DETERMINANTS OF FORAGING AND CACHING IN HETEROMYIDS

ECOLOGICAL DETERMINANTS OF FORAGING AND CACHING

BEHAVIOUR IN SYMPATRIC HETEROMYID RODENTS

By:

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Abstract

A series of studies was carried out in order to ascertain some of the ecological determinants of the foraging and caching behaviour of heteromyid rodents (kangaroo rats, *Dipodomys*, and pocket mice, *Chaetodipus*). The results show that heteromyids are sensitive to cues of predation while they are foraging. They put more effort into foraging under the safety of cover and in the dark of the new moon, when risk of predation from visually hunting predators is low. They also modulate their selectivity in relation to cues of predation risk, requiring a better pay-off (a more valuable food) as risk increases. The kangaroo rats and pocket mice compete for resources, and the pocket mice are at an aggressive disadvantage to the kangaroo rats at primary resource patches. However, the pocket mice compensate at least partially for their loss by engaging in cache pilferage. Finally, a study of the scatter caching decisions made by kangaroo rats demonstrates that they adaptively modulate cache spacing by placing more valuable seeds into caches that are more widely spaced. This differential spacing leads to decreased probability that pilferers conducting area-localised search after encountering one cache will be able to locate further caches. The results are discussed in relation to current theory and empirical findings.

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Finally, I thank the rodents, for tolerating my presence, for allowing me to watch and to follow them during their nightly activities and for treating fluorescent lentils as food.

Two of the papers in this thesis are co-authored by Lisa Leaver and Martin Daly (Chapter 2 and Chapter 4). The ideas in those papers were conceived by Lisa Leaver and Martin Daly. The research, analyses and writing of the papers was done by Lisa Leaver.

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Chapter 1-General Introduction

The application of economic cost-benefit analyses to feeding behaviour has led to the development of foraging theory (Stephens & Krebs 1986), integral to which is the notion that decisions about behaviour invariably result from multiple trade-offs. For instance, a foraging animal can be thought of as acting as if to maximise some consumptive currency like calories or nutrient intake, while minimising exposure to predation risk. A foraging animal must also consider the relative costs and benefits of continuing to forage at a food patch as resources are depleted, or moving on to another patch.

Predation has been a strong selective force over evolutionary time. The role of predation in shaping behaviour is a classic field of study in behavioural ecology (reviewed by Lima & Dill 1990; Lima 1998). Animals can adjust their behaviour in ways that affect predation risk, and behavioural control of predation risk has been the particular focus of many researchers investigating the trade-offs made by foraging animals (e. g. Lima & Dill 1990; Lima 1998). The studies presented in this thesis address the nature of some of the cost-benefit trade-offs made during foraging by a family of desert granivores, the Heteromyidae.

Heteromyid rodents have been the subjects of extensive study in a number of areas. They are interesting to researchers in diverse fields for various reasons. Their

physiology is striking in that they have multiple adaptations that allow them to conserve water in their desert habitat (Schmidt-Nielsen 1964). They provide a classic example of species-co-existence in the field of community ecology. As many as six behaviourally similar species can live sympatrically without one species out-competing the others. Despite hundreds of studies and decades of research on the subject (reviewed by Brown & Harney 1993) there is as yet no satisfactory answer as to how they co-exist. Heteromyid food hoarding decisions have been of interest to psychologists and neuroscientists because of the remarkable ability of some species to remember multiple cache locations (e. g. Jacobs 1992). Comparative studies of hippocampal volume have shown that among heteromyids, scatter caching species have greater hippocampal volume than larder hoarding species (Jacobs & Spencer 1994), paralleling the results of prior studies of the hippocampal complex in food storing and non-food storing birds (e. g. Krebs et al. 1989; Sherry et al. 1989).

The research that I present in this thesis touches on issues in a number of these fields, and provides a more comprehensive understanding of the foraging decisions made by the heteromyid rodents at one field site. The studies presented in chapters 2, 3 and 4 address the foraging, caching and competitive behaviour of the four species of heteromyid rodents on the alluvial plain of the University of California's Phillip L. Boyd Deep Canyon Desert Research Center in Palm Desert, California, USA. The heteromyid rodents present at that site consist of one species of kangaroo rat, Merriam's kangaroo rat (*Dipodomys merriami*), and 3 species of pocket mouse (*Chaetodipus fallax, C. formosus* and *C. penicillatus*). I examined the behaviour of these rodents in relation to some of the

ubiquitous ecological challenges that they face: risk of predation, obtaining and securing food and dealing with both conspecific and hetero-specific competitors.

The papers in this thesis are important because they report a series of studies conducted in the field rather than in a laboratory, where the majority of heteromyid behavioural studies have taken place. There are many potential problems associated with laboratory tests of hypotheses derived from theories about things like what permits co-existence or how food caching decisions are made. Laboratory studies involve the quantification of behaviour in spaces that are smaller by several orders of magnitude than home ranges in the field (e.g. cf. Behrends et al. 1986 and Leaver & Daly 1998). Natural predation and competition cues are absent, and it can be difficult to determine what cues are relevant in nature in order to recreate them in a laboratory. Any of these problems may account for some of the conflicting results reported when similar studies are conducted in slightly different laboratory set-ups. One important function of behavioural ecological field research is to determine what aspects of the environment are necessary to include in a laboratory environment (Ylonen & Wolff 1999). Field studies are also crucial for the meaningful interpretation of laboratory findings.

By conducting intensive focal observations of individual rodents, I provide a much more detailed understanding of their foraging behaviour than that presented in most ecological studies. Foraging effort in heteromyids has typically been measured by "quitting harvest rate" of animals foraging at trays of seeds mixed into a substrate such as sand. Species identity is inferred by footprint impressions in the sand after trays have

been left in the field for some period of time, usually overnight (e. g. Brown 1988). My approach has allowed me to gain some novel insight into the dynamics of species co-existence because rather than simply measuring net evidence of foraging effort, I observed the animals visiting foraging trays and interactions between individuals at those trays (Chapter 4), which allowed me to establish that the kangaroo rats are dominant over the pocket mice at food patches. By following individuals I was able to gather some of the first direct field evidence of cache spacing and food partitioning (see Daly et al. 1992 for the only other published field study of kangaroo rat caching). I located the caches of individual animals (Chapter 3 & 4), and measured pilferage, to estimate the costs and benefits of cache spacing as well as elucidating how species differences in cache pilferage may play a hitherto unrecognized role in the maintenance of heteroymid co-existence. Previous field studies of kangaroo rat caching have lacked the fine temporal and spatial resolution that I have been able to attain in these field studies.

The study presented in Chapter 2 was designed to test conflicting economic predictions about changes in selectivity during foraging between foods that differ in value. Some models predict decreased selectivity as the costs of foraging increase, since the costs of assessing food value also increase. These are called "reduced finickiness" models. Other models predict increased selectivity as predation risk increases, due to the fact that animals should require higher profit in order to tolerate the higher costs associated with increased exposure to predation risk. These models are called "higher requisite profit" models. The rodents in this study demonstrated increased selectivity

under high levels of predation risk, a finding that supports the predictions of the higher requisite profit models.

In Chapter 3, I present a field study of the caching decisions made by kangaroo rats when they are caching seeds that differ in value. I was interested in elucidating some of the factors involved in caching decisions made by Merriam's kangaroo rats, who scatter cache their food for future consumption. Since kangaroo rats live in a harsh desert environment in which the amount of available food can vary unpredictably, scatter caching seeds during times of plenty acts as insurance against future shortages. Furthermore, these animals do not have the opportunity to drink free-standing water so water conservation is essential. Consequently, they value seeds with a high carbohydrate-to-protein ratio since carbohydrates create a nontrivial amount of water when digested, whereas protein metabolism contributes to water loss (Schmidt-Nielsen 1964). I provisioned individual animals with seeds differing in their carbohydrate: protein ratio and observed their caching behaviour.

In order to determine the effect of differential spacing of caches containing different types of seeds, I also buried arrays of artificial caches differing in their spacing and in their food value and measured pilferage rates from those caches. I found that the rodents space caches of a more valuable food more widely and that increased cache spacing functions to protect those caches from area-localised search by would-be pilferers.

The study presented in Chapter 4 provides a test of a novel hypothesis about heteromyid co-existence. In addition to examining differences between the genera (*Dipodomys* and *Chaetodipus*) in extracting resources from primary sources and in their caching patterns, I examined genus differences in vulnerability to and perpetration of cache pilferage. The kangaroo rats are larger in size than the pocket mice. I begin by presenting results confirming that kangaroo rats and pocket mice have similar foraging preferences, and that the kangaroo rats have an aggressive advantage over the pocket mice. I then present the results of a systematic field study of genus differences in caching patterns. Such a field study has not been carried out before (to my knowledge). My results show that kangaroo rats are avid scatter cachers, whereas pocket mice tend to store their food in a single larder. The final part of this study is an examination of genus differences in cache pilferage. I found that the pocket mice engage in extensive cache pilferage, stealing from each other and from the kangaroo rats, whereas the kangaroo rats do not engage in such extensive pilferage. These findings suggest the possibility that asymmetries in cache pilferage may promote co-existence in these heteromyid rodents.

These three studies provide evidence that kangaroo rats and pocket mice behave in an adaptive manner. They compete over resources, and the avenues of competition are varied. They make predictable trade-offs between food rewards and predation risk. They value seeds with properties that aid in water conservation, and put more effort into foraging for and caching of seeds with those properties.

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Chapter 2

Effects of predation risk on selectivity and foraging efficiency in Heteromyid rodents

Running headline: Leaver & Daly: Heteromyid foraging and selectivity

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Abstract

Variations in predation risk affect the costs of foraging and may therefore warrant different foraging decisions. One class of models ("higher requisite profit") predicts that foragers should become more selective when predation risk increases, as low-profitability items that do not cover the increased costs are dropped from the diet. An alternative class of models ("reduced finickiness") predicts that foragers should become less selective when predation risk increases, because selectivity requires more extensive assessment and/or search behaviour, prolonging exposure to risk. We assessed the selectivity of foraging heteromyid rodents (Merriam's kangaroo rats, *Dipodomys merriami*, and pocket mice, *Chaetodipus* spp.) by comparing "giving up densities" (GUD: the quantity of cryptic food left in a patch by animals for whom the diminishing marginal gains from foraging have dropped below the threshold for continued search) for foods of different value, in patches varying in predation risk. Data collected over two field seasons revealed consistent main effects: under the cover of shrubs, during the new moon, and when a patch contained nutritionally more valuable seeds, the animals generally foraged patches down to a lower GUD. Interactive effects between food value and predation risk cues demonstrated that the rodents acted in accordance with the higher requisite profit model, showing increased selectivity for food type in the more dangerous open microhabitats. These findings of modulated selectivity and foraging effort in response to moonlight, microhabitat, season and food value are discussed in relation to models and empirical findings of foraging selectivity under predation risk.

Introduction

If food patches vary in value, an increase in predation risk may lead foragers to be more selective in decisions about where to forage and for how long (e.g. Cerri & Fraser 1983, Milinski 1985, Gilliam & Fraser 1987). This is because food qualities or encounter rates that are sufficient to warrant foraging effort under low predation risk are not profitable enough to cover the prospective fitness costs of exploiting them when risk increases, and the breadth of acceptable diet items or patch densities narrows. We call such models "higher requisite profit" models. Supportive studies have shown that the presence of either actual predators or predation risk cues such as a lack of protective cover can lead to increased selectivity with respect to the acceptable density of food patches (sticklebacks, Milinski & Heller 1978; surfperch, Holbrook & Schmitt 1988), with respect to the acceptable size (and hence the harvest rate) of nutritionally similar seeds (kangaroo rats, Bowers 1988, 1990), and with respect to the acceptability of seed species that differ in preference ranking (heteromyid rodents, Hay & Fuller 1981).

Other models, however, predict that foragers will be most selective when predation risk is low and will become relatively indiscriminate as risk rises (Real 1990; Crowley et al. 1991) because economizing on search and/or assessment can reduce the duration of exposure. We call these "reduced finickiness" models, and they have often found support in studies of mate choice (female pied flycatchers, Alatalo et al. 1988; female sticklebacks, Milinski & Bakker 1992; female gobies, Forsgren 1992; male pipefishes, Berglund 1993; female crickets, Hedrick & Dill 1993, female guppies, Godin

& Briggs 1996). It is perhaps unsurprising that the reduced finickiness model should be especially applicable to mate choice, because the goal in this case is seldom to maximize "consumption", and increased selectivity would translate rather straightforwardly into increased search time. However, the prediction of reduced selectivity under predation risk has also been supported in some studies of foraging for food (e.g. minnows, Cerri & Fraser 1983; salmon, Metcalfe et al. 1987; sticklebacks, Ibrahim & Huntingford 1989).

In the present study, we tested the conflicting predictions of the higher requisite profit and reduced finickiness models by measuring changes in selectivity and foraging effort in relation to changing levels of predation risk, in animals foraging for foods of different nutritional value. The foragers were heteromyid rodents, an ideal family for the study of selectivity under predation risk because they preferentially select and eat seeds high in carbohydrate and low in protein which produce metabolic water through oxidation (Schmidt-Nielsen 1964; Price 1983; Frank, 1988), and because they are sensitive to certain known cues of predation risk while active aboveground (Price et al. 1984; Daly et al., 1992) and during foraging (e.g. see Bowers 1988, 1990; Kotler 1984). The Heteromyidae are a family of New World rodents, most species of which are adapted to exist in the arid American southwest. The species of interest in this study are primarily granivorous, although they supplement their diet with insects and greens when available. We varied food value by using two seed types that differed in percent carbohydrate and protein.

We looked at foraging behaviour by measuring giving up densities (GUDs), a measure that facilitates fine estimation of foraging effort (Brown 1988). Seeds are mixed

into a substrate and left for animals to exploit. As seeds in the trays are depleted successive seeds are more difficult for foragers to detect so harvest rate decreases with tray depletion. The seeds remaining in the substrate in a tray after the foragers have 'given up' are measured (counted and/or weighed), and that residual amount is called the GUD: the density of seeds at which the utility of foraging was presumably too low to motivate the forager to continue at that patch. GUDs provide a better estimate of foraging effort than that used in previous studies of heteromyid selectivity (e. g. see Hay & Fuller 1981; Bowers 1988, 1990) which simply placed seeds in petri dishes with no substrate, because this tends to result in animals taking all or nothing from the pile of seeds as there are no diminishing marginal returns.

Foraging costs for heteromyids increase with increasing night-time illumination. As artificial or natural night-time illumination increases, heteromyid activities shift to the relative safety of microhabitat under the cover of shrubs, presumably in order to minimize risk from visually hunting predators (reviews: Munger et al. 1983; Price & Brown 1983). However, the costs of foraging under shrubs also appear to vary seasonally due to the fact that, in some areas, some snake species are less active in the winter months. Thus, heteromyids adjust their microhabitat use in ways that appear to reflect changing predation risk (Price 1978; Bouskila 1995).

The issues related to understanding heteromyid foraging decisions are further complicated by species co-existence which is mediated by multiple related factors (reviews by Price & Brown 1983; Brown & Harney 1993). Up to six species of heteromyids can co-exist in one area. In the present field study there were four sympatric

species on the study site. Pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) which are smaller than the kangaroo rats and are quadrupedal are thought to be specialists at foraging under shrub cover, whereas the larger bipedal kangaroo rats are thought to specialise on open microhabitats due to their superior predator avoidance abilities (reviewed in Price & Brown 1983). There is also some evidence that among co-existing heteromyids the foraging activity of the smallest species is restricted by the preferences of the larger species (e.g. Kotler 1984; Price et al. 1984). Thus, it is likely that pocket mice do not have behavioural preferences that differ from those of kangaroo rats, but rather that, due to interspecific competition, they are forced to concentrate their activity in those times and/or places when kangaroo rat activity is lowest. In order to determine whether kangaroo rats and pocket mice differ in their foraging habits, we measured their respective quitting harvest rates under varying levels of predation risk.

Methods

The study took place at Boyd Deep Canyon Desert Research Station, about 8 km south of Palm Desert, California in 1997, 1998 and 1999. The scrub-brush habitat of the study site has been described in detail by Zabriskie (1979). A permanent trapping grid, with traps set at 10 m intervals in a 10 x 10 array was used in this study. Traps were set at least one night each week during each field season. A trapping night consisted of leaving the traps open for a few hours, beginning at or soon after dusk, and then recording the identity, weight, and reproductive condition of captured animals and releasing them by 0100 hrs. The nocturnal rodent population on the study site consisted

of four heteromyid species, *Dipodomys merriami*, *Chaetodipus fallax*, *C. formosus*, *C. penicillatus* and one cricetid rodent *Peromyscus eremicus*.

Laboratory preference test

Seed species preferences were tested on 10 *D. merriami* (five male, five female), six *C. fallax* (three male, three female), one male *C. formosus* and one female *C. penicillatus*, all of whom were trapped in the wild and held in the field station laboratory for 24 hours for testing. Each animal was housed in a plastic 28 x 32 x 16 cm cage with approximately 3 cm of sifted sand on the bottom, a tin can for shelter, a leaf of lettuce or spinach, and 3 g each of whole oats and lentils. Animals were held under the guidelines of the Canadian Council on Animal Care, and trapped under scientific collecting permits issued to the authors by the State of California Department of Fish and Game.

We predicted that lentils which contain 61.7% carbohydrate, 24.1% protein, 1.1% fat and 33.6 calories/10 g (from Price 1983) would be the less valuable and therefore less preferred seed, while oats which contain 68.3% carbohydrate, 13.3% protein, 7.5% fat and 38.1 calories/10 g, would be the preferred food due to the fact that they contain higher carbohydrate, lower protein and higher caloric value (Arrowhead Mills nutrition information).

After 24 hours each animal was released at its point of capture and the remaining cage contents were sifted. Oats and lentils were separated and weighed to the nearest 0.1 gram on an electronic scale (Denver Instruments Company XD 400) in order to determine the amount consumed.

Open access GUD trials in the field

Selectivity data were collected over two field seasons; autumn 1997 and autumn 1998. Pairs of plates were placed side by side at stations on the trapping grid. Each station was located at least 25 m from any other station, at regular intervals. Each pair consisted of one plate containing 3 g of lentils and one plate containing 3 g of oats (all seeds were killed by microwave to prevent germination) mixed with 400 ml of sand sifted through a USA Standard Testing Sieve No. 18, with openings of 1mm. Each pair of plates was located in one of two microhabitat types, herein labelled "open" (at least 2 m from the nearest shrub or cactus) or "cover" (directly under the canopy of the nearest shrub or cactus).

In both field seasons, 16 pairs of plates were positioned each night just before dusk and collected two hours later. The contents of each dish were sifted and the seeds remaining in the plates were weighed to the nearest 0.01g. Data were collected in autumn 1997 on 16 nights: October 14-16 (full moon), October 30-November 1 (new moon), November 14-16 (full moon), November 28-December 1 (new moon) and December 11-13 (full moon). In autumn 1998, data were collected on 10 nights: November 2-4 (full moon), November 17-20 (new moon), and December 1-3 (full moon).

The GUD data were analysed in a repeated measures ANOVA using SPSS 10.0.5. Each pair of trays was treated as a "subject". Repeated measures ANOVA included tests for the within-tray-pair (repeated measures) factor of seed species (two levels: oats and lentils). Microhabitat (two levels: open and cover), moon phase (two levels: new and full

moon), and field season (two levels: autumn 1997 and autumn 1998) were treated as between-tray-pairs factors.

Limited access GUD trials in the field

On each of the three nights surrounding the new and full moon phases (two of each) from April 28 to June 15, 1999, 12 pairs of seed plates (one containing 3 g of oats and the other 3 g of lentils) containing seeds mixed in sand were placed at the same locations on the trapping grid as for the open access trials. The difference between these trials and those conducted previously involved the use of enclosures to control who had access to the plates, as described below. Plates were again positioned at dusk and picked up two hours later. GUDs were measured as before. Six pairs were placed directly under the cover of shrubs and six were placed out in the open at least 2 m from any form of cover. Each pair of plates was placed inside an enclosure (50 cm x 50 cm x 7.5 cm) with a removable plywood floor and a wire mesh top. Six pairs of plates (three in the open, three under cover) were placed in enclosures with a hole on each side wide enough to allow entry of pocket mice but not kangaroo rats (2.03 cm diameter). The other six pairs of plates (three open, three cover) were placed in enclosures with a hole in each side wide enough to allow entry of both kangaroo rats and pocket mice (3.75 cm diameter).

The GUD data were analysed in a repeated measures ANOVA using SPSS 10.0.5. Each pair of trays was again treated as a "subject". Repeated measures ANOVA included tests for the within-tray-pair (repeated measures) factor of seed species (two levels: oats and lentils). Hole size (two levels: small and large), microhabitat (two levels: open and cover) and moon phase (two levels: new and full moon) were treated as

between-tray-pairs factors. All data are expressed as mean $\pm$SE. All statistical tests presented are 2-tailed. We classified pairs of trays where both trays contained more than 2.97 g of seeds as 'not found' by the rodents. Most of these plates did not contain footprints, suggesting that any slight detected change in weight was probably due to desiccation or measurement error.

Results

Laboratory preference test

All the rodents tested exhibited a strong preference for oats over lentils. The 10 kangaroo rats showed a unanimous preference for oats over lentils, consuming an average of 2.7 g oats and 0.3 g lentils in 24 hours (Wilcoxon signed-ranks test: T=0, N=10, P<0.01). The six *C. fallax* also showed a unanimous preference for oats, consuming an average of 1.98 g *versus* only 0.44 g of lentils in 24 hours (Wilcoxon signed-ranks test: T=0, N=6, P<0.05). The *C. formosus* and *C. penicillatus* that were tested exhibited the same preference pattern: the former (N=2) consumed 2.66 g of oats and 0.56 g of lentils and the latter (N=1) consumed 2.39 g of oats and 0.20 g of lentils.

Open access GUD trials

The repeated measures ANOVA test included here is for moonlight and microhabitat differences in GUDs. The within-tray-pair factor of seed type was significant. GUDs for oats (0.07$\pm$0.01 g) were significantly lower than for lentils (0.16$\pm$0.02 g; ANOVA: $F_{1,382}$=21.75, P<0.001). The between-tray-pair factors of moon phase and microhabitat were also significant. GUDs were lower under the new moon

(0.07±0.02 g) than under the full moon (0.14±0.01 g; ANOVA: $F_{1,382}$=8.07, P<0.01) and lower under the relatively safe cover of shrubs (0.07±0.02 g) than in the open (0.16±0.02 g; ANOVA: $F_{1,382}$=15.18, P<0.001). "Season" was also a significant between-tray-pair factor (ANOVA: $F_{1,382}$=11.76, P<0.01). GUDs were lower in autumn 1998 (0.07±0.02) than in autumn 1997 (0.15±0.02).

There was no interaction between food type and season (ANOVA: $F_{1,382}$=0.17, NS). Moon phase also had no effect on the rodents' selectivity for food type (ANOVA: $F_{1,382}$=2.43, NS). Hence, there was no change in selectivity between the two field seasons and no effect of moon light on selectivity.

Selectivity was significantly influenced by microhabitat. The rodents were more highly selective for food type in the more dangerous open microhabitats (ANOVA: $F_{1,382}$=4.33, P<0.05; see Fig. 2.1, p. 29).

--Insert Fig. 2.1 about here--

Finally, there was a significant 3-way interaction between food type, moon phase and microhabitat (ANOVA: $F_{1,382}$=4.60, P<0.05). GUDs were lower under cover than in open microhabitat during the full moon, but there was no such microhabitat effect under the new moon (see Fig 2.2, p. 30).

--Insert Fig. .2.2 about here--

There was a significant positive correlation between GUD and temperature at dusk (Spearman's rho=0.561, N=24, P<0.01). Temperature at dusk ranged from 9 to 29 degrees celsius (see Fig. 2.3, p. 31).

--Insert Fig. 2.3 about here—

Limited access GUD trials

Seventeen of 191 pairs of trays were excluded because they were 'not found' by rodents. Of these 17 pairs of trays that were not found, 15 were in boxes with small holes and just two in boxes with large holes (Chi-square test: χ^2=9.94, P<0.001). More than twice as many trays were 'not found' under the full moon (including the two boxes with large holes) than under the new moon, but this difference was not significant (12 *versus* 5, Chi-square test: χ^2=2.88, P<0.10).

GUDs were analysed as an index of foraging effort at the remaining 174 pairs of seed trays. There was a significant effect of hole size on giving up density (ANOVA: $F_{1,166}$=28.77, P<0.001). GUDs were higher in 'pocket mouse' boxes with small holes (0.71 $\pm$ 0.09 g) than in 'kangaroo rat plus pocket mouse' boxes with large holes (0.08 $\pm$ 0.08 g). GUDs were higher for lentils (0.42 $\pm$ 0.07) than for oats (0.32 $\pm$ 0.06; ANOVA: $F_{1,166}$=7.98, P<0.01). Also, GUDS were again higher in the trays under the full moon (0.52 $\pm$ 0.09 g) than under the new moon (0.27 $\pm$ 0.09 g) but this difference was not quite significant (ANOVA: $F_{1,166}$=3.86, P=0.051).

The rodents were significantly more selective for food type in boxes where only pocket mice could enter than in boxes where both kangaroo rats and pocket mice could enter (ANOVA: $F_{1,166}$=9.47, P<0.01; see Fig. 2.4, p. 32).

--Insert Fig. 2.4 about here--

There was no relationship between GUD and temperature during this study (Spearman's rho=-0.035, N=16, NS). Temperatures ranged between 14 and 32 degrees celsius.

Discussion

Higher requisite profit models predict greater selectivity (that is, a greater difference in response to oats *versus* lentils) in the open and under the full moon, when risk from predators is higher. Reduced finickiness models predict that animals will show greater selectivity during foraging under the relative safety of cover and under the new moon. The rodents in this study consumed more and put more effort into foraging for the food of higher value. They showed microhabitat-related changes in selectivity when foraging for foods that differed in value. In accordance with the predictions of the higher requisite profit model, they were more selective in the open than under cover. The rodents' highest level of selectivity (i. e., differential response to the two foods) was in the open under the full moon, when risk from visually hunting predators was highest.

Other studies carried out in a single field season have also shown that heteromyids respond to increased predation risk by showing greater selectivity between two types of seeds (Hay & Fuller 1981; Bowers 1988, 1990). Hay and Fuller (1981) examined selectivity in relation to microhabitat in heteromyids. Bowers (1988 & 1990) examined selectivity in relation to both moon phase and microhabitat in Merriam's kangaroo rats. Neither study used GUDs to measure selectivity. Ours is the first study,

to our knowledge, to document changes in selectivity in relation to predation risk by measuring GUDs across field seasons.

Kangaroo rats and pocket mice could not be shown to differ in their behavioural response to predation risk during foraging. Similar results have been found in other studies (Longland 1994), suggesting that in the absence of competitors, various heteromyid species show similar foraging habits. However, the pocket mice demonstrated selectivity for seed type, whereas there was no evidence of selectivity in the boxes with holes large enough to allow entry to both kangaroo rats and pocket mice even though there had been selectivity for seed type in the open access (no enclosure) trials in previous years.

It is difficult to interpret changes in foraging effort with temperature. The metabolic costs of foraging increase with decreasing temperature (Brown et al. 1994), because of thermoregulatory demands. In the present study, we found that the animals foraged trays down to lower densities at lower temperatures. Temperature decreases are associated with decreases in snake activity as well as increases in metabolic costs, so it is not clear whether the rodents increased their foraging effort at lower temperatures in response to an increased need for food, or a decreased risk from snakes.

One potential problem with this study is that GUDs were compared for two species of seeds. It may be argued that differences in GUD may simply reflect different harvesting rates due to seed size and detectability. This could be the case, but since the lentils are larger, and more detectable (Leaver unpublished data), the fact that GUDs

were higher for lentils simply serves to reinforce the conclusion that lentils were not a highly preferred food.

In future studies, it might be useful for researchers to clarify the basis of changes in selectivity in relation to variation in the intensity of predation cues, since in the present study microhabitat, but not moon phase, influenced the animal's food choices. Another avenue of potential interest would be to determine whether the effect of a predation risk cue on selectivity in a single species such as kangaroo rats differs depending on whether an animal is making decisions in a foraging or a mate choice context.

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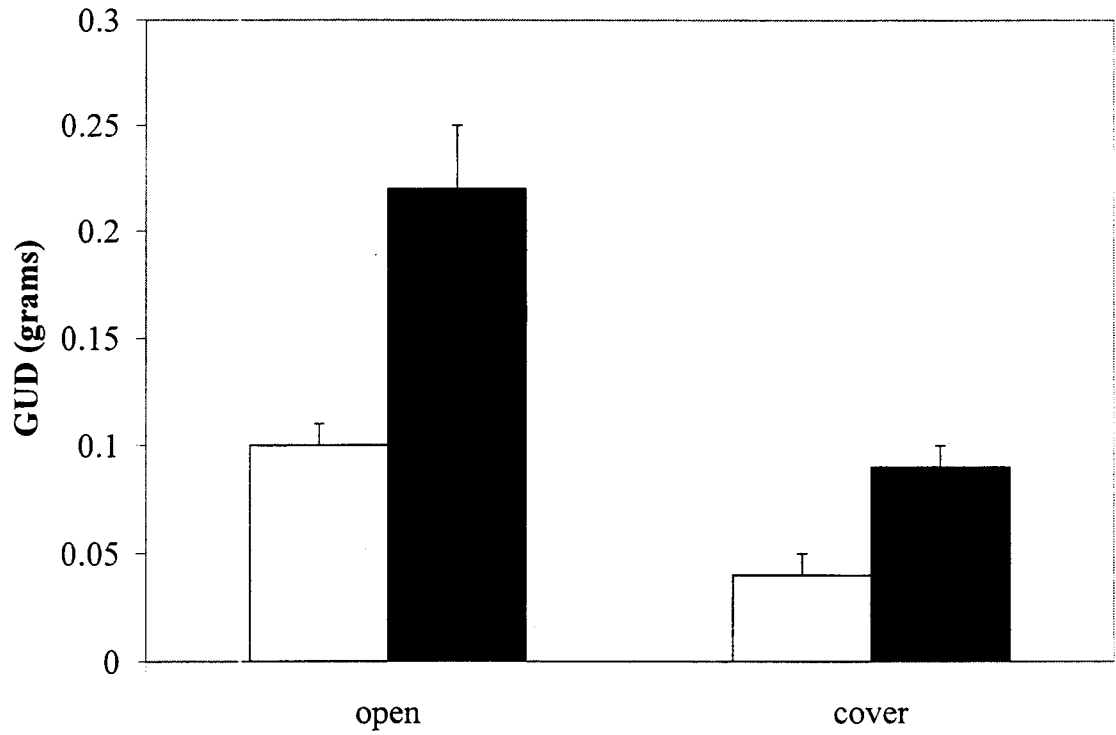
Figure 2.1 The GUDs (mean + SE) for oats (☐) and lentils (■) in open and cover

microhabitats.
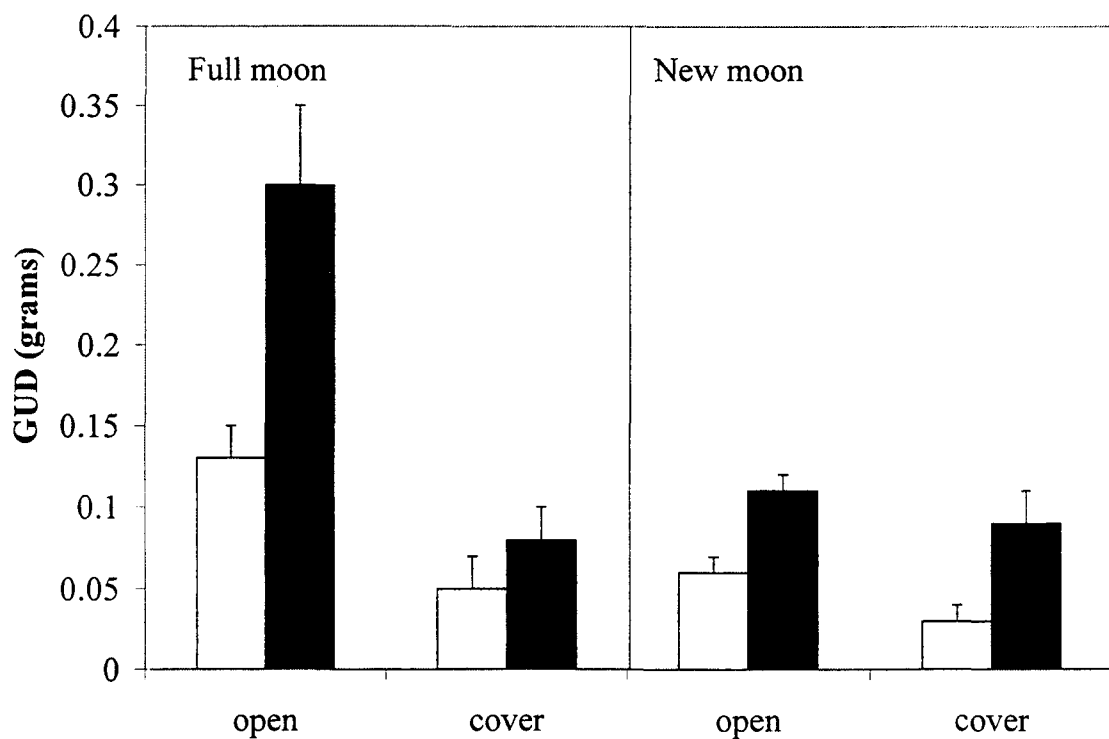
Figure 2.2 The GUDs (mean + SE) for oats (□) and lentils (■) in the open and under cover plotted separately for full and new moon phases.
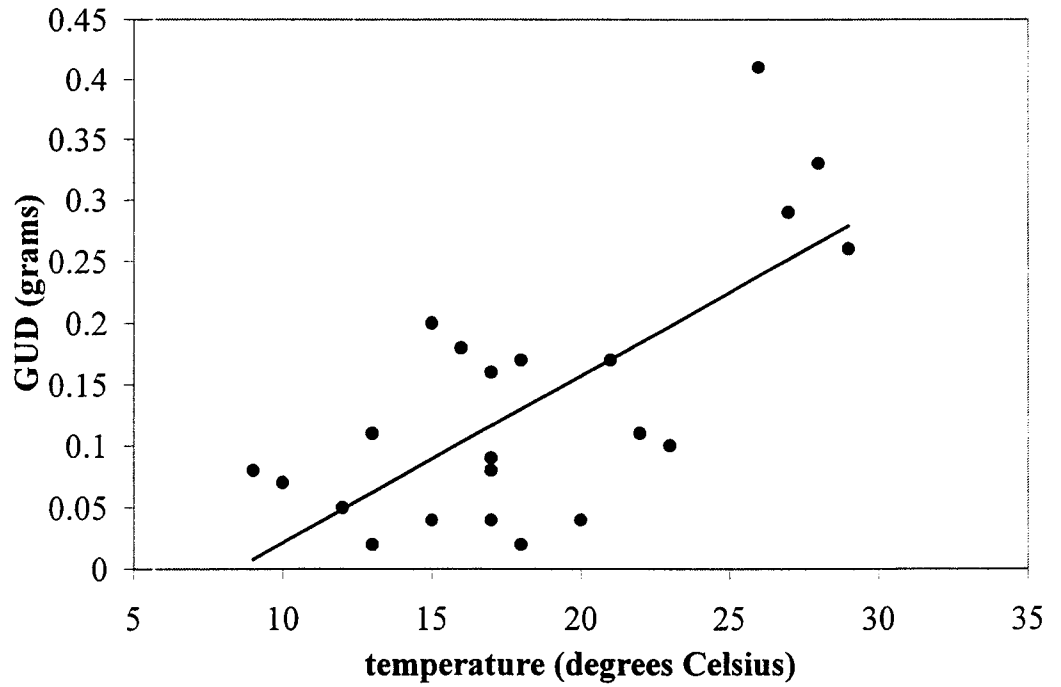
Figure 2.3 GUD plotted against temperature with trend-line. Data from two field

seasons.
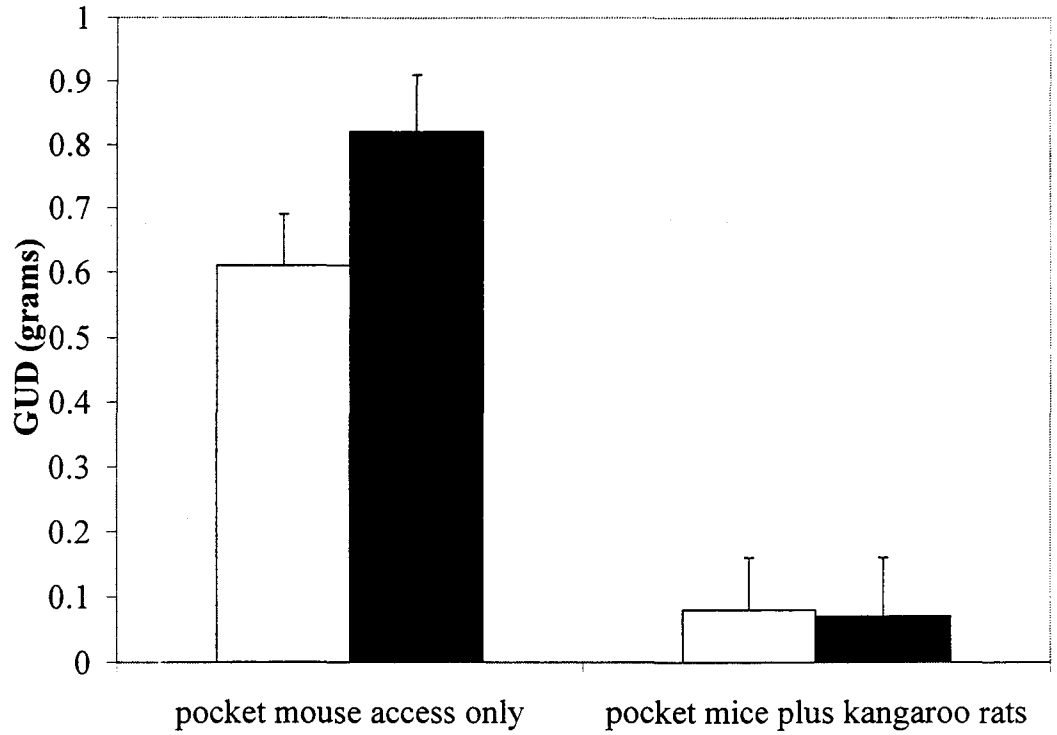
Figure 2.4 The GUDs (mean + SE) for oats (☐) and lentils (■) in boxes with small and large holes

Chapter 3

Effect of food value on caching decisions and cache pilferage by Heteromyid rodents in the field

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Running headline: Leaver: Heteromyid caching decisions

Abstract

I examined the scatter caching decisions made by Merriam's kangaroo rats (*Dipodomys merriami*) in the field. Based on the hypothesis that the effort expended in sequestering food should be adaptively modulated and on the results of previous laboratory studies, I predicted that they would partition a more valued and preferred food (oats) into a larger number of smaller sized caches, and that these caches would be more widely dispersed than caches of a less valued and preferred food (lentils). I also observed the probability of discovery of artificial caches of oats and lentils at two caching distances. *D. merriami* dispersed caches of oats significantly more widely, but caches of both oats and lentils were similar in size. Increased spacing of artificial caches decreased the probability of pilferage, but the species of the seeds in the caches had no effect on pilferage. The results suggest that the cache spacing decisions made by Merriam's kangaroo rats function to better protect more valuable seeds from loss to pilferers.

Introduction

For food storing animals, decisions related to the protection of caches from pilferers can be crucial for surviving periods of scarcity. Many animals store their food in numerous small caches, a method of food caching called scatter caching, as opposed to larder caching, which entails storing repeated loads of food in a single place (Vander Wall 1990). Scatter caching presumably provides protection against major loss to pilferers, and wide dispersion of scattered caches further protects caches from pilferage by increasing the area a pilferer must search (Stapanian & Smith 1978, 1984; Sherry et al. 1982; Clarkson et al. 1986; Daly et al. 1992b). However, there are costs involved in increased cache spacing. Memory demands are higher when an animal must retrieve a larger number of caches spread over a wider area (Sherry et al. 1989, 1992; Jacobs 1992; Jacobs & Spencer 1994), and predation risk increases as a function of exposure during travel time (e.g. Daly et al. 1990).

Most models of cache spacing share the assumption that a pilferer will conduct a more intensive area-localised search for caches after encountering a cache containing more valuable food (Stapanian & Smith 1978, 1984; Clarkson et al. 1986; Hurly & Robertson 1987). A number of studies show that scatter caching rodents and birds disperse caches of more valuable food more widely (red squirrels, *Tamiasciurus hudsonicus*, Hurly & Robertson 1987; yellow pine chipmunks, *Tamias amoenus*, Vander Wall 1995; willow and crested tits, *Parus montanus* and *P. cristatus*, Jokinen & Suhonen 1995; heteromyid rodents, Longland & Clements 1995; Leaver & Daly 1998; grey

squirrels, *Sciurus carolinensis*, Steele et al. 1996; Hadj-Chikh et al. 1996; Japanese squirrels, *S. lis*, Tamura et al. 1999). However, to my knowledge, there have been just two direct tests of the assumption that pilferers search more extensively upon finding a more valuable cache. Fox squirrels (*S. niger*) conduct more intensive searches in patches containing artificial caches of more valuable food (in terms of calories) (Stapanian & Smith 1984) whereas heteromyid rodents apparently do not search harder after finding larger sized caches since they were no more likely to find another nearby cache after locating a larger cache than a smaller cache (Daly et al 1992b). While there is conflicting evidence for search intensity in relation to cache value, there is evidence that increased spacing of artificial caches better protects them from pilferage (Stapanian & Smith 1978, 1984; Sherry et al. 1982; Clarkson et al. 1986; Daly et al. 1992b; Tamura et al. 1999).

Merriam's kangaroo rats (*Dipodomys merriami*) are predominantly granivorous and, like many other desert-dwelling heteromyid rodents, they prefer seeds that are relatively high in carbohydrate and low in protein (Lockard & Lockard, 1971; Price, 1983; Kelrick et al., 1986; Frank, 1988). For these desert rodents, food value is closely associated with water conservation. Carbohydrates produce a small amount of water during metabolism (Schmidt-Nielsen 1964) and protein ingestion results in water loss (Frank, 1988). In the laboratory, *D. merriami* preferentially cache a high carbohydrate, low protein food, placing it in a larger number of smaller sized, more widely spaced caches (Leaver & Daly 1998). Presumably they do this in order to better protect more valuable caches from pilferage.

The present study was conducted in order to test whether Merriam's kangaroo rats in the field show the same preferential caching of a more valuable food that they show in the laboratory and to see whether heteromyid rodent pilferers would conduct more intensive area-localised searches for caches containing seeds differing in carbohydrate to protein ratio. I did this by locating caches made by individual Merriam's kangaroo rats and by examining survival of arrays of artificial caches.

It is possible that heteromyid pilferers use the nutritional value of the seeds in a cache as an indicator of the value of surrounding caches, even though they do not use cache size (Daly et al. 1992b) because a caching animal gathering seeds from a single source can vary cache size more readily than seed value. Thus seed value may be a more reliable indicator to a pilferer of the utility of searching for surrounding caches. Since pilferers are more likely to find caches that are closer together in space and if seed storers scatter caches of a preferred food more widely, a pilferer might benefit by searching a wider area upon discovering a more valuable food cache. In the first experiment I tested two predictions: (1) a more valuable food will be partitioned into a larger number of smaller sized caches (2) these caches will be more widely spaced. In the second experiment I tested the prediction that area localised search by pilferers will be more extensive once caches are discovered if they contain more seeds that are more valuable to the pilferer.

Methods

Field site

The study took place at the University of California's Phillip L. Boyd Deep Canyon Desert Research Center in Palm Desert California, USA. The scrub brush vegetation of the alluvial plain has been described in detail by Zabriskie (1979).

Experiment 1: Cache partitioning and spacing in the field

In order to examine the nature of cache spacing by *D. merriami*, I provisioned them with seeds dusted in fluorescent powder and used portable ultraviolet lights to locate their caches (protocol from Longland & Clements 1995). Over 17 nights from November 4 to December 5, 1997, I placed 44 provisioning trays at separate locations in the field. I avoided new and full moon nights, since the extreme lighting conditions in these moon phases cause the animals to alter their foraging and activity patterns from that of the other nights (e.g. Daly et al. 1992a; Price et al. 1984).

Each provisioning tray consisted of a 30.6 cm round aluminium tray covered with sandpaper and dusted with fluorescent powder (Radiant Color). In the centre of each tray, I fastened a 7 cm round petri dish containing 40 g of whole oats (22 trays) or 40 g of whole lentils (22 trays) which had been mixed with 3g of green, blue or pink fluorescent powder. Oats are a relatively high carbohydrate, low protein food (68.3% carbohydrate, 13.3% protein; Arrowhead Mills nutrition information) and are preferred (Leaver & Daly unpublished data) over lentils, a relatively low carbohydrate, high protein seed (61.7% carbohydrate, 24.1% protein; Price 1983).

At sunset (~1700 hrs) on each of the 17 nights, I placed two to six trays at novel locations on the alluvial plain of Deep Canyon, spaced at least 30 m apart. I left the trays until 0200-0300 hours at which time I returned to each tray and checked whether or not it had been discovered by rodents. I conducted all searches around provisioning trays with the help of an assistant. At each of the trays that had been discovered by rodents, we used portable ultraviolet lights to follow any trails left by the animal. We also conducted a systematic search around each tray radiating outwards from the tray in concentric circles at 5 m intervals, covering approximately 70 m in diameter around each tray. By doing so we were able to find caches which had no trail leading to them. It was not possible to search a wider area thoroughly before dawn. Scatter caches were identifiable by conspicuous disturbance and signs of digging by the caching animal which left a distinctive sweep of fluorescent powder.

We marked trails that led to burrow entrances, caches, stray seeds, and burrow entrances with signs of powder around them with numbered pin flags. We removed the contents of any caches (and replenished them with a comparable amount of rolled oats) and placed them in labelled zip-lock bags for later weighing. We also collected and weighed any stray seeds. Caches were defined as consisting of two or more buried seeds. Single seeds were often scattered along trails as if accidentally dropped, and these were not counted as caches.

On the following day we measured the distance of each cache from the centre of the provisioning tray and the nearest neighbour distances for each cache. We did not measure the distance from the tray or the nearest neighbour for two cache locations at one

oat tray and one cache location at one lentil tray because the pin flags had been blown away in strong winds.

We identified the genus of visitor(s) to the tray by the footprints left around the tray by animals that had walked across fluorescent powder. In order to verify the species identity of the caching animals, in addition to the footprints, we used dyed seeds at some of the provisioning trays and subsequently set traps locally and examined the trapped animal's faeces for dye, in order to determine individual use of the seeds at the trays. We dyed oats at the provisioning trays with a solution of either Fast Green (Fisher Scientific) or Eosin Y (Fisher Scientific). Neither of these dyes affects the palatability of seeds for heteromyids (Daly et al. 1992b). It was not possible to dye the lentils since they did not take the dye.

At dusk on the night following discovery of an oat tray by a rodent, we set up a 5 x 6 grid of thirty Sherman live traps baited with rolled oats and set at 5 m intervals centred on the provisioning site. If trapping was not successful on the first night, we reset the traps at the same location the following night. We checked traps between 0000 hours and 0200 hours. We recorded the weight, sex, and reproductive condition of all trapped animals, checked them for traces of fluorescent powder and dye, and collected 1-2 faecal boluses from each subject before release. Seven animals did not produce faecal samples, four *Chaetodipus formosus* and three *D. merriami*, but two of each species had traces of dye and fluorescent powder around their mouths, inside their cheek pouches and around their anuses, so they were assumed responsible for depleting the respective dish.

We placed faecal samples inside small clear plastic vials and transported them to the station laboratory where a few drops of tap water were added to each. Subjective judgements were made more than 10 hours after the addition of water as to the presence or absence of dye. Twenty seven faecal samples were collected from trapped animals, and these were rated by four independent raters. Raters disagreed in three cases. Trapping records indicated that in two of these three cases, the animal had traces of fluorescent powder in its cheek pouches, and thus was likely to have been responsible for depleting the seeds at the provisioning tray. The third animal had no trace of powder on its body and thus was not considered to be responsible for depleting the tray in the vicinity in which it was trapped. Those animals that had traces of fluorescent powder on their bodies and/or who had dye present in their faeces were considered to be the animals responsible for caching around their respective trays. We also trapped at two lentil tray locations in order to ensure that the same species were present at both oat and lentil tray locations.

One-tailed Mann Whitney U tests (SPSS 10.0.5) were used to compare the mean number of caches, the mean nearest neighbour distance for scattered caches, the mean distance of caches from the source and the mean weight of caches at trays of oats *versus* lentils.

Experiment 2: Pilferage from artificial caches

In order to quantify the rate of discovery of caches of oats *versus* lentils, and to see if oats evidently inspired more intense or effective area-localised search than lentils,

we buried 603 triads of artificial caches and checked them for discovery after 23-25 hours. Caches were buried just outside of Boyd Deep Canyon Desert Research Station during three field periods, January 23 to March 2, 1997 (208 triads), October 11 to November 16, 1997 (175 triads) and October 14 to November 30, 1998 (220 triads). Triads were spaced at least 70m apart, so that it was unlikely that two triads would be discovered by the same rodent. Each triad consisted of either three caches of oats or three caches of lentils buried at each point of an equilateral triangle, measuring either 0.5 m or 2 m on a side. These cache distances differentially affect discovery by heteromyids (Daly et al. 1992b). Each cache contained eight seeds buried 1 cm deep in fine sand in plastic cups measuring 4.5 cm in diameter and 4 cm deep. These cups were themselves buried in the substrate so that their rims were flush with the surface. Locations were marked by yellow or orange tape tied to nearby (1-3 m away) shrubs or trees and exact cache locations were noted with reference to shrubs and compass directions.

After 24 hours, we checked artificial caches for discovery. At each triad, we recorded any sign of disturbance, the number of seeds left in each cache, and the number of caches disturbed in each triad. Any triad with a cache that had been noticeably disturbed and/or where there were seeds missing was considered to be 'discovered' by a pilferer. We removed triads where one or more caches had been discovered, and left triads where none of the three caches had been discovered for one more period of 24 hours. After removal, the same area was never reused for a subsequent group of triads.

We censused the nocturnal population by trapping for five nights in 1997 in different areas where the artificial caches had been made. Over five non-consecutive

nights 420 traps were set and left until dawn. Of the animals caught, 31 were *D. merriami* (53%), 22 were pocket mice (37%), either *Chaetodipus formosus* or *C. penicillatus* and six were cricetid rodents, *Peromyscus eremicus* (10%). Thus, it is likely that the majority of pilferers were heteromyid rodents.

In order to compare proportions of triads where more than one cache was pilfered, given that one cache was pilfered, I used a test for comparing two proportions to compare pilferage at the two spacings (0.5 and 2 m) and for the two seed types (oats and lentils) (Zar 1999). I used a test for comparing multiple proportions to compare pilferage rates between the three field seasons (Zar 1999).

Results

Experiment 1: Caching behaviour

Of the 44 provisioning trays, 26 (16 oat trays, 10 lentil trays) were discovered by rodents. There were two or more scattered caches in the vicinity of 13 (six oats, 6/16=37.5%; seven lentils, 7/10=70%) of these 26 trays [test for comparing two proportions: Z_2=1.21, NS, one-tailed]. Only one scattered cache was found at each of three tray locations (two oats, one lentils). Signs of larder caching (traces of powder around burrow entrances) were present in the vicinity of eight of the 13 trays with two or more scattered caches, two of the three trays with one scattered cache and at five seed trays with no scattered caches. No caches were found at the remaining five trays. I found a total of 171 scattered caches (71 oat, 100 lentil).

Contrary to prediction 1, which stated that rodents should partition a more valuable food into more, smaller sized caches, the rodents actually made slightly more caches of lentils than of oats (Table 3.1, p. 54), and caches of oats and lentils were almost identical in weight (Table 3.1, p. 54).

---Insert Table 3.1 about here---

In accordance with prediction 2, that caches of a more valuable food should be more widely spaced, the rodents distributed oat caches more widely than lentil caches: nearest neighbour distances were wider for oats than for lentils, but caches of oats and lentils were placed similar distances from the source (Table 3.1, p. 54). We recovered less of the total provisioned 40 g of oats per tray than lentils (Table 3.1, p. 54).

Identification of cachers

I set a total of 390 traps around 14 of the 16 oat tray locations that had been discovered by rodents. Inclement weather prohibited trapping at the two remaining tray locations. At one of the 14 trapping locations no animals entered any of the traps. Traces of fluorescent powder and/or faecal dye were present for 9/15 *D. merriami*, 5/11 *C. formosus*, 2/8 *C. penicillatus*, and 0/1 *C. fallax*.

I set thirty traps around each of two lentil tray locations. Traces of powder were present on 2/5 *D. merriami*, 0/4 *C. formosus*, and 0/1 *C. penicillatus*.

At the 11 trays from which I had both footprint identification and trapping data the species that was identified by its fluorescent tracks was also trapped and at nine of these locations had traces of dye or powder. At the remaining two tray locations, two

species had been identified by footprints, but only one had traces of dye or powder when trapped. In future studies, use of fluorescent powder to identify the caching animal by footprints seems sufficient.

I set traps at 11 of the 13 tray locations where I had found more than two scattered caches and kangaroo rats were present at all of them. Therefore, I attributed all scattered caches to kangaroo rats. Previous direct observations of habituated kangaroo rats and pocket mice collecting and hoarding provisioned food at Deep Canyon suggest that kangaroo rats scatter cache, while the pocket mice seldom do so (Leaver & Daly, unpublished data).

Experiment 2: Discovery of artificial caches

Five hundred twenty three of the 603 triads went 'undiscovered', so the pilferage rate was relatively low: 13.3%.

Discovery rate differed between field seasons, 32/208 (15.4%) in winter 1997, 13/175 (7.4%) in autumn 1997 and 35/220 (15.9%) in autumn 1998 [test for comparing multiple proportions; $\chi^2=7.30$, v=2, p<0.05]. Increased spacing reduced the probability that more than one cache in a triad would be discovered if at least one was, from 74% at 0.5 m to 45% at 2 m [test for comparing two proportions; $Z_2=2.35$, p<0.01, one-tailed; Table 3.2, p. 55]. There was no effect of seed type on the probability that a triad would be discovered [test for comparing two proportions; $Z_2=0.19$, NS, one-tailed; Table 3.2, p. 55].

---Insert Table 3.2 about here---

Discussion

Contrary to predictions, the kangaroo rats did not make a larger number of smaller sized, more widely spaced caches of the more valuable food. In fact, they made slightly more caches of the less valuable food and caches of both types of food were similar in size. However, more relevant to the issue of protecting more valuable food from pilferers, they distributed caches of the more valuable food more widely, as predicted. Wider cache dispersion entails a greater investment of time, energy, memory and exposure to predators, and the results of the artificial cache pilferage study showed that it also functioned to protect neighbouring caches from pilferage. Thus, the animals in this study adaptively adjusted cache spacing in a manner which protects more valuable food.

The spacing of artificial caches in the present study influenced their vulnerability to pilferage. Wider dispersion of artificial caches protected them better from discovery, as has been found in previous studies (see Introduction). However, heteromyid pilferers showed no evidence of searching more extensively for neighbouring caches upon discovering a more valuable cache. The type of seed in the cache did not affect probability of discovery. In a similar study carried out by Daly et al. (1992b) at the same study site, the number of seeds per cache was similarly irrelevant to the probability of discovery.

Whereas kangaroo rats in a laboratory environment were seen to make smaller caches of a more valuable food (Leaver & Daly 1998), the costs of partitioning a resource into a larger number of smaller caches might be too high for the rodents in the field. In the present study, the rodents spaced caches of a valuable food more widely. By doing

so, the rodents exposed themselves to higher predation risk by travelling greater distances during caching. The additional travel time that would have been incurred had the animals made these caches smaller and more numerous would further increase predation risk. By making smaller sized caches, in addition to spacing them more widely, an animal might reduce losses, but that benefit is likely outweighed by the corresponding increase in predation risk. The rodents dispersed caches, on average, more widely than the artificial caches were placed, so the risk that losing one cache will lead to the loss of another may be negligible, particularly for oat caches, which were spaced more widely by the rodents.

The conditional probability of finding additional caches in a triad after one was discovered was essentially identical for oats (0.61) and lentils (0.56). This suggests that rodents did not engage in more intense area-localised search after a more valuable food was discovered. The more widely dispersed natural caches of oats suggest that caching strategies eliminate any advantage that would accrue from doing so.

Discovery rates of artificial caches were significantly lower in autumn 1997 than in either winter 1997 or autumn 1998. This result was not predicted. However, in autumn 1997, there was an abundance of food and the kangaroo rats were heavier than average (39 g in autumn 1997 *versus* 36 g in winter 1997 and 34 g in autumn 1998). Thus artificial caches were less likely to be discovered when food was relatively abundant, presumably because more food (natural and provided) is left unharvested.

In this study, the species of the pilferer at artificial caches was not known. Time of pilferage was also unknown, so the possibility that more than one individual was responsible for discovery of a triad cannot be ruled out. Additionally, there were diurnal

animals that might have been responsible for cache pilferage, such as ground squirrels, birds and insects but the buried caches were likely safe from birds and ants. In future studies, it would be useful to directly determine which animals are primarily responsible for cache pilferage.

The fact the kangaroo rats made more caches of the less valuable food in this study might be an artefact of their closer spacing. More oat caches might have been discovered had we searched a wider radius around each tray. Unfortunately, due to time constraints, searching was biased to find the caches that were closest to the source. Daly et al. (1992b) used radiotelemetry to follow individual *D. merriami* as they cached. The maximum distance of caches from the source was 80 m in that study. Thus it is possible that there were caches beyond the area that was searched in the present study, and that the numbers were different for the two different food types. This possibility is reinforced by the fact that more of the oats than the lentils went unaccounted for. It is also possible that the rodents put more effort into hiding caches of oats than caches of lentils underneath shrubs and in brush where it was harder to search with portable lights.

In future studies, it would be informative to leave artificial caches for a longer time period that more closely mimics actual cache life in the field. By examining the caching behaviour of individuals more closely in the field, it will be possible to gain a better understanding of the nature of the decisions made by kangaroo rats and pocket mice when they cache seeds of different value.

Acknowledgements

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Table 3.1 Comparison of caches at 8 trays each of oats and lentils for number, weight and distance of caches from the source, and for a subset of those trays (6 trays of oats and 7 trays of lentils) where more than one cache was made for nearest neighbour distance

	Oats	Lentils		
	Mean[a]	Mean[a]	U[b]	p[c]
Number of caches	9.0±3.3	13.0±2.5	15	0.036
Weight of caches (g)	0.64±0.1	0.79±0.1	20	0.104
Nearest Neighbour (m)	11.7±5.5	3.61±0.6	9	0.043
Distance from source (m)	17.6±2.3	20.6±2.5	24	0.201
Amount recovered (g)	7.0±2.9	11.2±1.8	14	0.053

[a]average of the means ± SE from the caches at each tray.

[b]U is the value obtained by Mann Whitney U tests for each comparison.

[c]p is the probability that the means for oats and lentils differ significantly by a 1-tailed Mann Whitney U test.

Table 3.2 Conditional probability of finding additional caches in a triad after one was discovered. Data combined for 3 replicates of the experiment in fall and winter 1997 and autumn 1998

Spacing/seed	0.5 m	2 m	TOTALS
Oats	16/21=0.76	9/20=0.45	25/41=0.61
Lentils	12/17=0.71	10/22=0.45	22/39=0.56
TOTALS	28/38=0.74	19/42=0.45	

Chapter 4

Food caching and differential vulnerability to cache pilferage: a field study of co-existence in sympatric heteromyid rodents

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Abstract

Ecologists studying sympatric heteromyid rodents usually invoke species differences in primary foraging abilities and preferences and/or predation risk in order to explain co-existence. The present field study was conducted to test the hypothesis that co-existence is mediated by differences in caching patterns, which result in differences in vulnerability to pilferage. We examined differences between genera in foraging, caching and pilferage behaviour of kangaroo rats (Dipodomys spp.) and pocket mice (Chaetodipus spp.). Specifically, we examined aggressive interactions at food patches, differential food caching patterns and differential vulnerability to cache pilferage. Observations conducted at artificial seed patches showed that kangaroo rats chased other kangaroo rats and pocket mice away from seed patches, and pocket mice chased each other, but pocket mice rarely chased kangaroo rats. 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 only pilfered from each other.

KEY WORDS: co-existence, pilferage, food hoarding, Dipodomys, Chaetodipus

Introduction

The co-existence of ecologically similar rodent species has been a subject of interest for decades (e.g. see reviews by Brown & 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 & Harney 1993 for a review of body size patterns) and mode of locomotion (kangaroo rats and kangaroo mice are bipedal, pocket mice are quadrupedal). The heteromyid rodents that inhabit arid areas of the American southwest are nocturnal, burrow-dwelling granivores with behavioural and physiological adaptations that allow them to survive without drinking free water.

Most research on the co-existence of heteromyid species has focused on looking for differences among species in harvesting seeds from primary sources, or "primary foraging" abilities (reviewed by Kotler & Brown 1988). However, efforts to identify species differences in food preferences or foraging skills have mostly failed to explain species co-existence (reviewed by Randall 1993; Price et al. 2000). Neither foraging preferences (e. g. Smigel & Rosenzweig 1974; Reichman & Oberstein 1977; Hutto 1978; Price 1983a) nor abilities (e. g.; Price & Heinz 1984; Price & Podolsky 1989; Morgan & Price 1992; but see Rosenzweig and Sterner 1970) of different heteromyid species have been found to differ.

Behavioural differences permitting species co-existence may not exist exclusively in the realm of foraging skills and preferences. Other possibilities that have been investigated include vulnerability to predation (Kotler et al. 1988; Longland & Price 1991), aggressive dominance (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 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 co-exist 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 & Joyner 1997; Price et al. 2000). However, to our knowledge, there have been no field studies of species differences in caching patterns 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 co-existence. We focus on the simple question of why members of one genus do not out-compete members of another, rather than examining how up to six species can co-exist.

Co-existence may be mediated by a combination of 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 co-existence because although one species may be a better primary

forager of common resources, another species may be better at sequestering or pilfering

them. In the first experiment 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 the ecological variables of patch value, microhabitat and moon

phase by kangaroo rats versus pocket mice. We also report inter- and intra-genus

aggression at the food patches in order to determine whether the larger D. merriami

aggressively monopolized patches. In the second experiment, we compare the caching

behaviour of kangaroo rats and pocket mice in the field. In the last experiment, we

examine genus differences in vulnerability to and perpetration of cache pilferage.

EXPERIMENT 1-Competition over artificial food patches

We explored genus differences in use of artificial seed patches and aggressive

interactions at patches differing in seed value, microhabitat and moon phase. We

predicted that (1) D. merriami would aggressively monopolise patches, and (2) kangaroo

rats and pocket mice would show similar "preferences", as measured by visits to the

trays. The purpose of this experiment was to determine whether there were genus

differences at the level of primary foraging at our field site that might facilitate co-

existence.

Methods

We captured rodents on a trapping grid consisting of 100 traps spaced at 10 m intervals at the Boyd Deep Canyon Desert Research Center, approximately 8 km south of Palm Desert, California. We captured five species of nocturnal rodents during the course of the study: 4 heteromyid species (one kangaroo rat, D. merriami, and 3 pocket mice, C. fallax, C. formosus and C. penicillatus), and one cricetid (Peromyscus eremicus). We marked individual rodents with 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 hours 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 (October 10 to December 10, 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 (see Chapter 2, p. 14), 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 1983a). Both kangaroo rats and pocket mice prefer

seeds high in carbohydrate relative to protein (Price 1983a), since 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 oats or lentils. We placed seed trays in pairs at locations 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. Two to 2.5 hours later we collected the trays and brought them to a laboratory where the remaining seeds were sifted and weighed. We followed this procedure for 4 nights surrounding the new moon (17-20 November, 1998) and 3 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-hour period that they were available to the rodents, either by an observer seated 5 to 10 m from the tray with a dim headlight (4 Watt bulb), or by an infrared video camera on a tripod placed approximately 1 m from the seed dish. In total, we collected 42 hours of observational data. During observations we recorded the number 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 4 nights prior to the experiment.

Statistical analyses of 42 hours of observational data collected at 21 pairs of trays over 4 new moon nights from 17-20 November, and 3 full moon nights, 1-3 December, 1998, are presented below.

The amount of seeds left in the foraging trays in grams was analysed in repeated measures ANOVAs with pairs of trays treated as "subjects". The night of testing was included as a covariate. Seed species (2 levels: oats, lentils) was treated as a within-tray-pair factor. Microhabitat (2 levels: open, cover) and moon phase (2 levels: full, new) were treated as between-tray-pair factors.

Number of visits made to the seed trays was compared for genus, seed value, microhabitat and moon phase using Wilcoxon signed ranks tests and Mann Whitney U 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.

Results

The within-tray-pair factor of seed type was significant, with giving up densities (GUDs) for oats (0.04 ± 0.02 g) lower than for lentils (0.11 ± 0.03 g; ANOVA: $F_{1,154}=6.27$, p<0.05). The between-tray-pair factor of microhabitat was also significant, with GUDs lower under the cover of shrubs (0.02 ± 0.03g) than in the open (0.13 ± 0.03 g; ANOVA: $F_{1,154}=5.41$, P<0.05). There were no significant effects of moon phase on the amount of seeds left in the trays, and no significant interactions.

Kangaroo rats and pocket mice were the primary visitors to the seed trays. Only 2 visits were observed by P. eremicus, and these visits were not included in the analysis.

Kangaroo rats made more visits per tray (31 ± 15) than pocket mice (12 ± 14) at all but 3 of the 20 pairs of seed trays that were visited by rodents (Wilcoxon signed ranks test: $Z = -3.42$, $n = 20$, $p < 0.001$).

The rodents made significantly more visits to the oat trays (mean visits = 23 ± 3) at 11 of the 20 pairs of trays and more visits to the lentils (mean visits = 20 ± 2) at 6 pairs (Wilcoxon signed ranks test: $Z = -2.11$, $n = 20$, $p < 0.05$)

Significantly more visits were made to pairs of trays under the cover of shrubs (52 ± 7) than to trays in the open (31 ± 6; Mann Whitney test: $U = 18$, $n_A = 11$, $n_B = 9$, $p < 0.05$). There was no difference between the number of visits made to trays under the new (47 ± 7) versus full (37 ± 6) moon (Mann Whitney test: $U = 40.5$, $n_A = 11$, $n_B = 9$, NS).

A chase ensued in all but one of 69 instances in which 2 rodents were observed in the vicinity of a seed tray. The one exception occurred when 2 pocket mice foraged at a pair of trays. There was a significant effect of the genus of chaser and chasee on the number of chases made. Significantly more chases involved a kangaroo rat chasing a pocket mouse (38 chases) than a pocket mouse chasing a kangaroo rat (1 chase; $\chi^2 = 35.1$, $df = 1$, $p < 0.001$). A kangaroo rat chased another kangaroo rat in 21 of the chases and a pocket mouse chased another pocket mouse in 8 chases.

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, and 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 body size and the proportion of seeds larder hoarded by heteromyids were positively correlated in the six species they examined, but in a similar study, Price et al. (2000) reported an increase in scatter caching with increased body mass in the eight species of heteromyid rodents that were tested. Price et al. (2000) suggest the possibility that different methodology and apparatus may contribute to the different results reported in the two studies.

There are no such comparative studies of caching behaviour in the field. This experiment was conducted in order to determine whether there were any differences in food storage behaviours 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 October 28 and December 11, 1998. Eight individual kangaroo rats and 7 individual pocket mice were each provisioned with seeds by placing seed trays near burrows, and their caches were subsequently located. Each animal was only provisioned once.

One or 2 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 utilized. 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 aluminum tray, with a 7.5 cm round aluminum seed dish fixed in its center, at a place on the trapping grid where rodents had been observed. Caches were located following the protocol used by Longland and Clements (1995). The aluminum trays were lined with sandpaper, which was dusted with fluorescent powder (Radiant Color). The seeds in the center 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 2 caching trials, in which 1 kangaroo rat and 1 pocket mouse were provisioned, the seed dish in the center 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 minutes, 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 3600 m^2 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 visually 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 labeled bags for subsequent weighing. We replaced all caches immediately with a 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. A univariate ANOVA of number of caches, with species (D. merriami and C. fallax) as a between-subject factor and cache type (pit cache and burrow entrance) as a within-subject factor, was conducted using SPSS 9.0.1.

Results

The analysis revealed a significant interaction between species and cache type. Eight kangaroo rats each 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), whereas seven pocket mice each entered an average of 4.43 ± 0.92 existing burrows and made only 0.29 ± 0.92 pit caches ($F_{1,26}=20.13$, $p<0.001$). The multiple burrow entrances used by the 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 2 shallow pit caches were made by pocket mice. Although such pit caches are characteristic of scatter caching kangaroo rats, these 2 caches might best be characterized 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 (Vander 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-Pilferage in kangaroo rats and pocket mice

The third experiment explores the possibility that pocket mice might co-exist with kangaroo rats by specializing in cache pilferage. If kangaroo rats dominate initial natural resource patches, then the pocket mice may have an advantage in another realm, such as pilfering and/or protecting their seeds from pilferage. Smaller rodents might be 'forced' to scatter cache when they are unable to defend a larder hoard against larger bodied congeners, but it is also possible that there are benefits to larder hoarding that are enjoyed exclusively by the smaller bodied pocket mice. Jenkins and Breck (1998) have suggested that the small burrow entrances of pocket mice may prevent entry by the larger bodied 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 cricetid rodents, at this study

site. 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 parasitizing the kangaroo rats' foraging efforts.

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

Methods

In spring 1999, we trapped rodents for 10 nights between April 27 and June 8, 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 in the methods section of Experiment 1.

Batches of oats were dyed by soaking them in a solution of Fast Green and water for 30 minutes, 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 & 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. An observer sat close to the dish to ensure that only the targeted rodent took the dyed food, but at one tray location on November 23, 1998, 2 C. fallax shared 5 g of food. On June 1, 1999, a C. fallax female traveled 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. Five D. merriami were each

provisioned with 10-25 g of dyed oats on May 2 and 3, 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.

The provisioning trials were followed by a series of 3-5 trap nights, following the same procedures as used in Experiment 1. We collected fecal samples directly from each trapped animal when possible. We placed all fecal samples in labeled plastic vials. In the laboratory we added a few drops of tap water to each sample. The next day 2 independent raters who were blind to the identity of the animals rated fecal 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 feces. Raters disagreed on the presence of dye in just 3 of 95 cases where fecal 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 feces contained traces of dye.

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

Pilferage by kangaroo rats and pocket mice was compared by chi-square tests. Separate analyses were conducted for pilferers when pocket mice were provisioned and when kangaroo rats were provisioned. Expected values were generated from an

assumption that the relative numbers of kangaroo rats and pocket mice among the pilferers should be the same as their relative numbers among all animals.

Results

Details of each provisioning trial, including species provisioned, number of animals trapped, and number of pilferers identified on subsequent nights, are shown in Table 4.1 (p. 84).

---Insert Table 4.1 about here---

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 feces on at least one of the following trap nights. Pocket mice pilfered from other pocket mice significantly more than kangaroo rats. Twenty six pilferers were identified out of a total of 133 heteromyids trapped (38 kangaroo rats, 95 pocket mice), and all 26 of the pilferers were pocket mice (χ^2=10.34, df=1, p<0.001). Two individual P. eremicus out of 28 trapped were also identified as pilferers.

Five kangaroo rats were provisioned with dyed seeds, and all of them showed traces of fecal dye when trapped over the following 7 nights. Six pilferers were identified out of a total 50 heteromyids trapped (10 kangaroo rats, 40 pocket mice). One pilferer was a kangaroo rat and the other five were pocket mice (χ^2=0.04, df=1, NS). One of 10 P. eremicus trapped was also identified as a pilferer.

Discussion

The results of Experiment 1 indicate that kangaroo rats aggressively exclude pocket mice from food bonanzas that are attractive to both. Members of both genera visited trays under cover more often than in the open, regardless of moon phase, but used trays in both microhabitats. Both genera lingered longer in trays containing oats than in trays containing lentils. These observations reinforce the premise that kangaroo rats dominate access to food trays during primary foraging for resources.

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. It seems reasonable to conclude that kangaroo rats are capable of aggressively dominating seed patches. The aggressive advantage of larger heteromyids has been shown in other studies (Kenagy 1973; Congdon 1974; Blaustein & Risser 1976; Hutto 1978; Wondolleck 1978; Frye 1983; Kotler 1984; Bleich & Price 1995; Falkenburg & Clarke 1998).

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 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, P. baileyi and P. 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.

The results of the pilferage study 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 do not suffer pilferage from kangaroo rats, although kangaroo rat stores were pilfered by both genera. While provisioning pocket mice with seeds, we occasionally had to deter kangaroo rats waiting nearby and attempting to forage in the seed dishes. In one case, during a caching trial, a kangaroo rat was observed trying to follow a pocket mouse down a small hole, but the kangaroo rat was too large and could not fit. The following morning, the same hole showed signs of digging and the entrance was enlarged. This observation lends some support to the suggestion by Jenkins and Breck (1998) that

pocket mouse larders are relatively safe from kangaroo rats because their holes are too small.

It is possible that pilferage behaviour is an alternative strategy distinct from foraging at natural seed patches, maintained by natural selection in the event that foraging at seed patches is in large part denied by larger sympatric competitors. Microhabitat use of pocket mice shifts dramatically when kangaroo rat competitors are experimentally removed (e. g. Wondelleck 1978), supporting the hypothesis that kangaroo rats limit the foraging opportunities of pocket mice. Pilferage is likely not the answer to the food acquisition problems of the pocket mice, since in the present study they 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 since they are able to monopolize foraging opportunities. One might predict that pilferage by pocket mice would be reduced in areas where kangaroo rat competitors are few. The relative profitability of foraging and pilfering to pocket mice and kangaroo rats must be investigated in order to address these hypotheses.

Studies of changes in the population density of different rodent species over a number of years have found that populations of kangaroo rats are more stable than those of pocket mice (e. g. M'Closkey 1981). This leads to the speculation that perhaps pocket mice are at least partially reliant on kangaroo rat food stores. When food is scarce, kangaroo rats might not store as much food, and overall numbers of kangaroo rats drop, mainly because of limited reproduction during times of food scarcity. This, in turn,

might result in more dramatic decreases in the pocket mouse population, since there are not as many kangaroo rats from whose caches they can pilfer. However, experimental analyses are necessary to assess this possibility, since any number of other factors could influence these changes in population density. It would be interesting to look at the effect of pocket mouse removal on kangaroo rat densities.

Brown and Munger (1985) removed three species of kangaroo rats from semi-enclosed arenas and reported an increased population density in one species of pocket mouse, P. flavus, and 3 species of granivorous cricetid rodents. However, they reported no change in the density of P. penicillatus. They did not find perfect consumptive density compensation by the pocket mice following the removal of the kangaroo rats. They hypothesize that "[t]his suggests that processes other than straightforward competition for food among rodent species must also play important roles in determining the structure and function of this community." (p. 1558). The authors did not consider pilferage as a possible process, but if the pocket mice were relying even partially on pilferage when the kangaroo rats were present, any benefits gained by the removal of kangaroo rats as competitors may have been offset by the loss of kangaroo rat caches as a resource.

The results of this study show that the kangaroo rats tend to be scatter cachers, whereas the pocket mice are apparently larder cachers. Randall (1993) suggests 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 & 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.

Randall (1993) argues that because most studies of heteromyid microhabitat preferences are based on trapping data, they do not provide an accurate assessment of space use (see also Lemen & Rosenzweig 1978 and Thompson 1982 for similar arguments). Behavioural observation is indeed a superior method of determining space use and microhabitat preferences of different species, but the weight of concordant results from a large number of trapping studies should not be entirely dismissed. Thompson (1982) made naturalistic observations of heteromyid foraging activity. He found that D. deserti and D. merriami spent more time and effort foraging under or near cover than in the open, even though he live-trapped kangaroo rats more frequently in the open and pocket mice under cover. A few researchers have examined differential ingestion of labeled seeds scattered in open versus shrub or grass microhabitat (Price 1977; Lemen and Rosenzweig 1978; Wondolleck 1978), or by identifying species by footprints left in seed trays (Brown 1988). All of these studies showed that the majority of seeds consumed by Dipodomys spp. were collected in the open, whereas Chaetodipus spp. consumed more seeds collected in or near cover. However, Price (1977) found that her

estimates of microhabitat use from live-trapping were not perfectly concordant with estimates she made using labeled seed consumption.

The present study provides field evidence for differences between kangaroo rats and pocket mice in caching and cache pilferage. However, future studies are needed before the role of pilferage in co-existence can be verified. Such studies would 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.

Acknowledgements

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Table 4.1 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				
	No. Provisioned	Pilferers/ total number trapped				
Dates	No. with dye / No. provisionees trapped	D. merriami	C. fallax	C. formosus	C. penicillatus	P. eremicus
Provisioned: Nov. 23/98	6 C. fallax 1 C. formosus					
Trapped: Nov. 24, 26 & 28/98	7/7	0/12	5/23	1/2	0/3	1/11
Provisioned: Dec.4&5/98	2 C. fallax 1 C. penicillatus					
Trapped: Dec. 6, 8 & 10/98	3/3	0/13	5/27	2/2	0/2	0/12
Provisioned: June 1/99	5 C. fallax 1 C. penicillatus					
Trapped: June 2, 4, 6 & 8/99	5/5 C. fallax 0/1 C. penicillatus	0/13	10/19	1/11	2/6	1/5
Provisioned: May 2&3/99	5 D. merriami					
Trapped: May 4, 5, 6, 8 & 10/99	5/5	1/10	1/23	2/8	2/9	1/10

Chapter 5-General Conclusion

The results of the studies presented in the three previous chapters pave the way for the production of ecologically valid models of the foraging and caching behaviour of heteromyid rodents. My research has elucidated a number of parameters that should be considered in a dynamic model of heteromyid foraging. Costs and benefits change in relation to food value, predation risk and competitors, and these factors also have interactive effects on the decisions that are made during foraging and caching. Previous research has shown that heteromyids respond to cues of predation risk during foraging but none had examined the trade-offs in as much detail as is presented here.

The findings presented in the previous three chapters should generalise to other communities of sympatric heteromyids throughout the American southwest, as the habitat at Deep Canyon is fairly typical of Sonoran desert in terms of plants, animals and substrate. However, since the species make-up of sympatric communities varies so much, further research must be carried out in order to verify whether caching and pilferage might mediate co-existence in different communities.

My results provide some insight into the decisions made by heteromyid rodents during foraging and caching. Generally, they demonstrate that the rodents behave in an adaptive manner during foraging and food caching. They are capable of evaluating the risks and benefits that they face and they utilise this information, adjusting their

behaviour accordingly. While these studies present a fairly detailed picture, there is ample room for future research.

One avenue of particular interest is to uncover the varied ecological determinants of caching decisions made by kangaroo rats. Kangaroo rat caching is difficult to study in the field. It is tempting to carry out caching studies in enclosures where the sand can be sifted and burrows emptied, which facilitates the mapping of caches. However, field studies of caching behaviour provide us with a more ecologically-valid understanding of the caching decisions made by the rodents. By carefully habituating individual animals to experimenter presence and by utilising radio-tracking and food marked with fluorescent powder, it is possible to gain an understanding of heteromyid caching behaviour in the field. Each animal's intimate knowledge of its home range and the identity and behaviour of its neighbours must certainly have an effect on where and how it places and redistributes its caches (e. g. Jacobs & Spencer 1994). Predation cues such as overhead cover and moonlight likely play a role in caching, as must density of competitors. It is also possible that the relatedness of neighbours plays a role in caching decisions, since a higher degree of pilferage might be tolerated from relatives. Studies of dispersion have been carried out in bannertailed kangaroo rats (*Dipodomys spectabilis*; Jones et al. 1988; Waser & Elliot 1991) which show natal philopatry. However, detailed studies of dispersion are needed for Merriam's kangaroo rats and pocket mice in order to gain a better understanding of their kinship universe.

Long-term studies of heteromyid caching behaviour using radioactively labelled food (or some other new technology) are needed if we are ever to develop a good economic understanding of foraging and cache management because we do not yet really know how food is distributed over time and how it is depleted (and stolen) as a function of that cache dispersion. The management of caches over time and their use during times of food scarcity is a potentially fruitful area that warrants future investigation. Studies of caching decisions, long term memory for cache location, and cache recovery in parids (review by Sherry 1989; see also Hitchcock & Sherry 1990; Brodin 1994a, 1994b) have led to the production of models of hoarding, and the co-existence of hoarders and "cheaters" in parids (e. g. Brodin & Clark 1997; Smulders 1998).

It would also be useful to understand the foraging, caching and cache recovery behaviours of gestating and lactating females, particularly to see whether they show increased willingness to tolerate risk as the benefits of provisioning their young increase.

The use of and reliance on cache pilferage by both kangaroo rats and pocket mice is also an area where future research is warranted. Determining the nature of the caches stolen, for instance, whether caches in particular microhabitats are more or less vulnerable to pilferage, will facilitate an understanding of the vulnerability of particular types of caches. Individuals may only resort to pilferage at certain times (e. g. when resources are scarce) and/or under certain conditions (e. g. when rodent density is high). It is also possible that only a certain class of individuals specialise in pilferage. For instance, maybe juveniles engage in substantial pilferage until they gain experience and

skill at extracting resources from primary sources (e. g. see Goss-Custard et al. 1998). However, from the basis of the results presented in Chapter 4 alone, it is not yet clear whether pilferage is even a distinct activity from foraging, rather than merely from the perspective of the victim, such that animals must decide how to allocate efforts between them.

All of the studies in this thesis were carried out using food sources provisioned by an experimenter. Recently, researchers have been measuring the availability of seeds to heteromyids in their natural environments (e. g. Price & Joyner 1997), as has been done for ants (Crist & MacMahon 1992; Mehlhop & Scott 1983). Understanding how heteromyid rodents locate and sequester naturally distributed seeds should be the ultimate goal of future investigations of caching behaviour. The natural seed use of heteromyids was reported by Reichman (1975a), who found that they primarily ingest the seeds of forbs. Many of the seeds utilised by heteromyids are very small in comparison to oats and lentils. They are difficult and/or expensive to acquire, difficult to extract from a substrate, and nutritional analyses are scarce (but see Reichman 1975b). These factors make native seeds difficult to use in foraging and caching studies. However, such studies are needed before we can verify the ecological validity of results from studies using commercially available seeds such as oats, lentils and millet. Longland & Clements (1995) have conducted a study of heteromyid caching behaviour using naturally available seeds, and their results support the prediction that heteromyids treat more valuable seeds by caching them in more widely dispersed caches. They compared caching patterns in environments where the seeds were rare *versus* where the seeds were abundant, and

found that the rodents spaced caches more widely in the environment where the seeds were scarce. I have found that heteromyids respond to cues of predation risk while foraging for native seeds in GUD trays in the same way that they respond when foraging for oats and lentils (see Chapter 2), and that artificial caches of naturally available seeds are also subject to higher pilferage rates when those caches are closer together in space (see Chapter 3; Leaver unpublished data). On the basis of these findings, it seems fairly safe to assume that measures of foraging effort using commercially available seeds are ecologically valid.

I was interested in determining how the decision-making mechanisms that govern foraging and food storage behaviour have evolved to solve specific adaptive problems in different species. Optimal foraging models have been made more realistic with the inclusion of ecological constraints such as predation risk and nutrient requirements. However, current models of optimal cache spacing (Stapanian & Smith 1978; Clarkson et al. 1986) suffer from a lack of ecological validity. The 'best' or optimal answer to questions such as whether or not to scatter cache, how to distribute caches in space, and how much food to put in each cache should vary in relation to a number of complex, and often inter-related factors. These include predation risk, density of conspecific and hetero-specific competitors, relatedness of conspecific competitors, the value of the food being cached, and the nutritional status of the caching animal. Current models of cache spacing (Stapanian & Smith 1978; Clarkson et al. 1986) would benefit by incorporating these factors rather than assuming that cache spacing decisions are the result of a simple trade-off between pilferage risk *versus* travel time. More field research on the seed-

caching behaviour of heteromyids is necessary in order to further understand how different species have adapted to diverse ecological challenges. Such detailed studies of seed caching have been done in birds, and these have led to a relatively comprehensive understanding of their caching behaviour (e.g reviewed by Sherry 1989). Laboratory studies are valuable complements to field research in order to estimate the magnitude of the effects of relevant cues (e.g. illumination and overhead cover) on kangaroo rat caching decisions. A detailed understanding of kangaroo rat decision-making rules will be useful in generating more realistic models of caching economics in kangaroo rats and other species. By determining analogous ecological pressures that differ in their species-specific effects in terms of more abstract domains such as predation risk, competition, food value and other environmental factors including temperature, researchers will be able to build on current models of foraging and cache spacing and to define general models that more closely resemble the real world.

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