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Food caching and differential cache pilferage: a field study of coexistence of sympatric kangaroo rats and pocket mice

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Abstract Ecologists studying sympatric heteromyid rodents have sought evidence for species differences in primary foraging abilities and preferences and/or behavioural responses to predation risk in order to explain coexistence. The present field study was conducted to test the hypothesis that another factor may be involved, namely differences in caching patterns, which may result in differences in vulnerability to pilferage. We examined differences between kangaroo rats (*Dipodomys merriami*) and pocket mice (*Chaetodipus* spp.) in foraging, caching and pilferage behaviour. Specifically, we examined interactions at food patches, differential food caching patterns, and differential vulnerability to cache pilferage. Observations conducted at artificial seed patches showed that kangaroo rats dominated access to the patches by arriving and foraging first and by chasing pocket mice away. Individually provisioned pocket mice stored most seeds in underground burrows (larder hoarding), whereas kangaroo rats predominantly cached seeds in small, spatially dispersed caches in shallow pits in the surface of the sand (scatter hoarding). Pocket mice pilfered from each other as well as from the kangaroo rats, but the kangaroo rats rarely pilfered, and the only instance was from another kangaroo rat. Kangaroo rats and pocket mice were both vulnerable to cache pilferage. The results suggest that coexistence of kangaroo rats and pocket mice may be facilitated by a trade-off between primary harvest ability and the ability to exploit a resource that has been processed by another species, namely pilferage ability.

Keywords Coexistence · Pilferage · Food hoarding · *Dipodomys* · *Chaetodipus*

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Introduction

The coexistence of ecologically similar rodent species has been a subject of interest for decades (reviews by Brown and Harney 1993; Randall 1993). In the southwestern United States, it is not uncommon to find as many as six species of heteromyid rodents living sympatrically. Heteromyid species vary in size (kangaroo rats, *Dipodomys* spp., are larger than kangaroo mice, *Microdipodops* spp. and pocket mice, *Chaetodipus* spp. and *Perognathus* spp.; see Brown and Harney 1993 for a review of body size patterns) and mode of locomotion (kangaroo rats and kangaroo mice are bipedal; pocket mice are quadrupedal), but are otherwise similar in diet, burrowing habits, nocturnal activity, and physiological adaptations for water conservation.

Typically, coexistence mechanisms are thought to exist when there are trade-offs among species in their ability to utilise resources along an axis of resource heterogeneity (e.g. Kotler and Brown 1988; but see Basset 1995). This is often, but not always accompanied by resource partitioning. Most research on the coexistence of heteromyid species has sought differences among species in harvesting seeds from primary sources, or “primary foraging” abilities (reviewed by Kotler and Brown 1988). Studies of microhabitat use by kangaroo rats and pocket mice provide the strongest evidence for resource partitioning. *Dipodomys* spp. tend to forage in open microhabitats, whereas *Chaetodipus* spp. prefer to forage under cover (Price 1977; Lemen and Rosenzweig 1978; Wondolleck 1978; Brown 1988; Bouskila 1995; but see Thompson 1982). Whether this difference in microhabitat use reflects differential abilities to exploit resources in the open versus under cover is not known. However, differential vulnerability to predation does not seem to account for genus differences in microhabitat use, since both kangaroo rats and pocket mice are at greater risk of predation from owls in the open than under cover (Longland and Price 1991; Kotler et al. 1998).

Efforts to identify resource partitioning by examining food preferences or foraging skills have mostly failed to

explain species coexistence (reviewed by Randall 1993; Price et al. 2000). Species show concordant preferences for food items (e.g. Smigel and Rosenzweig 1974; Reichman and Oberstein 1977; Hutto 1978; Price 1983a) and perform best under the same conditions (e.g.; Price and Heinz 1984; Price and Podolsky 1989; Morgan and Price 1992; but see Rosenzweig and Sterner 1970). Species differences in microhabitat associations cannot yet be explained by trade-offs in foraging ability or predator avoidance. However, there is some evidence that the greater foraging efficiency of smaller heteromyids might contribute to coexistence by influencing patch choice (e.g. Price 1983a; Morgan and Price 1992).

Behavioural differences permitting species coexistence may not exist exclusively in the realm of foraging skills and preferences. Other possibilities that have been investigated include aggressive dominance (e.g. Kenagy 1973; Congdon 1974; Hutto 1978; Wondolleck 1978; Frye 1983; Kotler 1984; Bleich and Price 1995; Falkenburg and Clarke 1998), and caching (Price et al. 2000).

There is little evidence that the larger heteromyid species excel at one aspect of foraging, while the smaller species are superior at some other skill. So the question of how pocket mice manage to coexist with kangaroo rats remains unanswered. It has recently been suggested that species differences in caching patterns might promote coexistence by allowing different species differential access to food, not simply in primary foraging arenas, but also through cache recovery or pilferage (Price and Joyner 1997; Price et al. 2000). However, to our knowledge, there has been only one field study of species differences in caching patterns (Breck and Jenkins 1997) and no empirical tests of species differences in cache pilferage. The present study is an attempt to address this idea by providing field data on the foraging interactions, caching patterns and cache pilferage of kangaroo rats and pocket mice. Detailed knowledge of the interactions and behaviours of heteromyids in their natural habitat is necessary in order to gain a full understanding of the mechanism of coexistence. Here, we focus on the relatively simple question of why members of one genus do not out-compete members of another.

Coexistence may be facilitated by trade-offs in fitness returns, which are likely reflected in behavioural differences, and in this study we examine four possibilities: foraging, overt aggressive competition, food storage, and asymmetries in cache pilferage. Food storage and pilferage are examined as potential mediators of coexistence because although one species may be a better primary harvester of common primary resources, another species may be better at sequestering harvested food or pilfering that stored by others. Here we present the results of three studies that evaluated these possible coexistence mechanisms. In the first we present data on genus differences in visits to artificial food patches differing in seed value, microhabitat and moon phase in order to quantify differential response to these attributes of primary resources by kangaroo rats versus pocket mice. We also report inter- and intra-genus aggression at the food patches in or-

der to determine whether the larger *D. merriami* aggressively monopolised patches. In the second study, we compared the caching behaviour of kangaroo rats and pocket mice in the field. In the last study, we examined genus differences in perpetration of and vulnerability to cache pilferage.

The study took place at the University of California's Boyd Deep Canyon Desert Research Center, approximately 8 km south of Palm Desert, California, USA (approx. Lat. 33° 38' 10", Long. 116° 22' 30"W). The climate and habitat of this Sonoran desert site have been described by Zabriskie (1979). We captured five species of nocturnal rodents during the course of the study: four heteromyid species (one kangaroo rat, *D. merriami*, average weight 34 g, and three pocket mice, *C. fallax*, 13 g, *C. formosus*, 15 g and *C. penicillatus*, 13 g), and one cricetid (*Peromyscus eremicus*, 16 g).

Materials and methods

Experiment 1. Use of primary food resources

We explored genus differences in use of artificial seed patches and aggressive interactions at patches differing in seed value, microhabitat and moon phase, in order to determine whether kangaroo rats and pocket mice were partitioning primary food resources along any of these dimensions. Open microhabitat and bright moonlight are associated with higher predation risk for these rodents (Longland and Price 1991). We predicted that (1) *D. merriami* would aggressively monopolise patches, and (2) kangaroo rats and pocket mice would show similar "preferences", with respect to seed selection and predation risk avoidance during visits to the trays. The purpose of this experiment was to determine whether there were genus differences at the level of primary foraging behaviour at our field site.

Methods We captured rodents on a trapping grid consisting of 100 traps spaced at 10-m intervals. We marked individual rodents with subcutaneous PIT tags (Passive Integrative Transponders, Destron Fearing). We also marked all individual *D. merriami* with distinct patterns of clipped fur for visual identification.

We baited all traps at dusk with rolled oats and checked them for captures 3–5 h later. We identified all trapped animals by PIT tag number, weighed and checked them for reproductive condition, and then released them at the trap site. Sixteen trap nights over the course of 2 months (10 October to 10 December 1998) resulted in individual identification of 22 *D. merriami*, 41 *C. fallax*, 8 *C. penicillatus*, 10 *C. formosus* and 22 *P. eremicus*.

We examined the foraging behaviour of the heteromyid rodents by providing artificial seed patches (trays) in open and covered microhabitats, for a few nights around the full moon and again during the dark nights surrounding the new moon. Trays were placed in pairs (side-by-side) in each microhabitat, one tray containing seeds preferred by heteromyids in laboratory consumption tests, namely whole oats (68.3% carbohydrate, 13.3% protein), and the other containing seeds that were less preferred, namely lentils (59.4% carbohydrate, 25% protein) (Price 1983b). Both kangaroo rats and pocket mice prefer to consume seeds high in carbohydrate relative to protein (Price 1983b), presumably because metabolism of seeds high in carbohydrates provides a substantial contribution to water balance through production of oxidation water, and seeds high in protein contribute to water loss (Schmidt-Nielsen 1964). Each seed tray consisted of a 20-cm-diameter round shallow tray filled with 400 ml of sand (sifted through a USA Standard Testing Sieve No. 18, with 1-mm openings), mixed with 3 g of either whole husked oats or lentils. Individual lentils are slightly heavier than individual oats (mean lentil=0.05 g, mean oat=0.03 g). We placed seed trays in pairs at lo-

cations designated "cover" (directly under the canopy of a shrub, tree or cactus) or "open" (at least 2 m therefrom). Pairs of trays were placed at least 30 m apart.

We placed 16 pairs of trays out at dusk. We followed this procedure for four nights surrounding the new moon (17–20 November 1998) and three nights around the full moon (1–3 December 1998). On the nights of the full moon, we did not put the trays out until the moon had risen.

On each test night, 3 of the 16 pairs of trays were observed for the 2-h period that they were available to the rodents, either by an observer seated 5–10 m from the tray with a dim headlight (4 W bulb), or by an infrared video camera on a tripod placed approximately 1 m from the seed dish. Pairs of trays were observed in a rotating schedule on successive nights. In total, we collected 42 h of observational data. During observations we recorded the number and sequence of foraging visits to the tray, the duration of each visit, the genus of the visitor (species identification of pocket mice was not possible due to dim illumination and distance of observations), and chases from the dishes, including identification of chaser and chasee. Animals were habituated to these procedures over four nights prior to the experiment.

Numbers of visits made to the seed trays were compared with respect to rodent genus, seed species, microhabitat and moon phase using Wilcoxon signed ranks tests. Data are presented as mean \pm standard error and all tests are two-tailed. The statistical package SPSS 9.0.1 was used to carry out these analyses.

Experiment 2. Differences between genera in caching patterns

Heteromyids store seeds for extended periods in larder hoards, which are made up of multiple loads of food stored in a central place, as well as in scattered caches, which are made by placing single loads of seeds in multiple, spatially dispersed locations (Vander Wall 1990). Recently, species differences in caching behaviour have been examined, but the results of these studies are conflicting. Jenkins and Breck (1998) reported that the proportion of seeds larder-hoarded by five heteromyid species were positively correlated with body size, but in a similar study, Price et al. (2000) reported an increase in scatter caching with increased body mass in eight species of heteromyid rodents (three of which were also tested by Jenkins and Breck 1998). Price et al. (2000) suggested the possibility that different methodology and apparatus may contribute to the different results reported in the two studies.

Breck and Jenkins (1997) conducted a study of caching behaviour in the field and they reported that kangaroo rats scatter hoarded their food whereas pocket mice larder hoarded. The present experiment was conducted in order to determine whether there were any differences in food storage behaviour between *D. merriami* and the most numerous species of pocket mouse at the site, *C. fallax*.

Methods

Species differences in caching were examined on 10 nights between 28 October and 11 December 1998. Eight individual kangaroo rats and seven individual pocket mice were each provisioned with seeds by placing seed trays covered with fluorescent powder near their burrows, and caches were subsequently located using ultraviolet lights. Each animal was provisioned only once.

One or two observers waited quietly at least 8 m from the tray with a dim white light to illuminate the tray. It was difficult to target a specific individual for a caching trial so opportunistic encounters were utilised. Once a rodent found the tray, it was allowed to take the seeds, and if other rodents came to the tray once the trial had commenced, the experimenters deterred them from taking any seeds by chasing them away.

Each caching trial consisted of placing a 30.5-cm round aluminium tray, with a 7.5-cm round aluminium seed dish fixed in its centre, at a location on the trapping grid where rodents had been observed. Caches were located following the protocol used by Longland and Clements (1995). The aluminium trays were lined

with sandpaper, which was dusted with fluorescent powder (Radiant Color). The seeds in the centre dish were mixed with more of the same powder. The powder ensured that the target animal could be tracked and at least some of its cache sites could be located with portable ultraviolet lights.

In the first two caching trials, in which 1 kangaroo rat and 1 pocket mouse were provisioned, the seed dish in the centre of the tray was filled with 10 g each of oats and lentils. During one additional kangaroo rat trial, 7 g each of oats and lentils were provided. In the remaining 12 trials each animal was first allowed to cache 7 g of one food type, and then, once the target animal had depleted all of those seeds, the area was searched for caches before replenishing the provisioning tray with 7 g of the other seed type.

Once the target rodent had taken all of the seeds, or had failed to return to the tray for 20 min, the experimenters picked up the tray and searched the surrounding area with a portable ultraviolet light for seed caches. Footprint trails were followed to aid the search and to determine whether seeds were taken down holes. An area measuring 3,600 m² around each provisioning dish was thoroughly and systematically searched for caches, since not all caches were detectable by following trails. Scatter caches were defined as small shallow pit caches containing more than two seeds. Scatter caches were easily distinguishable by a small, distinct patch of fluorescent powder surrounded by a triangular sweep of fluorescent powder and sand. We excavated all caches and placed their contents in individually labelled bags for subsequent weighing, and replaced all caches immediately with a roughly similar amount of seeds. Larder caches were inferred when the animal's powder trail led into a burrow entrance, though we were not able to determine whether seeds had been deposited in the burrow. The locations of all scattered caches were marked and mapped. Wilcoxon signed rank tests were used to analyse the data.

Experiment 3. Pilferage in kangaroo rats and pocket mice

The third experiment explored the possibility that pocket mice might coexist with kangaroo rats, despite being dominated by them at primary food sources, because of an advantage in pilfering. Smaller rodents might be 'forced' to scatter cache when they are unable to defend a larder hoard against larger congeners, but it is also possible that there are benefits to larder hoarding that are enjoyed exclusively by the smaller pocket mice. Jenkins and Breck (1998) have suggested that the small burrow entrances of pocket mice may prevent entry by the larger kangaroo rats, thus providing some degree of protection to pocket mouse larders. Daly et al. (1992) demonstrated that kangaroo rats provisioned with dyed food suffered a high rate of pilferage from other kangaroo rats, pocket mice and cricketid rodents, at the study site used in the present study. It is not known whether the flow of resources from primary forager to pilferer is bidirectional and balanced or is instead more or less unidirectional, with the pocket mice in effect parasitising the kangaroo rats' foraging efforts.

The purpose of this experiment is to determine whether one genus had a competitive advantage by engaging in pilferage of stored seeds, and whether one genus could better protect stored seeds from pilferage.

Methods

In spring 1999, we trapped rodents for ten nights between 27 April and 8 June, which resulted in the individual identification of 16 *D. merriami*, 28 *C. fallax*, 5 *C. penicillatus*, 11 *C. formosus* and 11 *P. eremicus* on the same trapping grid described for experiment 1.

Batches of whole oats were dyed by soaking them in a solution of Fast Green (Fisher Scientific) and water for 30 min, then allowing the seeds to air dry on paper towels. Individual pocket mice were provisioned with 5 g of dyed whole oats on the nights of 23 November 1998 (6 *C. fallax* and 1 *C. formosus*) and 4 and 5 December 1998 (2 *C. fallax* and 1 *C. penicillatus*), and 10 g on 1 June 1999 (5 *C. fallax* and 1 *C. penicillatus*) at various locations

on the trapping grid. Individual *D. merriami* ($n=5$) were provisioned with 10–25 g of dyed oats on 2 and 3 May 1999 on the trapping grid. On each of these nights individual animals were targeted and allowed to empty a provisioning dish by returning to it multiple times. Individuals were identified by a PIT tag reader (Mini Portable Reader, Destron Fearing) upon which the provisioning dish was placed. An observer sat close to the dish to ensure that only the targeted rodent took the dyed food, but at one tray location on 23 November 1998, two *C. fallax* shared 5 g of food. On 1 June 1999, a *C. fallax* female travelled approximately 30 m after being provisioned by one experimenter to take another dish of dyed seeds from the other experimenter, thus receiving 20 g of dyed seeds.

Each provisioning trial was followed by a series of 3–5 trap nights, following the same procedures as used in experiment 1. We collected faecal samples directly from each trapped animal when possible (approximately 55%), and otherwise from traps. We placed all faecal samples in labelled plastic vials. In the laboratory we added a few drops of tap water to each sample. On the next day two independent raters who were blind to the identity of the animals rated faecal dye as present or absent. Only cases where both raters were in agreement concerning the presence of dye are reported here as positive identification of dye in faeces. Raters disagreed on the presence of dye in just three of 95 cases where faecal dye was detected by at least one rater. An animal was identified as a pilferer if it had not been provisioned with dyed seeds but its faeces contained traces of dye.

Trapping took place on nights 1, 3 and 5 following provisioning on 23 November 1998 and 5 December 1998, on nights 1, 2, 3, 5 and 7 after provisioning kangaroo rats on 2 and 3 May 1999 and on nights 1, 3, 5 and 7 following the provisioning trials on 1 June 1999.

We used logistic regression to evaluate the relationship between the provisioned genus, the genus of the pilferers and the number of animals that were provisioned.

Results

Experiment 1

Twenty of the 21 pairs of seed trays that were watched for 2 h each were visited by foraging rodents. Kangaroo rats and pocket mice were the primary visitors. Only two visits by *P. eremicus* were observed, and these visits were not included in the analysis.

A total of 856 visits were made to the seed trays. The observed ratio of visits to the trays by kangaroo rats and pocket mice respectively was 619:237. This differs significantly from the expected ratio of 232.5:623.5 based on the relative population size for each genus estimated from trapping ($\chi^2=882.1$, $df=1$, $P<0.001$). The kangaroo rats were the first to approach and forage at 14 of the 20 (70%) pairs of seed trays. (Expected ratio based on population size of kangaroo rats and pocket mice respectively=6:14, observed ratio=14:6; $\chi^2=15.24$, $df=1$, $P<0.001$). Furthermore, during the first 10 min at the seed trays, when foraging was likely most profitable, the kangaroo rats made significantly more visits (mean number of visits by kangaroo rats =6±1, mean by pocket mice =2±1; $Z=-2.24$, $n=20$, $P<0.05$). Though the kangaroo rats also spent more time foraging during the first 10 min than did the pocket mice (mean foraging time of kangaroo rats =3.9±0.7 min, mean for pocket mice =1.5±0.6 min) this difference was not significant ($Z=-1.90$, $n=20$, $P=0.06$).

Over the entire 2-h period, kangaroo rats made more visits per tray (mean =31±15) than pocket mice (mean =12±14; $Z=-3.42$, $n=20$, $P<0.001$). Kangaroo rats also spent more time foraging in each tray (mean=11.8±1.1 min) than did the pocket mice (mean 5.4±1.6 min; $Z=-2.28$, $n=20$, $P<0.05$).

The number of visits to seed trays made by kangaroo rats was significantly affected by seed type. They visited food trays containing oats (mean number of visits=17±2) more than they visited trays containing lentils (mean=14±2; $Z=-2.39$, $n=20$, $P<0.05$). Pocket mouse visits were not significantly affected by seed type (mean number of visits to oat =6±2, mean visits to lentils=5±1; $Z=-0.60$, $n=20$, NS). Similarly, the length of time that kangaroo rats spent foraging was significantly affected by seed type (mean visit length at oats=7.4±0.7 min, mean at lentils=4.4±0.5 min; $Z=-3.77$, $n=20$, $P<0.001$) whereas there was no significant effect of seed type on the length of time spent foraging at the trays by pocket mice (mean visit length at oat trays=3.2±1.0 min, mean at lentil trays=2.2±0.7 min; $Z=-1.73$, $n=20$, NS).

Further comparisons were made between kangaroo rats and pocket mice at the two moon phases. Kangaroo rats made significantly more visits to the seed trays than pocket mice under both new and full moon phases (New moon: mean visits made by kangaroo rats=34±5, mean pocket mouse visits=14±5; $Z=-2.40$, $n=11$, $P<0.05$; Full moon: mean kangaroo rat visits=28±5, mean pocket mouse visits=9±3; $Z=-2.37$, $n=9$, $P<0.05$). There was no significant difference between the amount of time spent foraging by kangaroo rats (mean=12.0±1.5 min) and pocket mice (mean=6.5±2.7 min) at the new moon ($Z=-1.25$, $n=11$, NS). However, kangaroo rats spent significantly longer foraging in the seed trays under the full moon (mean=11.7±1.6 min) than did pocket mice (mean=4.1±1.4; $Z=-2.31$, $n=9$, $P<0.05$).

In open microhabitats, where the rodents are more exposed to predators, kangaroo rats made significantly more visits to the seed trays (mean=24±3) than pocket mice (mean=7±4; $Z=-2.19$, $n=9$, $P<0.05$). There were no significant genus differences in time spent foraging in the open (mean time spent in 'open' trays by pocket mice=3.4±2.2 min, mean for kangaroo rats=9.9±1.0 min; $Z=-1.60$, $n=9$, NS). When the rodents were foraging at trays under the safety of cover, similarly, kangaroo rats made significantly more visits to the seed trays than did pocket mice (mean visits made by kangaroo rats =37±5, mean pocket mouse visits =15±4; $Z=-2.67$, $n=11$, $P<0.01$), but there were no significant differences between kangaroo rats and pocket mice in time spent foraging at the seed trays under cover (mean time spent in 'cover' trays by pocket mice=7.0±2.3 min, mean time for kangaroo rats=13.5±1.6 min; $Z=-1.60$, $n=11$, NS).

Chases were recorded at the seed trays as an index of dominance (see Table 1). In virtually all encounters, a chase ensued (68/69 encounters involved a chase). When kangaroo rats encountered pocket mice, the larger animal was significantly more likely to chase the smaller (38/39; $\chi^2=35.1$, $df=1$, $P<0.001$).

Table 1 Encounters between rodents at food trays that did or did not involve a chase. The genus of the chaser is identified in encounters that occurred between kangaroo rats and pocket mice

Encounter	<i>n</i> Chase	<i>n</i> No chase	<i>n</i> Chaser:	
			K. rat	P. mouse
Kangaroo rat versus pocket mouse	39	0	38	1
Kangaroo rat versus kangaroo rat	21	0	–	–
Pocket mouse versus pocket mouse	8	1	–	–
Total	68	1	–	–

Table 2 Number of animals of each species provisioned with dyed seeds on each of the provisioning nights in experiment 3, followed by a tabulation of the number of each species identified as pilferers over the number of each species trapped during the ensuing trap nights

Provisioning		Pilfering				
Dates	No. provisioned No. with dye / no. provisionees trapped	Pilferers/ total number trapped				
		<i>D. merriami</i>	<i>C. fallax</i>	<i>C. formosus</i>	<i>C. penicillatus</i>	<i>P. eremicus</i>
Provisioned: November 23/98	6 <i>C. fallax</i> , 1 <i>C. formosus</i>					
Trapped: November 24, 26 and 28/98	7/7	0/12	5/23	1/2	0/3	1/11
Provisioned: December 4 and 5/98	2 <i>C. fallax</i> , 1 <i>C. penicillatus</i>					
Trapped: December 6, 8 and 10/98	3/3	0/13	5/27	2/2	0/2	0/12
Provisioned: June 1/99	5 <i>C. fallax</i> , 1 <i>C. penicillatus</i>					
Trapped: June 2, 4, 6 and 8/99	5/5 <i>C. fallax</i> , 0/1 <i>C. penicillatus</i>	0/13	10/19	1/11	2/6	1/5
Provisioned: May 2 and 3/99	5 <i>D. merriami</i>					
Trapped: May 4, 5, 6, 8 and 10/99	5/5	1/10	1/23	2/8	2/9	1/10

Experiment 2

The kangaroo rats made significantly more scattered caches than larder caches ($Z=-2.25$, $n=8$, $P<0.05$). Kangaroo rats entered an average of 0.63 ± 0.86 existing burrows (potential larder hoards) and made an average of 4.50 ± 0.86 shallow pit caches (scatter hoards).

Conversely, pocket mice stored food in larders significantly more than in scattered pit caches ($Z=-2.38$, $n=7$, $P<0.05$). Pocket mice entered an average of 4.43 ± 0.92 existing burrows and made only 0.29 ± 0.92 pit caches.

We were able to recover an average of 0.35% of the original mass of the seeds harvested from the scattered caches of kangaroo rats, versus just 0.04% of the seeds harvested by pocket mice ($Z=-2.69$, $n=15$, $P<0.01$).

The multiple burrow entrances used by pocket mice usually appeared to be different entrances to the same burrow system, as they were close together, and the same animal (identified by fluorescent powder) was often seen entering one hole and exiting from another. Thus it is likely that the pocket mice were larder caching seeds in a single burrow with multiple entrances, whereas the kangaroo rats were scatter caching seeds.

Only two shallow pit caches were made by pocket mice. Although such pit caches are characteristic of scat-

ter caching kangaroo rats, the two that were made by pocket mice might best be characterised as larders since they were both fairly large, each containing over 3 g of seeds, which is more than a pocket mouse can carry in its cheek pouches at one time (Van der Wall et al. 1998), so these caches must have been made with more than one load of food. In contrast, the caches made by kangaroo rats weighed an average of 0.86 ± 0.10 g, and a maximum of 2.0 g, which is less than their maximum cheek pouch capacity.

Experiment 3

Details of each provisioning trial, including species provisioned, number of animals trapped, and number of pilferers identified on subsequent nights, are shown in Table 2.

In total, 16 individual pocket mice (13 *C. fallax*, 2 *C. penicillatus* and 1 *C. formosus*) were provisioned. All but one of the provisioned pocket mice, a *C. penicillatus*, showed traces of dye in its faeces on at least one of the ensuing trap nights. Twenty-six pilferers were identified out of a total of 133 heteromyids trapped. Two individual *P. eremicus* out of 28 trapped were also identified as pilferers.

Logistic regression showed that there was an overall effect ($\chi^2=16.98$, $n=183$, $df=3$, $P<0.001$). Pocket mice pilfered significantly more than kangaroo rats (23% of trapped pocket mice had dye in their faeces, whereas only 2% of kangaroo rats had dye; $\chi^2=15.30$, $df=1$, $P<0.001$). There was no significant effect of genus of the provisioned animal on pilferage (probability of pilferage was 12% for provisioned kangaroo rats and 20% for provisioned pocket mice; $\chi^2=2.23$, $df=1$, NS). The number of rodents provisioned in each trial had no significant effect on the model ($\chi^2=0.15$, $df=1$, NS).

Discussion

The results of experiment 1 indicate that kangaroo rats exclude pocket mice from food sources that are attractive to both. Not only did kangaroo rats chase pocket mice away from seed dishes, they also made proportionally more visits to the seed trays, arriving and foraging at them before the pocket mice. This suggests that kangaroo rats have better access to primary food resources, since the first animals to arrive and forage are likely to get more food than the ones who arrive later. Kangaroo rats, but not pocket mice, foraged preferentially for oats over lentils, making more visits and spending more time foraging at seed trays containing oats. Kangaroo rats made more visits to the seed trays during both new and full moon phases, and they spent more time foraging at the trays under the full moon than did the pocket mice, indicating that the pocket mice may be more sensitive to the risk of predation associated with greater visibility under the full moon. Kangaroo rats made more visits to trays in both the open and covered microhabitats, but kangaroo rats and pocket mice spent similar amounts of time foraging in both microhabitats.

When an encounter occurred between a kangaroo rat and a pocket mouse, the kangaroo rat was the aggressor in almost all cases. Pocket mice chased other pocket mice in most instances when two visited a tray simultaneously, so their lack of aggression towards the kangaroo rats indicates that they are aggressively subordinate to the larger kangaroo rats rather than less aggressive generally. Kangaroo rats get to rich patches first and are capable of aggressively dominating them when pocket mice arrive. The aggressive advantage of larger heteromyids has been shown in other studies (e.g. Kenagy 1973; Congdon 1974; Blaustein and Risser 1976; Hutto 1978; Wondolleck 1978; Frye 1983; Kotler 1984; Bleich and Price 1995; Falkenburg and Clarke 1998). These observations reinforce the premise that kangaroo rats dominate access to food trays during primary foraging for resources by getting to the food first and excluding the pocket mice that come to the patches. Kangaroo rats likely enjoy a speed advantage both in searching for patches and in harvesting them once they are encountered (Price and Heinz 1984). In order to determine whether the pocket mice had an advantage in cache pilferage, we examined differences in caching patterns and cache pilferage in the next experiments.

The results of experiment 2 show that the kangaroo rats tend to be scatter cachers, whereas the pocket mice are apparently larder cachers. Randall (1993) suggested that species with the ability to scatter cache might enjoy a competitive advantage over species that do not because they are able to store food as insurance against future shortages. However, larder hoards are also a potential insurance against shortages. Scatter caching species have more neural capacity devoted to brain structures involved in spatial memory, specifically the hippocampus, than do non-scatter caching species (Sherry et al. 1992; Jacobs and Spencer 1994). This may imply that scatter caching is an adaptation that evolved in species with a competitive disadvantage in terms of their ability to protect larder hoards, forcing them to devote neural capacity to spatial memory, presumably at the expense of some other cognitive function.

The results of the pilferage study (experiment 3) provide strong evidence that pilferage is asymmetrical among these heteromyid rodents. Daly et al. (1992) provisioned *D. merriami* at the same site using similar methods as in this study and reported substantial pilferage by both pocket mice and kangaroo rats. The present study indicates that pocket mice engage in pilferage more than kangaroo rats, but both are vulnerable to cache pilferage.

The results presented in the previous three experiments suggest that the foraging advantage gained by the kangaroo rats due to their ability to dominate access to seed patches is at least partially balanced by the greater use of pilferage by the pocket mice. Perhaps these foraging and pilferage differences facilitate coexistence between the kangaroo rats and the pocket mice.

Despite the fact that there were more than twice as many pocket mice as kangaroo rats present on the study site, kangaroo rats made significantly more visits to the seed trays presented in experiment 1 than pocket mice. The individual identity of kangaroo rats visiting the seed trays was recorded because they were individually marked with distinctive patterns of clipped fur, but the pocket mice were not visually marked so the identity of the pocket mice was not recorded. In future, it would be interesting to individually mark the pocket mice as well as the kangaroo rats in order to determine the number of individuals visiting each tray.

It is possible that pocket mice did not visit the seed trays as frequently as kangaroo rats because their diets have a heavier reliance on insects and vegetation. However, the available evidence is contrary to this hypothesis: Reichman (1975) examined the stomach contents of hundreds of heteromyid rodents, and found that seeds made up a larger proportion of the diets of the three pocket mouse species he studied (*P. amplus*, *C. baileyi* and *C. intermedius*) than of the diet of *D. merriami*. These results support the hypothesis that pocket mice are excluded by the kangaroo rats from seed patches, but that they compensate for the seed losses by engaging in pilferage activities.

Pilferage behaviour may be an alternative strategy distinct from foraging at natural seed patches, main-

tained by natural selection in the event that foraging at seed patches is in large part denied by larger sympatric competitors due to aggression or the ability to harvest resources more quickly. The microhabitat use of pocket mice shifts dramatically when kangaroo rat competitors are experimentally removed (e.g. Wondelleck 1978; Price 1978), providing further support for the hypothesis that kangaroo rats limit the foraging opportunities of pocket mice. However, it does not appear that there is a direct trade-off between primary foraging and pilferage, since in the present study the pocket mice continued to spend considerable time and effort foraging at seed patches, risking aggressive attacks from the larger kangaroo rats while doing so rather than using a pure pilferage strategy. Perhaps kangaroo rats do not invest as much effort in pilferage as pocket mice because they are able to monopolise foraging opportunities. One might predict that pilferage by pocket mice would be reduced in areas where there are relatively few kangaroo rat competitors. The relative profitability of foraging and pilfering to pocket mice and kangaroo rats must be investigated in order to address these hypotheses. Furthermore, it remains to be established that the pocket mice recognise caches per se, rather than treating them as any other small seed patch.

The present study does not address the possibility that the caching or pilfering of seeds provisioned in a feeder differs from that of seeds that are naturally foraged and cached, as is the case for birds (Bardin and Markovets 1991; Brodin 1994). Kangaroo rats may concentrate caches around a provisioning tray more than they do when caching naturally foraged seeds and this may result in an artificially elevated level of pilferage in the present study. Studies of the caching patterns of and pilferage from caches made by naturally foraging animals are needed in order to corroborate the findings reported in this study.

The present study provides field evidence for differences between kangaroo rats and pocket mice in foraging access to seed patches, caching patterns and cache pilferage. However, future studies are needed before the role of pilferage in coexistence can be verified. Such studies would also benefit from quantifying the prevalence of pilferage in different heteromyid communities at different times of the year. We are currently investigating the characteristics that influence the vulnerability of kangaroo rat caches to pilferage.

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