3; $R^2 = 0.27$); and (*B*) the mean number of Indian ricegrass seeds placed in each cache (Seeds/cache = 1.6[Body mass] + 138.1; $R^2 = 0.20$). Dashed lines show the 95% confidence interval.

2007), and this varation may partially overwhelm interspecific differences that underlie body mass variation among the species we tested.

Even though interspecific differences in cache sizes were directly related to body mass and cheek pouch volume, cache sizes were much smaller for all species than the respective estimated cheek pouch capacities for Indian ricegrass seeds, based on data from Vander Wall (1998). This finding suggests that animals in our trials either made multiple caches per pouch load or did not fill their pouches to full capacity. The latter explanation seems more likely, because animals in our trials had to separate seeds from sand, whereas Vander Wall et al. (1998) presented piles of seeds unmixed with substrate. Our method would have reduced harvest rates in the present study relative to Vander Wall et al. (1998) and may have discouraged animals from filling cheek pouches to capacity. Interestingly, there was an inverse relationship between body size of heteromyid species and cache size as a percentage of cheek pouch capacity. The smallest species we tested, *P. longimembris,* made caches that were >50% of their pouch capacity, and the largest species, *D. deserti,* made caches that were only about 10% of pouch capacity. This observation implies that, relative to larger species, smaller species either filled their cheek pouches to greater capacity or placed a larger proportion of the seeds in their pouches in individual caches.

Microdipodops pallidus made nearly twice the mean number of caches per trial in our experiments than the species that made the second most, *D. merriami* (Table 1). Because number of seeds per cache was related to body size of animals tested and because *M. pallidus* is a small species, it made smaller caches than other species. Mean cache size of *M. pallidus* individuals still exceeded 140 seeds (Table 1). A previous experiment at our field site found that Indian ricegrass seedlings in clumps of 100 seeds emerged at a rate between 67.2% and 70.3% (Longland et al. 2001). Therefore, a cache as small as 140 seeds would still yield >90 seedlings, which far exceeds the number that can survive in clusters of Indian ricegrass seedlings (Longland and Dimitri 2016). Another field experiment demonstrated greater initial survival of individual Indian ricegrass seedlings within clumps of 25 seedlings than within clumps of 35, although individual seedling survival in these 2 clump sizes converged by the end of the experiment (Longland and Dimitri 2016). In a greenhouse study, McMurray et al. (1997) compared survival of Indian ricegrass seedlings as a function of number of seedlings in clumps and found that survival was maximized in the 2 largest clump size categories considered; comparing these, the 26–48 seedling category showed a small, but nonsignificant, reduction in survival relative to the 12–25 seedling category. Results of these studies suggest that mean cache sizes of all species we tested in our trials should yield seedling densities that greatly exceed the optimal density for survival of Indian ricegrass seedlings, which is the density at which competition among clumped seedlings begins to overcome facilitation. Even though *M. pallidus* individuals placed far more seeds per cache than would be optimal for maximizing seedling survival, the fact that other species deposited even more seeds per cache suggests that *M. pallidus* cache sizes were more economical for Indian ricegrass seedling establishment than cache sizes made by the other species. Our results thus suggest that among the heteromyid species we tested *M. pallidus* is the most effective disperser of Indian ricegrass seeds when these quantitative aspects of disperser effectiveness are considered (Schupp et al. 2010). Similarly, Hollander and Vander Wall (2004) concluded that 2 congeneric rodent species (*Peromyscus maniculatus* and *P. truei*) constituted effective dispersers of singleleaf piñon pine (*Pinus monophylla*) among a community of 6 granivorous rodent species, primarily because they distributed smaller numbers of seeds to more locations than the other 4 species.

The larger species we tested in caching trials (*D. deserti* and *D. merriami*), both kangaroo rats, placed seeds at greater depths than the smaller *M. pallidus* and *P. longimembris* (Table 1). However, the 2 kangaroo rat species placed caches at similar depths despite a large difference in their body masses, and our results did not support the predicted relationship between body size and caching depth. The optimal planting depth for establishment of Indian ricegrass seedlings ranges from approximately 5 mm to 20 mm; these depths yielded 61%–93% seedling emergence in greenhouse trials with 2 varieties of Indian ricegrass seeds (Young et al. 1994). While this depth range overlaps depths of caches made by all the species we tested, it is most closely matched by the top and bottom cache depths measured for *P. longimembris* caches, and secondly by those measured for *M. pallidus* caches (Table 1). Caches made by the kangaroo rat species extended deeper than this optimal depth range for seedling emergence (Table 1). However, Indian ricegrass seeds that were planted deeper showed greater seedling emergence in field trials than those planted in the optimal depth range based on greenhouse results (Young et al. 1994); seeds at greater depths experience less seed predation by rodents naïve to cache locations. Therefore, seeds placed deeper than the optimal depth for seedling establishment may actually occur in locations more favorable for reducing the chance of seed removal. Due to this uncertainty, and given the overlap between planting depths that favor Indian ricegrass seedling emergence and cache depths of all rodent species tested, we cannot confidently rank the species for disperser effectiveness based on depths that they placed seeds.

Of course, there are many factors beyond those measured here that can influence the probability of Indian ricegrass seedlings becoming established. For example, in comparing the effects of different rodent species on seedling establishment, species densities need to be considered along with effects at the level of individual animals. Based on data given in Longland et al. (2001) from intensive live trapping at the site during 1994–1996, *D. merriami* was generally far more abundant than the other species tested in our trials. Among the 4 species that yielded statistically testable results in our caching trials, *D. merriami* represented 44.0%–64.1% of trap captures; each of the other 3 rodent species was second-most abundant in one of the 3 years of trapping, but represented only 13.9%–23.6% of captures. Therefore, at the species level, *D. merriami* may account for the most establishment of Indian ricegrass seedlings at our site.

We found no support for the prediction that quadrupedal heteromyid species place caches closer to shrub cover than bipedal species do. The quadruped in our trials, *P. longimembris,* did not differ from any of the bipedal species in mean caching distance from shrubs. The only species pair that differed in this regard was *D. merriami* and *M. pallidus,* which scatter-hoarded seeds at distances nearest and farthest from shrubs, respectively, although the former species' caches were still nearly a meter from shrub cover (Table 1). The rodent species we tested also showed no differences in numbers or proportions of caches placed beneath shrubs. Another study at our site used very similar methods to consider whether interspecific differences in caching behavior may promote coexistence of desert rodent species (Swartz et al. 2010). Curiously, it found that *P. longimembris* and *M. pallidus* placed most caches under shrubs, while *D. merriami* generally cached in the open. For the 3 heteromyid species included in both studies, our sample sizes of individuals tested were considerably greater than those of Swartz et al. (2010) for *D. merriami* (16 individuals vs. 5 individuals) and *M. pallidus* (9 individuals vs. 2 individuals), but both studies had few *P. longimembris* individuals (5 individuals vs. 4 individuals). Methodological differences in the 2 studies may also have influenced caching behavior. For example, Swartz et al. (2010) used fewer Indian ricegrass seeds per trial (9 g, in 3 piles of 3 g each) than the 25 g of seeds we used per trial, and they did not mix the seeds with substrate as we did. The latter should have resulted in faster seed harvest in the Swartz et al. (2010) study, which may have influenced how animals cached seeds.

Although it is often advantageous for seedlings to emerge near established plants (Howe and Smallwood 1982), especially in arid environments (Flores and Jurado 2003), the degree to which this placement may provide a benefit for Indian ricegrass is unclear. In a field experiment testing survival of Indian ricegrass seedlings growing singly versus those growing in clumps typical of seedlings from caches (Longland and Dimitri 2016), all seedlings were planted in the open away from protective shading. Although seedling mortality was high among all seedlings, no single seedlings survived the summer heat, but a small percentage of clumped seedlings survived. Based on casual observation, the vast majority of mature Indian ricegrass bunches occur in open spaces away from shrubs. However, because desiccation causes most Indian ricegrass seedling mortality (Longland and Dimitri 2016), it is quite possible that proximity to an established shrub that provides partial shade would benefit even a species adapted to such xeric environments. Revegetation experiments by Petersen et al. (2004) demonstrated greater establishment of Indian ricegrass seedlings adjacent to rocks or logs than those in open microsites, suggesting that shading from other plants may benefit seedling establishment. Regardless of whether proximity to established plants benefits Indian ricegrass seedling establishment, the mean distances that the heteromyid species we tested placed caches from shrubs (approximately 1–2 m; Table 1) are probably too far to provide any significant shading.

Among the 4 heteromyid species that provided sufficient data for statistical analysis, we found no overall differences in numbers of larders made per trial or in number of seeds placed in larders. Our focus was primarily on seed dispersal through scatter hoarding, and except for one extremely large cache made by a single *D. microps* individual (Table 1), this species made no surface caches. However, all 3 of the *D. microps* individuals that cached seeds in our trials made at least one larder. Along a hypothetical continuum of purely scatter-hoarding versus purely larder-hoarding species, *D. microps* may fall more toward the latter end of the spectrum. Jenkins and Breck (1998) conducted laboratory caching trials and found that among 5 sympatric heteromyid species, *D. microps* cached the greatest proportion of seeds in larders. In another laboratory study, Barkley and Jacobs (2007) found that *D. microps* was less adept at retrieving caches than *D. merriami* and attributed this result to the former species being a specialized consumer of saline foliage, unlike the latter species and other heteromyids, which are largely granivorous.

Based on factors that influence qualitative effectiveness of dispersal (Schupp et al. 2010), such as location and depth of seeds, all the heteromyid species we tested appear to be effective dispersers of Indian ricegrass seeds with the exception of *D. microps,* which may be primarily a seed predator because it stores seeds in a larder. *Microdipodops pallidus* was the most effective species at our site at the level of individual animals for quantitative aspects of dispersal, particularly because this species made the most caches per trial and made caches closest to the optimal cache sizes for Indian ricegrass seedling establishment. However, the substantially greater abundance of *D. merriami* relative to other heteromyid species at the site suggests that individuals of this species may account for more recruitment than other rodent species. Land managers responsible for areas with Indian ricegrass as an important component of herbaceous vegetation should be aware of the species composition of the local granivorous rodent community, and should consider how quantitative and qualitative aspects of the rodents' seed-caching behavior may affect dispersal services and local persistence of Indian ricegrass populations.

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