

University of Nevada, Reno

**Differences in cache placement and pilferage by
desert rodents (Family: Heteromyidae)**

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science in Biology

by

Maryke Justine Swartz

Dr. Stephen H. Jenkins, Thesis Advisor

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THE GRADUATE SCHOOL

We recommend that the thesis
prepared under our supervision by

MARYKE JUSTINE SWARTZ

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**Differences in cache placement and pilferage by desert rodents (Family:
Heteromyidae)**

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

MASTER OF SCIENCE

Stephen Jenkins, Ph.D., Advisor

Stephen Vander Wall, Ph.D., Committee Member

William Longland, Ph.D., Graduate School Representative

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

May, 2009

ABSTRACT

Desert rodents in the family Heteromyidae cache seeds throughout their home ranges either concentrated in one location (larder hoard) or in multiple, small seed piles (scatter hoards). In order to maintain seed resources and minimize cache pilferage (removal by other rodents), heteromyid species may use different behavioral strategies. I examined caching and pilfering behaviors of heteromyid rodents in the field and laboratory.

I first conducted a field experiment to determine which microhabitats species use for caching and pilfering for three coexisting heteromyid rodent species: Merriam's kangaroo rat (*Dipodomys merriami*), the pale kangaroo mouse (*Microdipodops pallidus*), and the little pocket mouse (*Perognathus longimembris*). I tracked cache placement by rodents in outdoor enclosures and measured pilferage of artificial caches of radio-labeled Indian ricegrass (*Achnatherum hymenoides*) seeds. *M. pallidus* and *P. longimembris* preferred to cache seeds under shrubs, whereas *D. merriami* placed caches predominately in open microhabitat. However, *D. merriami* showed a significant preference for pilfering caches under shrubs, whereas *P. longimembris* did not show a significant preference for pilfering caches in either open or under-shrub microhabitats. I suggest that rodents may be selecting their scatter hoarding microhabitats to recover a higher proportion of food and lower the probability of caches being detected and pilfered. For each species, there are trade-offs between costs (e.g. predation risk,

pilferage risk) and benefits (e.g. predator-avoidance, pilferage-avoidance) of cache placement and cache removal in each microhabitat.

I also conducted a laboratory test and demonstrated that sandbathing behavior by *D. merriami* increases cache pilferage. During sandbathing, kangaroo rats deposit sebum from a specialized sebaceous dorsal gland and oils from other glands in the skin when they extend their bodies, slide forward on their sides, and rub their ventral regions along the sand. Most males removed more seeds from areas where either they or a conspecific had sandbathed compared to the control area. Moreover, kangaroo rats placed new caches in areas where no sandbathing occurred. However, sandbathing did not affect space use between familiar *D. merriami* individuals; kangaroo rats spent similar amounts of time in control areas and those with self and conspecific sandbathing loci. I suggest that the olfactory cues left by a sandbathing rodent signal a pilferer that another rodent was there, stimulating a cache search, and thus increase cache pilferage. *D. merriami* can avoid cache pilferage by sandbathing away from scatter hoard locations. In order to maintain seed resources and minimize cache pilferage by heterospecifics and conspecifics, heteromyid species can employ various behavioral strategies including cache placement in separate microhabitats and cache placement at a distance from sandbathing loci.

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GENERAL INTRODUCTION

Desert rodents in the family Heteromyidae temporarily cache, or bury, seeds throughout their home ranges either concentrated in one location (larder hoard) or in multiple, small seed piles (scatter hoards) in order to maintain resources for future consumption. Seed caching is an important behavioral adaptation for animals living in environments with unpredictable, limited food resources (Giannoni et al. 2001). However caches are often pilfered, or removed by other animals (Vander Wall and Jenkins 2003). Heteromyid species may employ behavioral strategies to minimize cache pilferage by either heterospecifics or conspecifics (Daly et al. 1992; Preston and Jacobs 2001).

I conducted complementary field and laboratory experiments to study different aspects of caching and pilfering behaviors of heteromyid rodents. In my field experiment, I examined whether heteromyid species cache seeds in distinct microhabitats to maintain resources and minimize cache pilferage. I compared microhabitats where rodents cache seeds and pilfer caches for three coexisting species: Merriam's kangaroo rats (*Dipodomys merriami*), pale kangaroo mice (*Microdipodops pallidus*), and little pocket mice (*Perognathus longimembris*) (Chapter I). Comparing foraging behaviors such as caching and pilfering between heteromyid rodents is important because it offers empirical insight into their mechanisms for coexistence.

I demonstrated that *M. pallidus* and *P. longimembris* preferred to place seed caches under shrubs, whereas *D. merriami* placed caches predominately in open microhabitat. However, *D. merriami* showed a

significant preference for pilfering caches under shrubs, whereas *P. longimembris* did not show a significant preference for pilfering caches in either open or under-shrub microhabitats.

Rodents may be selecting their scatter hoarding microhabitats to recover a higher proportion of food and lower the probability of caches being detected and pilfered. For each species, trade-offs between costs (e.g. predation risk, pilferage risk) and benefits (e.g. predator-avoidance, pilferage-avoidance) of cache placement and cache pilferage make some microhabitats optimal.

Although coexisting species can spatially separate caches to avoid pilferage by heterospecifics (Chapter I), they may also use strategies to prevent pilferage by conspecifics in their preferred microhabitat. One mechanism which can mediate space use between conspecifics and help maintain resources is scent marking. Kangaroo rats deposit scent during sandbathing, a behavior in which they extend their bodies, slide forward on their sides, and rub their ventral regions along the sand (Eisenberg 1963; Quay 1953; Randall 1981, 1991).

In my second study, I conducted a laboratory experiment to determine whether sandbathing affects cache detection and cache pilferage by Merriam's kangaroo rats (*D. merriami*) (Chapter II). I hypothesized that kangaroo rats use olfactory cues from sandbathing to recover their own caches and as a scent mark to avoid cache pilferage by conspecifics. Alternatively, olfactory cues left by a sandbathing rodent could signal a

pilferer that another rodent was there, stimulating a cache search, and thus increase cache pilferage.

I demonstrated that sandbathing affects cache removal by *D. merriami*. Males removed more seeds from areas where either they or a conspecific had sandbathed compared to the control area. Moreover, kangaroo rats placed new caches in areas where no sandbathing occurred. However, sandbathing did not communicate ownership of space between familiar individuals of *D. merriami*. Although some mammals scent mark near food stores to help maintain resources (Clapperton 1989; Henry 1977; Merti-Millhollen 2006; Randall 1987), I demonstrated that for *D. merriami*, scent deposition at sandbathing loci increases cache pilferage. Therefore, in order to maintain food resources, *D. merriami* should spatially separate their caching and sandbathing behaviors.

In summary, I found that spatial separation of food caches by coexisting heteromyid species will not completely prevent pilferage by other rodents, but differences in microhabitat preferences could allow species to recover a higher proportion of food and lower the probability of cache pilferage (Chapter I). In addition, I demonstrated that olfactory cues from sandbathing by Merriam's kangaroo rats increases cache pilferage by conspecifics, so kangaroo rats can avoid pilferage by placing caches away from sandbathing loci (Chapter II). In order to maintain seed resources and minimize cache pilferage by heterospecifics and conspecifics, heteromyid species employ various behavioral strategies.

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Chapter I: COEXISTING DESERT RODENTS DIFFER IN MICROHABITAT PREFERENCES FOR CACHE PLACEMENT AND PILFERAGE

ABSTRACT

Seed caching by desert rodents in the family Heteromyidae is an important behavioral adaptation for animals living in environments with unpredictable, limited food resources. Heteromyid species cache seeds throughout their home ranges either concentrated in one location (larder hoard) or in multiple, small seed piles (scatter hoards). In order to maintain resources and minimize cache pilferage (removal by other rodents), coexisting species may scatter hoard seeds in distinct microhabitats. In this field study, I examined interspecific differences in caching and pilfering behaviors to determine if caching microhabitat affects likelihood of pilferage between three coexisting heteromyid rodent species: Merriam's kangaroo rat (*Dipodomys merriami*), the pale kangaroo mouse (*Microdipodops pallidus*), and the little pocket mouse (*Perognathus longimembris*).

In outdoor enclosures, I tracked cache placement and measured pilferage of artificial caches using radio-labeled Indian ricegrass (*Achnatherum hymenoides*) seeds. *M. pallidus* and *P. longimembris* preferred to place seed caches under shrubs, whereas *D. merriami* placed caches predominately in open microhabitat. However, *D. merriami* showed a significant preference for pilfering caches under shrubs, whereas *P. longimembris* did not show a significant preference for pilfering caches in

either open or under-shrub microhabitats. The two species pilfered similar numbers of caches.

For each species, trade-offs between costs (e.g. predation risk, pilferage risk) and benefits (e.g. predator-avoidance, pilferage-avoidance) of cache placement and cache removal make some microhabitats optimal.

Coexisting heteromyid rodent species may create environmental heterogeneity in terms of available resources by caching in different microhabitats, thereby minimizing cache pilferage by other species.

INTRODUCTION

Seed caching by desert rodents in the family Heteromyidae is an important behavioral adaptation for animals living in environments with unpredictable food resources (Giannoni et al. 2001). Andersson and Krebs (1978) proposed that food-caching could only become evolutionarily stable if the individual caching food has a higher probability of recovering its caches than other individuals in a community. However a recent review demonstrated that heteromyid rodents pilfer 26-51% of artificial caches (Vander Wall and Jenkins 2003). Rodents pilfer artificial caches and real caches at a similar rate (Vander Wall et al. 2006). To minimize cache pilferage, heteromyid species may cache seeds in distinct microhabitats. In this study, I examined interspecific differences in caching and pilfering behavior to determine if caching microhabitat affects likelihood of pilferage. Comparing foraging behaviors such as caching and

pilfering between heteromyid rodents is important because it offers empirical insight into their mechanisms for coexistence.

As many as six species of heteromyid rodents can coexist in a community (Brown 1973), a phenomenon of continuing interest for community ecologists due to the ecological similarity of heteromyids (Randall 1993). Coexisting heteromyid rodents are all nocturnal and fossorial, they utilize the same food resources, and they share the same predators (Brown et al. 1979). Since most heteromyid species are granivores, they depend on the seed production of various desert plant species. The availability of seeds is limited and varies temporally and spatially. In order to maintain seed resources, these rodents bury seeds throughout their home ranges, either concentrated in one location (usually a burrow) or in multiple, small seed “piles”. These food-hoarding behaviors are termed larder hoarding and scatter hoarding, respectively.

Despite the large body of literature on heteromyids, it has not yet been determined how foraging behavior contributes to coexistence. Traditionally, mechanisms of coexistence were studied in terms of the initial acquisition of seed resources (i.e. resource partitioning; Brown et al. 1979; Kotler and Brown 1988; Price 1978a; Wondolleck 1978). However, studies showed that most heteromyids are generalist granivores that do not have strong preferences for seed species (Reichman 1975; Smigel and Rosenzweig 1974) or seed sizes (Lemen 1978). Trapping and bait-station data suggest that heteromyids partition microhabitats during foraging; quadrupedal pocket

mice (*Perognathus* and *Chaetodipus* spp.) more readily take seeds from shrub-covered microhabitats, whereas bipedal kangaroo rats (*Dipodomys* spp.) and kangaroo mice (*Microdipodops* spp.) more readily exploit open areas (Daly et al. 1992; Harris 1984; Lemen and Rosenzweig 1978; Price 1978a; Price 1978b; but see Thompson 1987, Leaver and Daly 2001). However, it is not clear how this relates to selection of cache sites and pilfering of caches made by other individuals.

Although the acquisition of seeds is important for desert rodents, maintaining these limited resources is essential for survival. Resource maintenance involves three stages: 1) harvesting seeds, 2) burying or caching seeds, and 3) retrieving stored seeds. Researchers have recently begun studying the implications for species coexistence of the latter two stages in heteromyid seed management (Leaver and Daly 2001). Differences in caching strategies (larder hoarding versus scatter hoarding; Price et al. 2000), cache recovery, and pilferage ability (Price and Mittler 2003) have been suggested to facilitate coexistence. Supporting this possibility, Price and Mittler (2003, 2006) used models to demonstrate that species coexistence was facilitated when cache exchange occurred between heteromyids and when species exhibited behavioral differences, including in the ability to pilfer caches. The ability to exploit different microhabitats for caching versus pilfering may be one behavioral difference involved in coexistence.

Although studies have demonstrated that caches made by rodents are at risk of pilferage by other rodents (Daly et al. 1992; Leaver and Daly 2001; Murray et al. 2006; Preston and Jacobs 2001), we do not have a complete understanding of whether species differ in their abilities to avoid seed pilferage by competitors. Heteromyids use behavioral strategies to prevent pilferage, including optimal spacing of caches (Daly et al. 1992) and changing food-hoarding strategies from scatter hoarding to larder hoarding in response to pilferage by conspecifics (Preston and Jacobs 2001). Animals may also avoid pilferage by transporting food to areas where potential pilferers are absent or uncommon. In an evolutionary arms race scenario, a caching species should conceal their caches in locations where costs are greater for a potential pilferer. For example, kangaroo rats may cache mainly in open microhabitat, where they can evade aerial predators by jumping erratically more effectively than quadrupedal pocket mice (Longland and Price 1991), and therefore reduce pilferage by pocket mice.

In this study, three different hypotheses were examined. First, if species exhibit caching preferences for certain microhabitats, it may limit their encounters with other species' caches and, therefore, their opportunity to pilfer. Thus, if species prefer distinct microhabitats for caching and pilfering, pilferage by heterospecifics is unlikely.

Second, species use a broad range of microhabitats for both cache placement and pilfering. Thus, caches are at risk of both intraspecific and interspecific pilferage; however, cache pilferage may be tolerated. According

to Vander Wall and Jenkins (2003), communities with high pilferage rates, including heteromyid rodent communities, can be stable if the exchange of seeds is a reciprocated behavior between conspecifics or perhaps between heterospecifics. Therefore, reciprocal pilferage could occur between species that utilize the same microhabitats.

The third hypothesis is that species prefer distinct microhabitats to make caches but pilfer caches in different or all microhabitats. In this case, preferring a certain microhabitat for cache placement is not entirely driven by avoiding pilferage by heterospecifics since other species may pilfer in the microhabitat. Preferring a certain microhabitat for cache placement could be due to various non-mutually exclusive factors, including predation risk, soil moisture, social dominance, and avoidance of pilferage by other species that do not utilize that microhabitat for caching. Pilferage of caches by heterospecifics may be reduced because a microhabitat may be more costly to a pilferer in terms of predation risk for certain species. In this hypothesis, pilferage between species is reduced relative to pilferage between conspecifics, but reciprocal pilferage still occurs between conspecifics and heterospecifics.

In this study, caching and pilferage behaviors were compared between three coexisting heteromyid rodent species: Merriam's kangaroo rats (*Dipodomys merriami*), pale kangaroo mice (*Microdipodops pallidus*) and little pocket mice (*Perognathus longimembris*). Specifically, I compared the species in terms of 1) preferred microhabitat for scatter hoarding seeds and

2) preferred microhabitat for pilfering caches. The first hypothesis (see above) predicts that heteromyid rodent species will prefer separate microhabitats for cache placement and pilferage that are similar to their microhabitat preferences for space use and seed harvesting. Thus, it predicts that pocket mice (*P. longimembris*) will prefer to scatter hoard seeds and pilfer caches under shrubs, whereas kangaroo rats (*D. merriami*) and kangaroo mice (*M. pallidus*) will prefer open microhabitat for scatter hoarding and pilfering. The second hypothesis predicts that heteromyid rodents will not show a microhabitat preference to scatter hoard or pilfer caches, which would facilitate reciprocal pilferage. The third hypothesis predicts that heteromyid rodents will prefer distinct microhabitats to scatter hoard seeds but will not have a microhabitat preference for pilferage.

METHODS

Study site

This study was conducted during the summers of 2007 and 2008 in outdoor enclosures at the Hot Springs Mountains, ~14 km east of Fernley, Nevada (11 323007 E, 4395366 N). This site was a sand dune habitat with perennial shrub species including *Sarcobatus baileyi*, *Atriplex confertifolia*, *A. canescens*, *Psoralea polydenius*, *Tetradymia spinosa*, and *T. tetrameres*. Annual plant species, including cheatgrass (*Bromus tectorum*), Indian ricegrass (*Achnatherum hymenoides*), and Russian thistle (*Salsola paulsenii*, and *S. tragus*) were also abundant at this site. Other plants included *Camissonia*

claviformis, *Sphaeralcea munroana*, *Gilia leptomeria*, *Phacelia bicolor*, *Streptanthella longirostris*, *Malacothrix sonchoides*, *Mentzelia albicaulis*, and *Halogeton glomeratus*. The rodent community consisted of several nocturnal heteromyid species as well as one diurnal sciurid rodent, *Ammospermophilus leucurus*.

Trials were conducted in two enclosures of approximately 5 m by 5 m. The enclosures were built in 1994 using four corner poles and fencing of reinforced 0.6-cm mesh hardware cloth. Fences were 0.75 m aboveground and 0.5 m below ground. Along the top of the fences, 30 cm wide strips of sheet aluminum were attached to prevent rodents from entering and escaping.

Outside of enclosures, I buried artificial burrows which had been made to mimic the diameter of natural burrows of different species. For trials with the larger species, *D. merriami*, an artificial burrow (18.9-L bucket) was buried outside of the enclosure with two attached PVC tubes (55 cm length and 3.8 cm diameter) that extended into the enclosure and rested on top of the sand. A smaller artificial burrow (7.6-L bucket) with two PVC tubes (65 cm length and 2.5 cm diameter) was used in trials with *P. longimembris* and *M. pallidus*.

To prevent harvester ants (*Pogonomyrmex salinus*) from entering the enclosures and removing seeds, 30 cm wide strips of sheet aluminum were buried approximately 45 cm away from the fence and stood approximately 20 cm aboveground. I removed an ant colony in one enclosure by shoveling the ants and sand away from the enclosure and applied commercial insecticide between the fence and sheet aluminum on the ground at both enclosures.

The vegetation inside the enclosures included *A. canescens*, *B. tectorum*, *P. polydenius*, *A. hymenoides*, *S. tragus* and *S. paulsenii*. I removed Indian ricegrass and Russian thistle seedlings to enhance differences between shrub cover and open microhabitats. I also trimmed seed heads from Indian ricegrass plants within the enclosure to decrease the likelihood that rodents would forage from natural sources. I calculated percent cover of vegetation inside each enclosure by dividing the area covered by vegetation by the total area in an enclosure. I assumed each plant was circular with an area of $\pi*r^2$ and estimated the diameter of each plant by averaging length and width measurements.

Seed bank

To assess the seed bank prior to scatter hoarding trials, I collected 20 soil samples (10 from open microhabitats, 10 from under shrubs) using random coordinates in each enclosure. Each sample was collected using a 165 mL metal container and was placed into a Ziploc[®] bag. In the lab, I drained each sample through a sieve with a 1 mm opening. Using a dissecting microscope, I identified and counted seeds in each sample. Based on known heteromyid preferences for seed species, only Indian ricegrass (*A. hymenoides*), cheatgrass (*B. tectorum*), and Russian thistle (*Salsola* spp.) were quantified (McAdoo et al. 1983, Kelrick et al. 1986, Longland 2007).

Soil moisture

Since soil moisture can affect a rodent's ability to find buried caches (Vander Wall 2000), I collected soil samples on 15 and 21 August 2008. On both days, I collected four soil samples from each enclosure using a 165-mL metal container—two from open microhabitats, two from under-shrub microhabitats. I placed each sample in a Ziploc[®] bag and weighed them at the lab. I then dried the 16 soil samples in an oven at 80°C for three days. The samples were reweighed after the drying period. Due to an apparent measuring error, one sample was removed from the analysis.

Radiolabeling seeds

In order to locate and map caches in scatter hoarding and pilfering trials, commercial “Nezpar” Indian ricegrass (*Achnatherum hymenoides*) seeds (Granite Seed, Lehi, Utah, USA) were labeled using scandium-46, a biologically inactive, gamma-emitting radionuclide with a half-life of 84 days. The decay product is titanium-46 which is not radioactive and non-toxic (Emsley 2001; National Nuclear Data Center). I used a Geiger counter to find each cache location. This technique has been used in several rodent-caching studies, including in my study area, and showed no apparent harmful effects on the rodents (e.g. Hollander and Vander Wall 2004; Longland et al. 2001; Vander Wall 2000). Indian ricegrass seeds were labeled with the radioisotope at the University of Nevada, Reno, by sealing them in containers with ScCl₃ and distilled water for approximately 1 hour. After seeds absorbed the moisture, they

were dried for 48 hours. I transported radiolabeled seeds to the field site following radiation safety protocols.

Scatter hoarding trials

In May 2007, before scatter hoarding trials were conducted, I removed rodents from the outdoor enclosures during three trap nights. The outdoor enclosures had been accessible to rodents in previous studies via small openings at the base of the fences, so I covered these openings with mesh hardware cloth. I captured four individuals during trapping and relocated them approximately 8-16 km away in a similar habitat. Scatter hoarding trials were conducted between June and August 2007 in the outdoor enclosures.

To obtain study subjects, I set up a 10 x 5 trapping grid with 50 traps spaced 10 m apart approximately 50 m north of the enclosures using long Sherman live traps baited with commercial mixed bird seed. Trapping was conducted the night before a trial. During trapping sessions, I gave each rodent left and right ear tags and recorded its weight, sex, and reproductive status. For each trial, I transported an individual trapped on the grid to an enclosure and placed it into the artificial burrow outside of the enclosure.

I gave each individual 12 g of radio-labeled Indian ricegrass seed. Indian ricegrass is an abundant, native plant in the study area and its seeds are highly preferred by heteromyid rodents (McAdoo et al. 1983). I set out three 4 g piles of seed at different locations (using random coordinates of the enclosure) in an open area, under a shrub and along the periphery of a shrub. Placing seed piles

in different microhabitats controlled for the possibility that the placement of caches by rodents could be the result of rapid sequestration of an abundant resource (Jenkins and Peters 1992). For example, if rodents scatter hoard seeds close to the seed source to sequester resources as quickly as possible in each microhabitat type, then I would not find a preference for a caching microhabitat. During scatter hoarding trials, each individual was allowed 24 hours to cache seeds.

The day following a caching trial, I located caches using a Geiger counter, removed the caches using a spoon and sieve, and counted the seeds in each cache. In addition, the coordinates of each cache location and the distance to the nearest shrub or fence were measured. Seeds found inside the artificial burrow or in a rodent burrow (larders) were not considered in analyses. If a rodent did not run out from a burrow while I was removing caches, the animal was trapped the following night and returned to its original location on the trapping grid. Trials were successfully conducted with four *P. longimembris* (three females, one male), five *D. merriami* (three females, two males) and two *M. pallidus* (one male, one female). Due either to low population size or low capture success on my trapping grid, three *P. longimembris* and one *M. pallidus* had to be collected from another trapping grid that was being used for a different study, approximately 100 m from the enclosures.

Pilfering trials

Between June and August 2008, I conducted trials comparing cache pilferage behavior in the same outdoor enclosures used in 2007. I set up a 9 x 8 trapping grid with 72 traps spaced 10 m apart approximately 100 m north of the trapping grid used in 2007. One individual *D. merriami* and one *P. longimembris* from this grid were used for pilfering trials. However, due to poor trapping success of *P. longimembris*, I set up a new 9 x 8 trapping grid with 72 traps approximately 150 m west of the enclosures, which I used from July to August. Six individual *D. merriami* and six *P. longimembris* were used in pilfering trials from this grid. Traps were again baited with a commercial bird seed mix. I used the same trapping and marking methods that were used in 2007, except that I marked only *P. longimembris* that were used in trials with a unique ear punch pattern. In 2007, *P. longimembris* captures were so few that each captured individual was used in a trial, but in 2008 the capture rate was much higher (Table 1). Ear tags consistently fall off little pocket mice, so in order to ensure that individuals were only used in one trial, an ear punch technique was used. Both ear tags and ear punches left notches in rodents' ears. *M. pallidus* was not captured in 2008 and therefore was not used in pilfering trials.

I trapped rodents the night preceding pilfering trials. Before I placed a trapped individual into the artificial burrow of an enclosure, I made 12 artificial caches to mimic real caches in the enclosure, six in open microhabitat and six in under-shrub microhabitat. Conducting studies using artificial caches is

informative because any removal of seeds can be attributed to pilferage (Vander Wall and Jenkins 2003). Furthermore, Vander Wall et al. (2006) found that artificial caches and real rodent caches are pilfered at similar rates by *Tamias amoenus*.

I made the artificial caches using Indian ricegrass seeds labeled with a scandium isotope (see above). I determined locations of artificial cache sites by using random coordinates within the enclosure. All caches were spaced at least 0.5 m apart to reduce the chance of a pilferer finding an additional cache after discovering one (Leaver 2004). Caches in open microhabitat were placed at least 10 cm from the fence or edge of a shrub. Caches in shrub microhabitat were placed anywhere from the edge of the shrub to the base or stem. If a random location did not fit these criteria, a new location was chosen.

I created each cache using a 1.9 cm hollow, aluminum tube with a fitted wooden dowel inside. I placed the dowel and tube 1 cm into the sand to create a hole. *Dipodomys* spp. and *Perognathus* spp. can detect caches at this depth (Hollander and Vander Wall 2004; Johnson and Jorgensen 1981). Once I removed the dowel from the tube, I dropped 0.5 g (~130 seeds) of radio-labeled Indian ricegrass seeds through the tube into the hole. This is approximately the mean size of Indian ricegrass caches made by heteromyid rodents (Longland and Clements 1995). When I lifted the tube out of the sand, the seeds remained 1 cm deep while the fine sand covered the cache.

Using gloves, I “patted down” each artificial cache to remove any visual evidence of disturbance of the sand.

Each *D. merriami* or *P. longimembris* individual was given 24 hours to pilfer the artificial caches. I then removed the pilferer and located caches using a Geiger counter. For each cache, I recorded the coordinates, counted the number of seeds, and measured the distance to the edge of the nearest shrub or fence. Seven *P. longimembris* (three females, four males) and seven *D. merriami* (four females, three males) were used in trials, but data for one male *P. longimembris* was not analyzed due to its inactivity.

RESULTS

Percent cover of vegetation in enclosures

In 2007, the percent cover of vegetation was 11.4% in one enclosure and 13.3% in the second. In 2008, corresponding values were 22.6% and 19.2%. The difference in vegetation cover between years was due to new growth of *Salsola* spp. Although the amount of vegetation cover was different between years, it was similar between enclosures in each year.

Seed bank

A two-way analysis of variance (ANOVA) was conducted using the total number of seeds (*A. hymenoides*, *B. tectorum*, and *Salsola* spp.) per sample as the response variable and microhabitat type and enclosure as predictor variables. There was no difference in number of seeds in the seed bank

between enclosures ($F_{1, 39} = 0.01$, $P = 0.936$) or between microhabitat types ($F_{1, 39} = 0.04$, $P = 0.833$), and there was no significant interaction between enclosure and microhabitat type ($F_{1, 39} = 0.86$, $P = 0.359$). Thus, I did not expect cache placement to be affected by the number of available seeds in an enclosure's seed bank.

Soil moisture

Percent soil moisture in samples was compared using a two-way ANOVA with microhabitat type and enclosure as predictor variables. There was no difference in percent soil moisture between open and under-shrub microhabitats ($F_{1, 14} = 35.78$, d.f. = 1, $P = 0.105$) or between enclosures ($F_{1, 14} = 0.01$, $P = 0.942$). The interaction between microhabitat type and enclosure was also not significant ($F_{1, 14} = 0.05$, $P = 0.830$). On average (\pm SD), soil from both enclosures contained $0.47 \pm 0.03\%$ water which indicates very dry conditions. In fact, the average monthly precipitation was $1.18 \text{ mm} \pm 1.06$ from June to August 2007 and $0.59 \text{ mm} \pm 0.82$ from June to August 2008 (Western Regional Climate Center).

Rodent community composition

In 2007, the heteromyid rodent community consisted of *D. deserti*, *D. merriami*, *D. microps*, *M. pallidus*, and *P. longimembris* (Table 1). The community composition was similar in 2008 except that *M. pallidus* was not captured and one *Chaetodipus formosus* was captured. Although the majority

(85.2%) of the captures in 2007 were *D. merriami*, only 50% of captures were *D. merriami* in 2008 while 20.7% were *P. longimembris* (Table 1).

Scatter hoarding trials

D. merriami made caches of similar size in the two microhabitats (paired t-test: $t = -1.08$, $N = 4$, $P = 0.359$; Table 2). Only one *M. pallidus* and one *P. longimembris* placed caches in the open. The *M. pallidus* made similar size caches in both microhabitats (two-sample t-test: $t = -0.01$, d.f. = 9, $P = 0.994$). However, the *P. longimembris* made caches with more seeds under shrubs compared to the cache it made in the open (one-sample t-test: $t = 10.0$, $N = 2$, $P = 0.063$). Moreover, the *M. pallidus* and *P. longimembris* individuals that did place caches in the open made fewer caches compared to the caches they made under shrubs (Table 2).

To analyze scatter hoarding trials, a one-way ANOVA was calculated using species as the predictor variable and the mean distance of caches to a shrub edge or fence as the response variable. Since the number of seeds per cache varied, each distance to a shrub edge or fence was weighted by the number of seeds in a cache. Pairwise comparisons between species were calculated using Tukey's test with a family-wide error rate of 0.05.

The mean distance (\pm SD) of caches from a shrub edge or fence was 25.14 cm \pm 11.70 for *D. merriami*, -2.37 cm \pm 2.31 for *M. pallidus*, and -11.64 cm \pm 2.77 for *P. longimembris*. Zero is considered the shrub edge, so negative distances for *M. pallidus* and *P. longimembris* indicate that caches were placed

under shrubs. The weighted mean distances of scatter hoarded caches from shrub edges or fences were significantly different between species ($F_{2, 10} = 14.68$, $P = 0.002$; Figure 1). Even when cache distances were not weighted by number of seeds, species were different in cache placement ($F_{2, 10} = 22.29$, $P = 0.001$; Appendix Figure A1).

All pairwise comparisons using Tukey's test showed that *D. merriami* differed in cache placement from *M. pallidus* and *P. longimembris*. However *M. pallidus* did not significantly differ from *P. longimembris*. Thus, *D. merriami* placed caches away from shrub edges, whereas *P. longimembris* and *M. pallidus* placed caches under shrubs.

Pilfering trials

On average (\pm SD), individual Merriam's kangaroo rats pilfered seeds from $65.5 \pm 14.8\%$ of artificial caches whereas little pocket mice pilfered $52.8 \pm 18.0\%$ of available caches. Caches were considered pilfered if a cache contained ≤ 120 *A. hymendoides* seeds (although 0.5 g of *A. hymendoides* ≈ 130 seeds, a more conservative estimate was used to adjust for measuring error). Merriam's kangaroo rats and little pocket mice did not differ in the proportion of caches pilfered (two sample t-test: $t = 1.38$, d.f. = 9, $P = 0.202$).

Kangaroo rats had more seeds remaining in artificial caches that were in the open compared to the under-shrub microhabitat (Appendix Figure A2). Some individual pocket mice had more seeds remaining in caches in the open whereas other individuals had more seeds remaining in caches under shrubs (Appendix

Figure A3). In order to statistically compare cache removal, or pilfering behavior, in the two microhabitats for each species, each individual's twelve caches were ranked by the number of seeds remaining. The rank sum was then compared between the two microhabitat types for each species using a paired t-test. *D. merriami* showed a significant preference for pilfering caches under shrubs (paired t-test: $t = 2.61$, $N = 7$, $P = 0.04$; Figure 2). *P. longimembris* did not show a significant preference for pilfering caches from open or under-shrub microhabitats (paired t-test: $t = 0.46$, $N = 6$, $P = 0.666$; Figure 2).

Four individual *P. longimembris* and four *D. merriami* made new caches during trials. Cache placement was compared to the results I obtained in 2007 during scatter hoarding trials using a general linear model. Similar to my analysis used in 2007, the response variable was the mean cache distance to nearest shrub edge or fence which was weighted by the number of seeds per cache. Species and year were both fixed factors used in the model. Cache distances were again significantly different between species ($F_{1, 16} = 7.37$, $P = 0.018$) and did not differ significantly between years ($F_{1, 16} = 2.29$, $P = 0.154$). In addition, the species by year interaction was not significant ($F_{1, 16} = 2.72$, $P = 0.123$).

DISCUSSION

Merriam's kangaroo rats preferred to place their caches in open microhabitat whereas little pocket mice and pale kangaroo mice scatter hoarded seeds predominately under shrubs. For kangaroo rats and pocket mice, this finding is similar to their microhabitat preferences for space use and harvesting

seeds (Daly et al. 1992; Harris 1984; Lemen and Rosenzweig 1978; Price 1978a, 1978b; but see Thompson 1987; Leaver and Daly 2001). This result is also consistent with a finding by Hollander and Vander Wall (2004) for preferences of two other heteromyid species' for scatter hoarding seeds: Panamint kangaroo rats (*Dipodomys panamintinus*) preferred open microhabitat whereas Great Basin pocket mice (*Perognathus parvus*) preferred under-shrub microhabitat. However, kangaroo mice in this study preferred to scatter hoard seeds under shrubs, despite their preference for harvesting seeds in the open (Harris 1984).

Preferences for harvesting microhabitats have been attributed to heteromyid locomotion and anti-predator behavior; bipedal rodents (kangaroo rats and kangaroo mice), which are more closely related to each other than to pocket mice (Hafner et al. 2008), use their erratic jumping ability to evade predation attempts more effectively in the open (Longland and Price 1991) compared to quadrupedal rodents (pocket mice) that tend to use shrub cover to avoid predators. The two *M. pallidus* I studied tended to cache near the edges of shrubs, which would still allow them to use their erratic jumping ability to escape predators. Alternatively, kangaroo mice may be excluded from open microhabitat by competitive interference from kangaroo rats. Thus, body size (kangaroo mice and pocket mice are smaller than kangaroo rats) may be as important as locomotion in determining space use. Interspecific differences in body size may make one microhabitat type more preferable for caching seeds. For example, soil under shrubs may be looser, allowing a smaller-bodied rodent to dig more effectively. Another non-mutually

exclusive possibility is that kangaroo mice use a caching strategy in which they not only use shrub edges to minimize pilferage by heterospecifics, but also make smaller caches (Table 2) to make their caches less apparent to foragers. Although heteromyids have incredible olfactory abilities (Johnson and Jorgensen 1981), caches with fewer seeds have a lower chance of being discovered and removed by pilferers (Geluso 2005) especially in dry soil. Kangaroo mice have not been studied as extensively as kangaroo rats and pocket mice. More studies of the foraging behavior of kangaroo mice should be conducted to fully understand coexistence mechanisms of heteromyid rodent communities.

Although Merriam's kangaroo rats and little pocket mice preferred distinct microhabitats to place caches in, the rodents preferred to pilfer caches in other or all microhabitat types, which supports the third hypothesis discussed earlier. Preferences for caching microhabitats may be due to various non-mutually exclusive factors, including predation risk and avoidance of pilferage by other species.

The finding that Merriam's kangaroo rats preferred to pilfer caches under shrubs has two alternative explanations. First, kangaroo rats could find caches under shrubs if they use this microhabitat to harvest seeds or make scatter hoards. However, most studies suggest that they primarily use open microhabitats during seed acquisition (e.g. Daly et al. 1992; Harris 1984; Lemen and Rosenzweig 1978; Price 1978a, 1978b), and this study demonstrated that they also prefer to cache seeds in open microhabitat.

Alternatively, kangaroo rats may prefer to eat or move caches from under-shrub microhabitat to open microhabitat in order to maintain and enhance their own resources. In fact, kangaroo rats in this study did move caches into open microhabitat. The more caches that are available for a kangaroo rat in the open, a microhabitat which may be more costly for pocket mice to use, the more likely a kangaroo rat will survive, especially when seed production is low.

My results show that some individual pocket mice preferentially pilfer caches in the open despite the greater risk of predation. Moreover, pocket mice and kangaroo rats in this study pilfered at similar rates. These rates of cache removal may be affected in natural conditions (i.e. outside of enclosures) by competitive interference. Kangaroo rats dominate access to artificial seed patches by chasing away pocket mice (Leaver and Daly 2001). However, pocket mice may have an advantage over kangaroo rats in their ability to pilfer larder hoards in burrows of other pocket mice as well as kangaroo rats. Larger-bodied kangaroo rats are unable to enter pocket mice burrows.

Price (1978) found that in the absence of competitors in enclosures, *Perognathus* spp. used a broader range of microhabitats whereas *D. merriami* maintained its microhabitat preference for large, open spaces. However, microhabitat use between species remained heterogeneous (Price 1978), which suggests that microhabitat preferences are not only the result of competitive interactions. Other causal explanations include interspecific differences in foraging efficiency or predator avoidance in certain microhabitats.

The rate of pilferage was high in this study (Merriam's kangaroo rats pilfered $65.5 \pm 14.8\%$ of artificial caches and little pocket mice pilfered $52.8 \pm 18.0\%$ of caches). Although this rate may be amplified by the fact that they did not have their own caches to recover elsewhere, artificial cache pilferage has been shown to be similar to the rate of pilferage of real rodent caches (Vander Wall et al. 2006). Despite the possibility that rates of pilferage are high under natural conditions, cache makers still have a recovery advantage over naïve pilferers because they can use spatial memory to retrieve their caches (Jacobs 1992, Vander Wall et al. 2006). Moreover, scatter hoarding rodents prefer to remove their own caches (Vander Wall et al. 2008).

One lab study showed that microhabitat use of cache makers shifts after pilferage events (Preston and Jacobs 2001). However, pilferage may occur so frequently in the field that these rodents may deal with pilferage throughout their lives so that continuously changing caching strategies would not be beneficial. Reciprocal pilferage may be a more efficient strategy for these coexisting rodents.

The ability to detect and remove seeds is critical for survival of scatter hoarding rodents during times when there is little or no seed production. To retrieve caches, rodents can remember precise locations of cache sites (Jacobs 1992; Vander Wall et al. 2006) or use a subset of microhabitats for cache sites and search only those types of locations. Studies of tits and chickadees (*Parus* spp.) have shown that birds preferentially use certain cache microhabitats to increase the probability of cache recovery (Brodin

1994; Petit et al. 1989) and certain species avoid caching in the same sites as other species (Suhonen and Alatalo 1991). Similarly, rodents may be selecting their scatter hoarding microhabitats to recover a higher proportion of food and lower the probability of caches being detected and pilfered. For each species, trade-offs between costs (e.g. predation risk, pilferage risk) and benefits (e.g. predator-avoidance, pilferage-avoidance) of cache placement and cache removal make some microhabitats optimal.

Coexistence mechanisms are thought to exist when there are trade-offs among species in their abilities to utilize resources in environments with heterogeneity. Coexisting heteromyid rodent species may contribute to environmental heterogeneity in terms of available resources by caching in different microhabitats, thereby minimizing cache pilferage by other species.

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TABLES

Table 1. Number and percent of captures per year of rodent species at the Hot Springs Mountains, Nevada in 2007-2008. Capture rate = (number of captures/number of trap-nights) X 100.

Species	Year (number of trap-nights)			
	2007 (490)		2008 (720)	
	No. of Captures (% of captures)	Capture rate (%)	No. of captures (% of captures)	Capture rate (%)
<i>Ammospermophilus leucurus</i>	1 (0.4)	0.2	2 (1.7)	0.3
<i>Chaetodipus formosus</i>	0	0	1 (0.9)	0.1
<i>Dipodomys deserti</i>	21 (8.4)	4.3	18 (15.5)	2.5
<i>Dipodomys merriami</i>	213 (85.2)	43.5	58 (50)	8.1
<i>Dipodomys microps</i>	5 (2.0)	1.02	13 (11.2)	1.8
<i>Microdipodops pallidus</i>	1 (0.4)	0.2	0	0
<i>Perognathus longimembris</i>	6 (2.4)	1.2	24 (20.7)	3.3
<i>Peromyscus maniculatus</i>	3 (1.2)	0.6	0	0

Table 2. Mean number of seeds per cache (cache size) and mean number of caches in different microhabitats for individuals of three heteromyid rodent species. SD=standard deviation. * indicates that only one individual had cache(s) in the microhabitat.

Species	n	MICROHABITAT			
		Open		Under-shrub	
		Cache size (SD)	No. caches (SD)	Cache size (SD)	No. caches (SD)
<i>Dipodomys merriami</i>	5	154.1 (167.7)	4.6 (1.9)	113.0 (122.3)	2.5 (1.7)
<i>Microdipodops pallidus</i>	2	30.5 (*)	3(*)	56.9 (37.4)	5.5 (3.5)
<i>Perognathus longimembris</i>	4	6.0 (*)	1(*)	92.0 (56.2)	5.8 (5.5)

FIGURES

Figure 1. Cache placement by three heteromyid rodent species in relation to the nearest shrub or fence edge. Mean distances to the nearest shrub or fence for each individual (open circles) are weighted by seeds per cache. Triangles indicate species' means and the dotted line indicates the shrub or fence edge. Negative distances indicate caches were underneath shrubs. *Dipodomys merriami* significantly differs from *Microdipodops pallidus* and *Perognathus longimembris* (pairwise comparisons using Tukey's test).

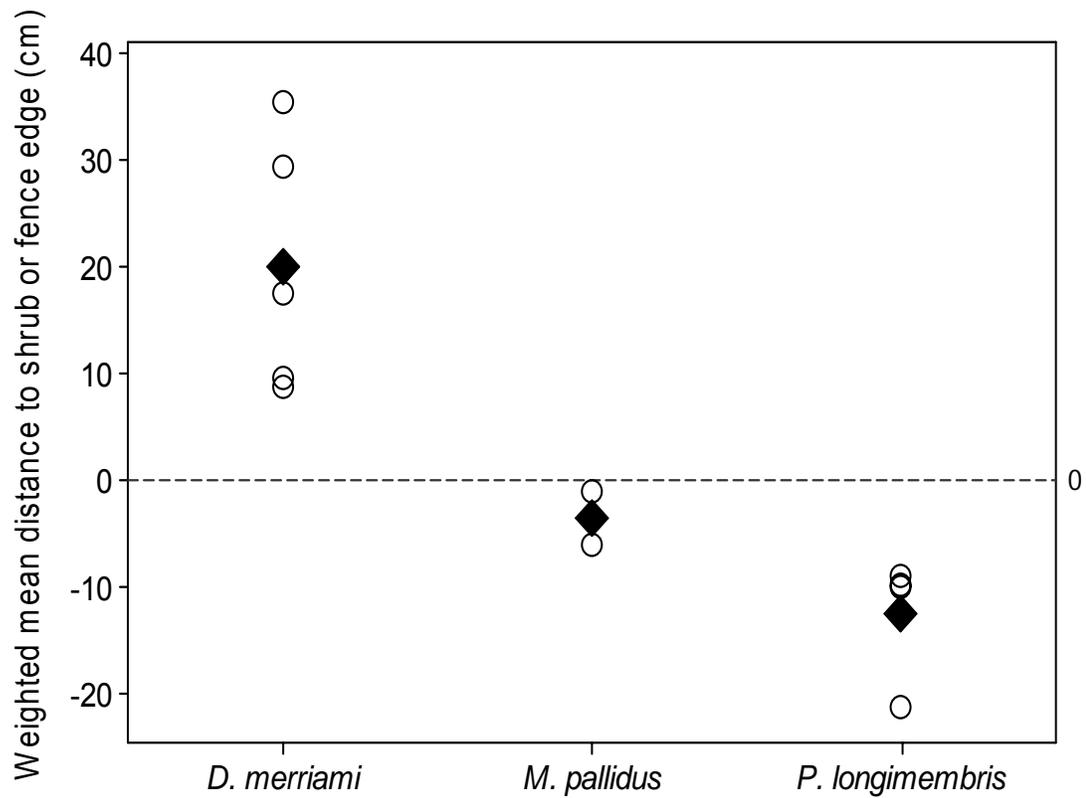
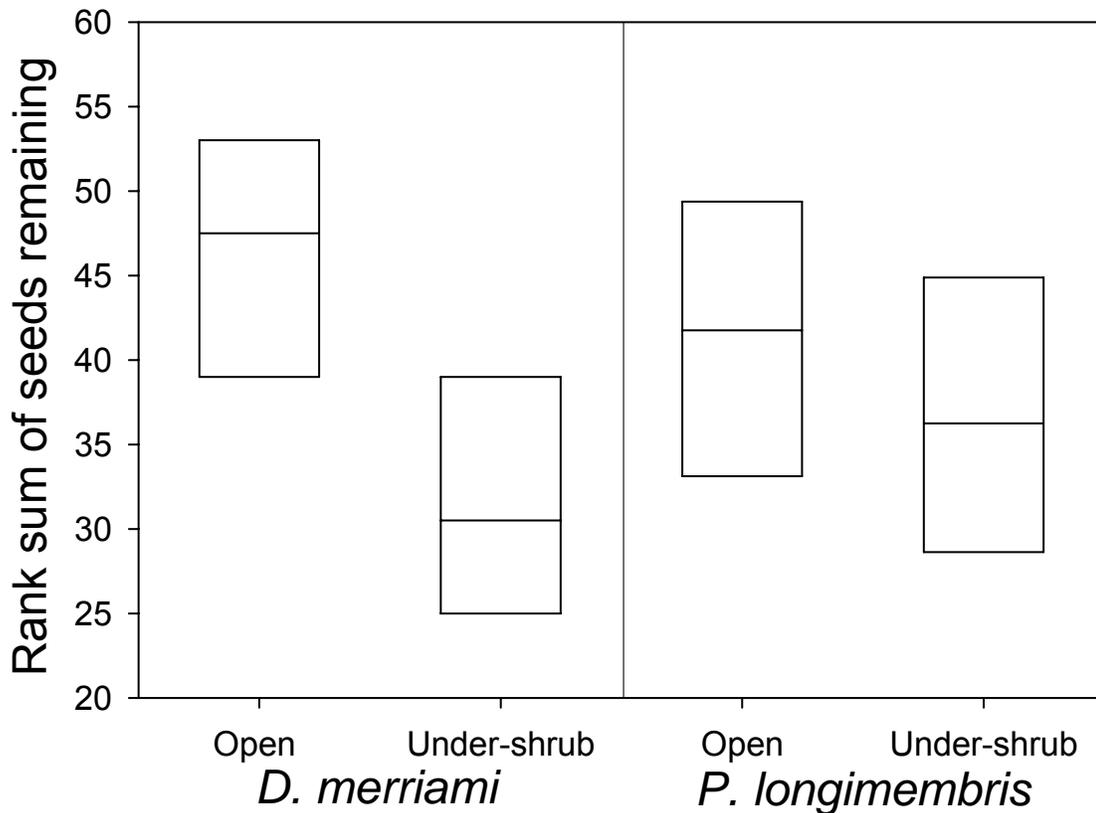


Figure 2. Rank sum of seeds remaining in artificial caches provided to *D. merriami* and *P. longimembris*. Each individual searched for 6 caches of approximately 130 seeds in open and under-shrub microhabitats. *D. merriami* pilfered significantly more caches in under-shrub microhabitat than in open microhabitat, whereas *P. longimembris* did not show a significant preference. The line within each box represents the median, the boundary above the median represents the 75th percentile, and the boundary below the median represents the 25th percentile.



APPENDIX

Figure A1. Cache placement for three heteromyid rodent species in relation to a shrub or fence edge. Triangles indicate species' means and the dotted line indicates the shrub or fence edge. Negative distances indicate caches were underneath shrubs.

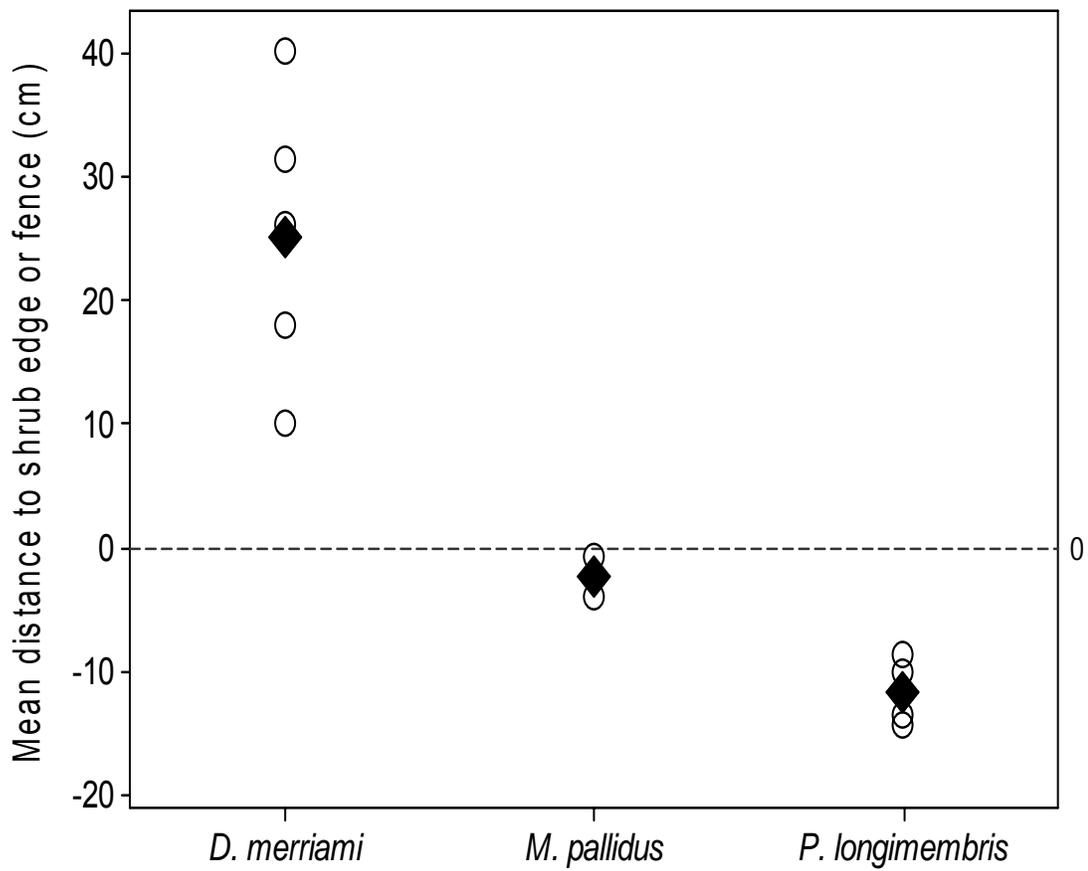


Figure A2. Number of seeds remaining in artificial caches after pilferage trials for seven *D. merriami* individuals. Six artificial caches of approximately 130 seeds were provided in both under-shrub and open microhabitats.

Individual

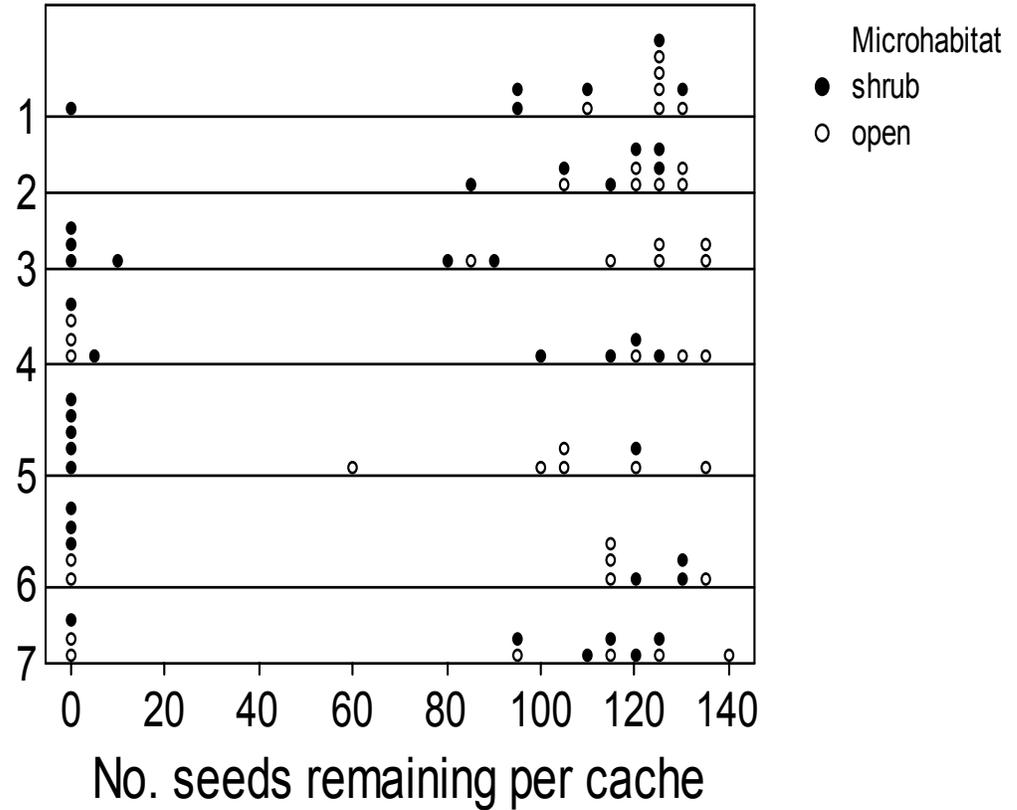
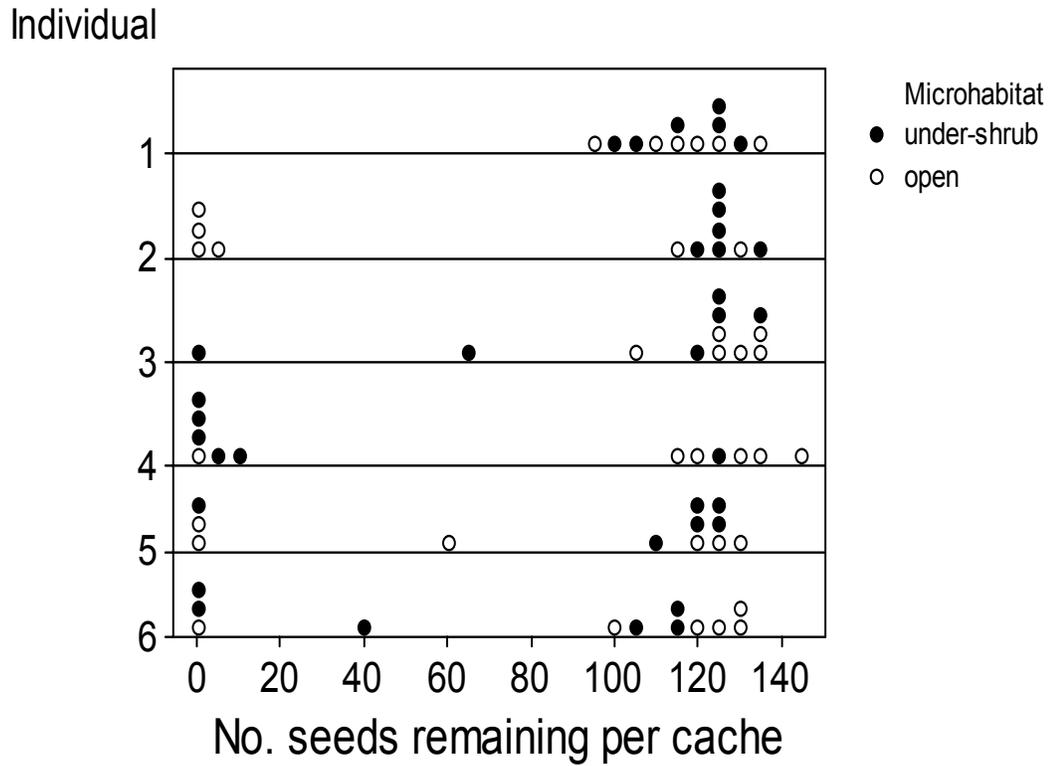


Figure A3. Number of seeds remaining in artificial caches after pilferage trials for six *P. longimembris* individuals. Six artificial caches of approximately 130 seeds were provided in both under-shrub and open microhabitats.



Chapter II: DOES CACHE PILFERAGE BY *DIPODOMYS MERRIAMI* INCREASE NEAR SANDBATHING LOCI?

ABSTRACT

Kangaroo rats deposit scent during sandbathing, a behavior in which they extend their bodies, slide forward on their sides, and rub their ventral regions along the sand. This study examined whether sandbathing by kangaroo rats affected their ability to detect and remove buried seed caches, which are critical to their survival. Kangaroo rats may use olfactory cues from sandbathing to recover their own caches and as a scent mark to avoid cache pilferage, which is the removal of caches by other animals. Alternatively, olfactory cues left by a sandbathing rodent may signal a pilferer that another rodent was there, stimulating a cache search, and thus increase cache pilferage.

A lab study was conducted using male Merriam's kangaroo rats (*Dipodomys merriami*) to test the following hypotheses: (1) scent marking affects the probability that seed caches are found and (2) sandbathing communicates ownership of space between familiar individuals.

D. merriami spent similar amounts of time in control quadrants and those with self and conspecific sandbathing loci in arenas and therefore, sandbathing did not affect space use. However, sandbathing did affect cache removal. Individual kangaroo rats varied in their preferences to harvest caches from quadrants with different sandbathing treatments. Most males removed more seeds from areas where either they or a conspecific had sandbathed compared to the control area. Moreover, seventy-five percent of kangaroo rats placed new

caches in areas where no sandbathing occurred. In order to avoid cache pilferage by conspecifics, *D. merriami* should sandbathe away from scatter hoard locations.

INTRODUCTION

Many mammals communicate with conspecifics by scent marking with specialized apocrine or sebaceous glands. Scent marking can have different functions, depending on the species. Scents can be used for defense, such as in skunks (*Mephitis* spp.), territorial marking, as in deer (Family Cervidae, Ralls 1971), defense of food resources, as in foxes (*Vulpes* spp., Monclus et al. 2009), as well as other social interactions. Kangaroo rats (*Dipodomys* spp.) scent mark to communicate information to other individuals by depositing scent during sandbathing (Eisenberg 1963; Randall 1981b), a behavior in which individuals extend their bodies, slide forward on their sides, and rub their ventral regions along the sand. During sandbathing, sebum from a specialized sebaceous dorsal gland and oils from other glands in skin are deposited (Eisenberg 1963; Quay 1953; Randall 1981a, 1991). Sandbathing functions not only to maintain the pelage but also to communicate information (Eisenberg 1963; Randall 1981a, 1981b).

Although several studies have demonstrated that scents deposited at sandbathing sites convey information about an individual's identity to conspecifics (Eisenberg 1963; Randall 1981a, 1981b, 1991), it is unclear how kangaroo rats use this information. Randall (1991) suggested that olfactory

signals from sandbathing function in neighbor and mate recognition. Another potentially important and non-mutually exclusive function of scent marking, which has not yet been studied, is its role in food cache recovery. Other animals use scent marks to maintain their resources and increase foraging efficiency (Begg et al. 2003; Clapperton 1989; Henry 1977; Mertl-Millhollen 2006; Stout and Goulson 2001). Kangaroo rats may use olfactory cues from sandbathing to relocate and recover their own caches (i.e. buried seed “piles”) and scent mark to avoid cache pilferage, which is the removal of caches by other animals. Alternatively, olfactory cues left by a sandbathing rodent may signal a pilferer that another rodent was there, stimulating a cache search, and thus increase cache pilferage.

Kangaroo rats are primarily granivorous rodents that maintain their food resources by burying seeds throughout their home ranges either concentrated in one location (usually a burrow) or in multiple, small seed piles in shallow soil. These food-hoarding behaviors are termed larder hoarding and scatter hoarding, respectively. The bannertailed kangaroo rat (*D. spectabilis*) larder hoards its food resources in its burrow and sandbathes primarily around the burrow entrance. According to Randall (1987), sandbathing helps *D. spectabilis* maintain its food resources and social relationships through advertising competitive ability and mediating space use. Olfactory cues from sandbathing may also mediate space used by scatter hoarding kangaroo rat species and help them maintain their food resources.

The ability to detect and remove seeds from caches is critical for the survival of scatter hoarding rodents during times when there is little or no seed

production. Rodents recover their own caches using random digging, spatial memory (Barkley and Jacobs 2007, 1998; Jacobs 1992; Vander Wall et al. 2006), visual cues (Pyare and Longland 2000), and olfactory cues (Johnson and Jorgensen 1981). Olfactory cues deposited during sandbathing may assist or deter a rodent during cache recovery.

In order to maintain resources, individual kangaroo rats should avoid or minimize cache pilferage. Studies have demonstrated that caches made by rodents are at risk of pilferage (Leaver and Daly 2001; Murray et al. 2006; Preston and Jacobs 2001), and rodents use different behavioral strategies to prevent pilferage (Daly et al. 1992). Instead of actively defending scatter hoards, kangaroo rats may deposit an olfactory cue during sandbathing to reduce cache pilferage. Other animals may associate individual scents with positive or negative experiences, and scents of some animals could discourage a conspecific from entering the territory of the marker (Halpin 1986). Therefore scent marking may result in the reduction of cache pilferage. Individuals that are submissive (Blaustein and Risser 1976; Hargett 2006; Newmark and Jenkins 2000) may not remove caches with scent from a more dominant individual. Avoidance behavior can increase foraging efficiency and decrease aggressive interference (Perri and Randall 1999).

Alternatively, scent from an aggressively dominant individual may not deter a rodent from pilfering a cache when it is not present, especially during times of low seed production. Furthermore, if sandbathing provides an olfactory cue to a rodent retrieving its own caches, it could also provide a cue to a

conspecific about the relative location of caches. The olfactory cue left by a sandbathing rodent would then increase cache pilferage. If this is the case, we would not expect kangaroo rats to sandbathe near cache sites or cache near sandbathing loci.

Mechanisms of social spacing, including odor, may function to allow coexistence between overlapping species and individuals (Perri and Randall 1999). Odors are important in the spacing of many mammal species (Gosling 1982). Different desert rodent species partition microhabitats for caching and foraging (Chapter I; Brown et al. 1979; Kotler and Brown 1988; Price 1978; Wondolleck 1978), and olfactory cues from sandbathing may help space overlapping conspecifics within a microhabitat and minimize cache exchange. For example, in open microhabitat, kangaroo rats may scent mark to assist in cache retrieval and also to avoid cache pilferage. Scents at sandbathing loci seem to communicate ownership since kangaroo rats can distinguish between familiar and unfamiliar conspecifics (Randall 1991). Furthermore, recognition of the scents of neighbors minimizes aggression and promotes tolerance in non-social species (Randall 1991; Shier and Randall 2007).

I conducted a lab study with male Merriam's kangaroo rats (*D. merriami*) to test the following hypotheses: (1) scent marking affects the probability that seed caches are found and (2) sandbathing communicates ownership of space between familiar individuals. *D. merriami* sandbathe and scatter hoard seeds throughout their home ranges (Perri and Randall 1999). Since *D. merriami* males have overlapping home ranges (Perri and Randall 1999; Randall 1993)

and repeatedly encounter their neighbors, a behavioral signal, like a scent mark, that reflects motivation or fighting ability can reduce the cost of aggressive interactions (Shier and Randall 2007). Thus, scent marks from aggressively dominant individuals near caches may help to avoid pilferage by other rodents.

Alternatively, olfactory cues from sandbathing may primarily function in neighbor and mate recognition and indirectly provide a signal that another rodent was present that may have been caching seeds. Although kangaroo rats do not spend as much time investigating scent from familiar individuals (Randall 1991), a brief investigation at sandbathing loci could increase the likelihood of encountering and pilfering caches. If sandbathing provides a general cue for cache location, then more seeds will be pilfered from sandbathing loci compared to a control. Furthermore, if sandbathing mediates space use, then kangaroo rats will spend less time near sandbathing loci of a conspecific compared to his own sandbathing loci and control areas.

METHODS

I captured four male Merriam's kangaroo rats in the Hot Springs Mountains, Nevada (11 323824E, 43 98103N), in July 2007; and five males at Nightingale Flat, Nevada (11 328465E, 44 10172N), in September 2007 using long Sherman live traps baited with a commercial bird seed mixture. Individuals were housed in a 12:12 light:dark cycle in the animal care facility of the Biology Department of the University of Nevada, Reno. Each animal was maintained in a 47 x 27 x 15 cm cage with sand, a plastic tube for a "burrow", and cotton material

for nesting. Subjects were fed ad libitum amounts of commercial bird seed and were given lettuce as a periodic source of supplemented water.

I conducted foraging trials between June and September 2008. I removed sand from the kangaroo rats' cages three days prior to trials to allow body oils to accumulate and to stimulate sandbathing behavior upon receiving sand. The kangaroo rats were housed in the lab in close proximity; however, to ensure that individuals were familiar with each other, I presented them with scent from a conspecific on the day of a foraging trial. Males were familiarized with each other to minimize investigation of conspecific sandbathing loci during cache-removal trials.

I collected body oils from the conspecific by pressing a microscope slide along each side of its body four times, moving in an anterior to posterior direction. I then pressed the microscope slide over the dorsal gland two times to collect sebum. I placed the "scented" microscope slide inside the burrow of the test (focal) kangaroo rat after ensuring that the animal was awake. I moved to the opposite side of the room, out of sight from the individual, and waited quietly. Usually, after less than a minute, I heard the kangaroo rat moving and presumably investigating the slide. I presented a slide for 5 minutes every hour for five hours before foraging trials began. Kangaroo rats become familiar with conspecifics' scent in this time period (Randall 1987, 1991).

After the fourth scent presentation, I transported individuals that would be used in foraging trials from their housing room to an arena room. The kangaroo

rats acclimated to the arena room for 30 minutes, and then I presented the focal male with the conspecific-scented slide for the fifth time.

The arena room had red lighting and contained two 91 cm by 81 cm arenas. I positioned cameras above each arena and connected them to a television in a separate, adjacent room so that I could record and observe trials without disturbing animals. Each arena was divided into quadrants by wooden dividers and was filled with sand \approx 4 cm deep for each trial.

Prior to the cache-removal phase of a trial, two males sandbathed in separate quadrants of an arena. First, I placed the focal subject (i.e. the cache remover) in a quadrant (Figure 1) to sandbathe twenty times before being removed. I watched the individual from the television in the adjacent room and counted the following sandbathing behaviors: side rolls, side rubs or extensions, and ventral rubs or extensions. After the focal male completed sandbathing (which usually took less than 5 minutes), I placed him in a clean, sand-filled cage to allow him to continue to sandbathe. Then, I placed the conspecific male that was familiarized earlier with the focal male into the quadrant opposite where the focal male had sandbathed (Figure 1). I waited for the conspecific male to sandbathe twenty times before he was returned to his cage. I used one of the two remaining quadrants that neither male sandbathed in as a control (Figure 1) by disturbing the sand with a wooden dowel to mimic tail drags. I used the fourth quadrant as a release site for the focal male during the cache-removal phase (Figure 1). For each trial, treatments applied to quadrants and male pairings

were randomly selected, except that I adjusted the ordering to ensure that individuals had at least one week between trials.

After both males had sandbathed and were back in their respective cages, I removed the wooden dividers in the arena and created artificial caches in the two quadrants where sandbathing occurred and the control quadrant. In each of these three quadrants, five artificial caches containing 1 g of white millet seed were made and spaced approximately 10 cm apart in an “x-shaped” pattern, resembling the five on a die. The average size of white millet caches made by *D. merriami* is 1 g (Price et al. 2000). I made artificial caches using a hollow, aluminum tube with a wooden dowel that fit inside. I inserted the aluminum tube and wooden dowel 2 cm into the sand, removed the dowel, and poured the millet into the tube. When I lifted the tube out of the sand, the seeds remained 2 cm deep and the fine sand covered the cache. Using the wooden dowel, I made squiggles through the sand on top of caches to mimic tail drags and to minimize any obvious disturbance. *D. merriami* can detect caches at a 2 cm depth (Reichman and Oberstein 1977).

I conducted the cache-removal phase of trials approximately 1 hour after the focal male initially sandbathed. I released the focal male into the quadrant which did not contain artificial caches, and he was allowed 20 minutes to explore and harvest artificial caches. To stimulate foraging, kangaroo rats were food deprived for twelve hours prior to trials. Trials were videotaped and the program *JWatcher* (version 1.0, Blumstein 2007) was used to quantify the time kangaroo rats spent in each quadrant.

At the end of each trial, I put the kangaroo rat back in his cage and took both males back to their housing room. Eighteen trials were conducted using 9 individuals as both focal and conspecific males in two trials. Focal males were paired with a different conspecific male in each trial.

In order to determine the mass of seeds pilfered during a trial, sand was removed from the arenas. Bottoms of arenas contained a fine-mesh screening over a removable wooden board. When I removed the board, sand drained out of the arena, and caches remained in place. I then weighed remaining caches and noted any new caches.

DATA ANALYSIS

To determine if sandbathing treatments affected time spent in quadrants, a general linear model with a repeated measures design was conducted using MINITAB. Individual variation was examined using subject as a random factor. Trial number and quadrant treatment (i.e. the focal subject sandbathing, a conspecific sandbathing, or control) were also predictor variables in the model and were defined as within-subject fixed factors. The position of the quadrant in arenas was also included as a within-subject fixed factor since arenas were mounted to a wall and therefore could not be changed for each trial. The response variable was the natural logarithm of the ratio of the proportion of time spent in treatment quadrants divided by the proportion of time spent in the release quadrant. Since the proportion of time spent in one quadrant was not independent of the time spent in other quadrants and the proportions of time sum

to 1, proportions of time were transformed to natural logarithmic ratios using the proportion of time spent in the release quadrant as the denominator (Aebischer et al. 1993).

A second general linear model was conducted to determine if the predictor variables (sandbathing treatments, trial number, quadrant position, and subject) affected the amount of seed kangaroo rats removed from quadrants in the arena. Trial number, quadrant treatment, and quadrant position were within-subject fixed factors in the model, and subject was a random factor. The response variable was the mass of seeds removed by kangaroo rats.

RESULTS

Merriam's kangaroo rats spent similar amounts of time in all quadrants of the arena regardless of their sandbathing treatments (Figure 2) and position in the room (Table 1). The interactions of subject and quadrant treatment, trial number and quadrant treatment, subject and trial number, and trial number and quadrant position were also not significant (Table 1).

Kangaroo rats harvested more seed from the quadrant where they sandbathed and from the quadrant where a conspecific male sandbathed compared to the control quadrant (Figure 3, 4). Although quadrant treatment by itself was not a significant factor, the subject by quadrant treatment interaction was significant (Table 2). Thus, treatment affected which quadrants individual kangaroo rats preferred to remove seeds from. Subjects either harvested more seed from the quadrant where the conspecific male sandbathed or preferred to

take seed from the quadrant where it had sandbathed compared to the control, except one male that did not show a treatment preference during cache removal (Figure 4).

The quadrant position in the arena did not significantly affect the amount of seeds harvested (Table 2). The interactions of trial by quadrant treatment and trial by quadrant position were both not significant (Table 2). However, individual kangaroo rats significantly differed in the amount of seeds they removed, and there was a significant trial by subject interaction (Table 2; Figure 5).

In order to compare the amount of seed taken from caches with sandbathing treatments and the control, a third general linear model with a repeated measures design was conducted. Subject was a random, fixed factor and the within-in subject factors were trial number and sandbathing occurrence. When the mass of seeds removed from both quadrants in which sandbathing occurred were averaged and compared to the mass of seeds removed from the control quadrant, kangaroo rats preferred to remove seed from quadrants with sandbathing treatments ($F_{1, 35} = 4.85$, $P = 0.037$). Again, subjects significantly differed in the amount of seed removed ($F_{8, 35} = 8.04$, $P < 0.0001$). Trial number was not a significant effect ($F_{1, 35} = 0.14$, $P = 0.712$).

Kangaroo rats usually removed a relatively small amount of seed from caches; only 4.1% of the total artificial caches had more than half (0.5 g) of the seed removed. This may be due to the fact that the rodents only had twenty minutes to forage. However, ten of eleven of the caches (90.9%) that had more

than 0.5 g of millet removed were harvested from quadrants where either the focal male or conspecific male sandbathed.

Four kangaroo rats made new caches during cache-removal trials. The average cache size (\pm SD) of the kangaroo rats was 1.05 g (\pm 0.18) which supports other findings noted earlier and my justification for the cache size used in this study. Three of four individuals placed their new caches in the control or release quadrants where neither individual sandbathed. The fourth male made seven new caches during two trials; three caches were placed in the quadrant where he sandbathed, three were placed in the release quadrant, and one cache was placed in the quadrant where a conspecific male sandbathed.

DISCUSSION

Kangaroo rats spent equivalent amounts of time in quadrants where sandbathing occurred and did not occur, which indicates that sandbathing did not mediate space use between *D. merriami* in this experiment. However, it is possible that the experimental design did not allow for differences in space use to be apparent. For example, the arena size used in this experiment may not have been large enough for the kangaroo rats to show preferences for areas with or without specific sandbathing treatments. Randall (1987) found that sandbathing behavior by *D. spectabilis* was different in larger field enclosures than in neutral laboratory arenas (Lepri and Randall 1983); *D. spectabilis* did not sandbathe over other individuals' sandbathing loci, as was observed in the lab, but instead sandbathed in its own area within a larger enclosure. However, Randall (1991)

used an even smaller arena than mine (60 cm in diameter) to show that kangaroo rats could distinguish between scent of familiar and unfamiliar conspecifics. Moreover, male Merriam's kangaroo rats have overlapping home ranges, so presumably they should be able to make distinctions even within a small area.

Another possible explanation for the lack of differences in the time spent in different quadrants in this study is that the novelty of the arena may have had a greater effect on behavior than the olfactory cues from sandbathing. In the field, *D. merriami* sandbathes throughout its home range (Randall 1981b) and immediately after emerging from its burrow (Randall 1981a) which indicates that sandbathing has some sort of scent-marking function. Perhaps sandbathing can only mediate space use once home ranges and dominance hierarchies are established. Future studies should be conducted correlating sandbathing loci and space use by *D. merriami* in the field before this hypothesis is rejected.

Although sandbathing did not affect space use by *D. merriami*, it did affect the amount of seed kangaroo rats pilfered from artificial caches. Eighty-nine percent of males preferred to pilfer seeds from where they sandbathed or from sandbathing loci of a conspecific male (Figure 4). Individuals varied in their preference for either self-scented or conspecific-scented loci. This is consistent with past studies that have demonstrated that Merriam's kangaroo rats show individual variation in different behaviors including food hoarding and response to cues from conspecifics (Dochtermann and Jenkins 2007; Jenkins et al. 1995; Murray et al. 2006).

These differences in preference for self-scented loci versus conspecific-scented loci may reflect dominance status. Perhaps dominant males preferred removing caches from subordinate males, whereas subordinate males may not have been willing to risk costly interactions by foraging near the sandbathing loci of a dominant conspecific. Shier and Randall (2007) suggested that male *D. heermanni* communicate their dominance status during sandbathing. Dominant males sandbathed at higher frequencies, possibly to advertise their competitive ability, whereas subordinate males sandbathed less frequently and were unwilling to interact with dominant males (Shier and Randall 2007). Since dominance status was not measured in this study, its effect on cache removal and pilferage remains unclear.

Perhaps males were attracted to scents at sandbathing loci regardless of dominance status and then “discovered” artificial caches. Randall (1981b) found *D. merriami* was attracted to sandbathing loci of conspecifics. However, once males were familiarized with scent from conspecific males, they did not spend as much time investigating scents (Randall 1991). Males were familiarized with each other in this study; however it is possible that they were still attracted to these areas which then led to an increase in cache pilferage. Consistent with this, human scent also increased the rate of cache removal by rodents (Wenny 2002).

The fact that 75% of males put their new caches in “unscented” quadrants suggests that sandbathing may not only affect cache removal by kangaroo rats, but also cache placement. Thus, in order to avoid cache pilferage by

conspecifics, *D. merriami* should scatter hoard seeds away from sandbathing loci or sandbathe away from cache locations.

For some mammals, including the bannertailed kangaroo rat (*D. spectabilis*), scent marking near food stores helps maintain resources (Clapperton 1989; Henry 1977; Merti-Millhollen 2006; Randall 1987). I have demonstrated that for *D. merriami*, scent deposition at sandbathing loci increases cache pilferage. In order to maintain food resources and maintain familiarity with conspecifics, *D. merriami* should spatially separate their caching and sandbathing behaviors.

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TABLES

Table 1. ANOVA results for ln(proportion of time in treatment quadrant/proportion of time in release quadrant) for *D. merriami* during cache-removal trials in arenas with three treatment quadrants (focal male sandbathed, conspecific male sandbathed, and no male sandbathed) and a release quadrant.

Effect	SS	d.f.	MS	<i>F</i>	<i>P</i>
Subject	20.527	8	2.719	1.08	0.453
Trial No.	0.028	1	0.030	0.01	0.910
Subject*Trial No.	24.866	8	2.116	2.65	0.075
Quadrant Treatment	0.688	2	0.396	0.36	0.705
Subject*Quad Treatment	20.051	16	1.148	1.44	0.283
Trial No.*Quad Treatment	2.039	2	1.177	1.48	0.274
Quadrant Position	4.478	3	1.071	1.34	0.315
Trial No.*Quad Position	3.877	3	1.292	1.62	0.246
Error	7.975	10	0.798		
Total	84.530	53			

Table 2. ANOVA results for mass of seeds removed by *D. merriami* during cache-removal trials in laboratory arenas. Significant *P* values are bold.

Effect	SS	d.f.	MS	<i>F</i>	<i>P</i>
Subject	7.581	8	0.861	4.06	0.009
Trial No.	0.007	1	0.003	0.02	0.883
Subject*Trial No.	1.064	8	0.132	5.87	0.006
Quadrant Treatment	0.581	2	0.144	1.68	0.215
Subject*Quad Treatment	1.562	16	0.095	4.21	0.013
Trial No.*Quad Treatment	0.157	2	0.082	3.65	0.065
Quadrant Position	0.195	3	0.053	2.35	0.134
Trial No.*Quad Position	0.042	3	0.014	0.62	0.616
Error	0.225	10	0.022		
Total	11.414	53			

FIGURES

Figure 1. Arena setup for trials comparing foraging behavior of *D. merriami* in self-scented and conspecific-scented areas. The focal (F) male sandbathed in one quadrant, and a male conspecific (C) sandbathed in another quadrant. The control was in the third quadrant for cache-removal trials. The focal rodent was released into the fourth quadrant.

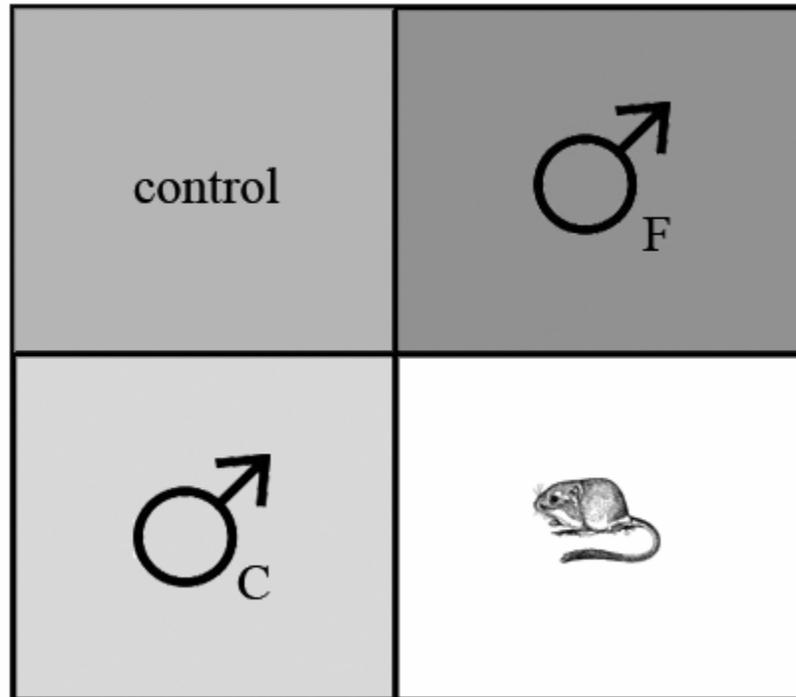


Figure 2. Proportion of time nine *D. merriami* males spent in different quadrants of an arena during two cache-removal trials. Quadrants had one of the following treatments: 1) a focal male sandbathed and I created artificial caches 2) a conspecific male sandbathed and I created artificial caches 3) no rodent sandbathed but I created artificial caches. Zero indicates that individuals spent equal time in a treatment quadrant compared to a release quadrant. The line within a box represents the median, the boundary above the median represents the 75th percentile, and the boundary below the median represents the 25th percentile. Whiskers above the box indicate the 90th percentile and whiskers below the box indicate the 10th percentile.

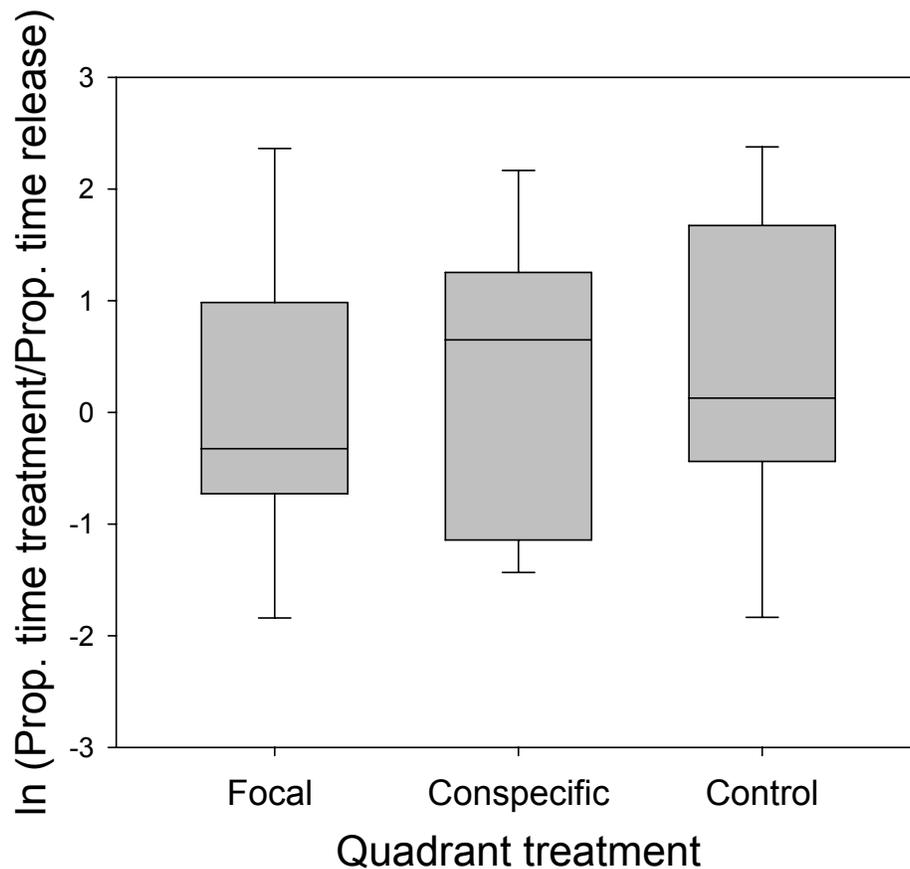


Figure 3. Average mass of seeds removed from artificial caches by nine male *D. merriami* during two laboratory trials. Seeds were harvested from an arena which had three quadrants with the following treatments: 1) the harvesting (focal) male sandbathed 2) a conspecific male sandbathed 3) no male sandbathed (control). Standard error bars are shown.

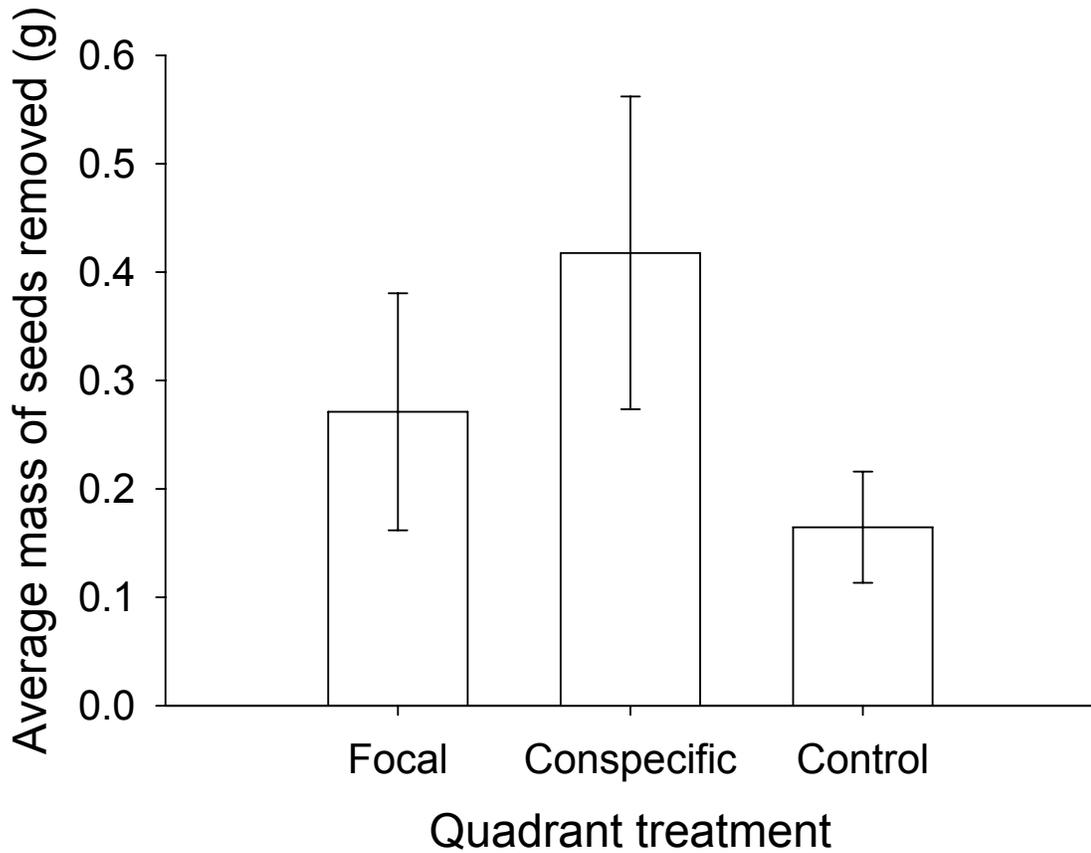


Figure 4. Ternary plot of the proportions of seed removed by nine *D. merriami* from three different treatment quadrants within an arena totaled across two trials. The bottom axis represents the proportion of seed removed from the quadrant in which a conspecific male sandbathed. The right axis represents the proportion of the seed taken from the quadrant where the focal male had self-sandbathed. The left axis represents the proportion of seed removed from a control quadrant where neither kangaroo rat sandbathed. Point in center represents a male that did not have a pilferage preference.

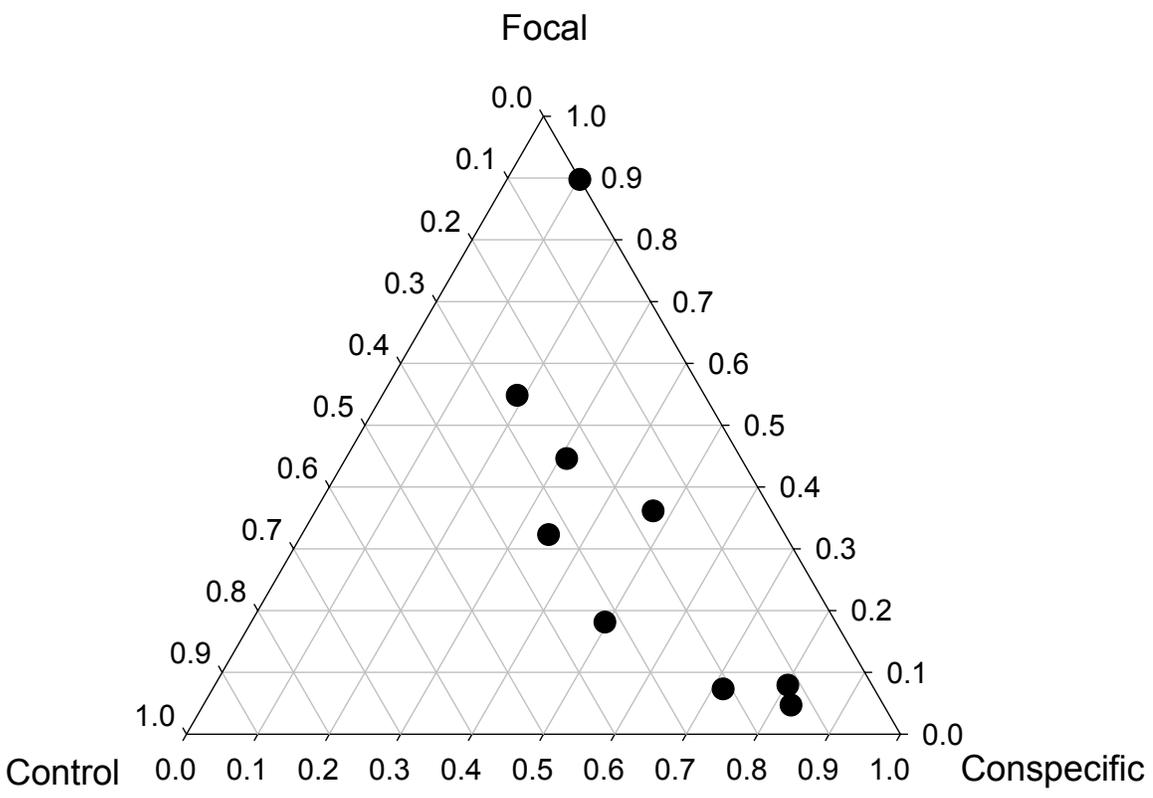


Figure 5. Mass of seeds removed from artificial caches by *D. merriami* during two cache-removal trials. The dashed line represents equality and therefore no difference in the mass of seeds removed in trial 1 compared to trial 2. Points above the dashed line indicate that individuals removed more seed in trial 2 compared to trial 1, whereas the opposite is true for points below the dashed line.

