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Author(s): Lisa Leaver and Martin Daly

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EFFECTS OF FOOD PREFERENCE ON SCATTER-HOARDING BY KANGAROO RATS (*DIPODOMYS MERRIAM*)

by

LISA LEAVER¹⁾ and MARTIN DALY²⁾

(McMaster University, Department of Psychology, Hamilton, Ontario, L8S 4K1, Canada)

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Summary

Two laboratory studies were conducted to determine whether Merriam's kangaroo rats invest greater effort in the caching of a more preferred food. As predicted, more of the preferred food was cached and yet the individual caches were smaller. The second experiment showed wider dispersion of the preferred food, and these caches were placed further away from the source. These findings imply that investment in protecting food from pilferage is adjusted in relation to the animal's evaluation of that food.

Keywords: kangaroo rat, scatter-hoarding, food caching, food preferences.

Introduction

Scatter-hoarding refers to the dispersion of food caches, each cache typically made with a single load of food, by a storing animal. Scatter-hoarding presumably entails energetic and time costs, both in the caching and cache recovery activities themselves and in travel to and from cache sites, and it also entails demands on memory (Sherry, 1985). Its principal adaptive value appears to reside in 'risk-averse' avoidance of major losses to pilferers, rather than simply in minimizing expected mean loss (Vander Wall, 1990, p. 101).

¹⁾ Corresponding author; e-mail address: leaverl@mcmaster.ca

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Scatter-hoarding may be considered an 'investment' in securing food, and there are at least two potentially distinct components to the magnitude of this investment: partitioning of the resource into caches and cache spacing. Where caches contain numerous small items, hoarders can partition a given amount of food into a variable number of caches, with a relatively large number of relatively small caches representing a relatively great investment. Moreover, increasing cache spacing reduces the effectiveness of area-localized search by would-be pilferers and attendant risk of major loss (Stapanian & Smith, 1978; Clarkson *et al.*, 1986; Daly *et al.*, 1992). Thus, if investment in scatter-hoarding is a domain of adaptive decision making, we may expect animals to invest more in the hoarding of foods to which they attach more value, assuming that consumption of all available food is not possible. If the food that is preferentially eaten over other foods is also preferentially scatter-hoarded two predictions follow:

- (1) the preferred food will be cached in a larger number of smaller caches than the less preferred food, and
- (2) the spatial dispersion of caches will be greater for the preferred food than for the less preferred food.

Among scatter-hoarding rodents, some evidence for these two predictions has been found. Red squirrels (*Tamiasciurus hudsonicus*) carry larger and therefore more valuable food items farther from the source for caching than smaller food items (Hurly & Roberston, 1987). Yellow pine chipmunks (*Tamias amoenus*) distribute caches of larger, nutritionally more valuable Jeffrey pine seeds (*Pinus jeffreyi*) farther from the source than the less valuable antelope bitterbrush seeds (*Purshia tridentata*) (Vander Wall, 1995). Grey squirrels (*Sciurus carolinensis*) are sensitive to perishability of acorns and will preferentially cache acorns with various qualities related to non-perishability, and these caches are more widely dispersed (Steele *et al.*, 1996). Finally, heteromyids will disperse caches of Indian ricegrass (*Oryzopsis hymenoides*) more widely in an environment where these seeds are rare than in an environment where these seeds are plentiful (Longland & Clements, 1995).

Merriam's kangaroo rats (*Dipodomys merriami*) are predominantly granivorous desert-dwelling rodents, suitable for testing the predictions stated above. They scatter-hoard in the wild, where it has been shown that pilferage is common but that the scatter-hoarder is able to retain most of the

food it caches, and where increased cache spacing has been shown to reduce losses (Daly *et al.*, 1992). Conveniently, they will also scatter-hoard in arenas in captivity, where it has been shown that they remember cache sites (Jacobs, 1992) and that they may re-cache food to increase its spacing after initial rapid sequestering (Jenkins & Peters, 1992; Jenkins *et al.*, 1995). Moreover, there are at least two sorts of evidence that scatter-hoarding by *D. merriami* entails costs. One is that an individual's likelihood of being preyed upon increases as a function of distance travelled (Daly *et al.*, 1990). Another is that a larger proportion of neural tissue and cognitive capacity is invested in spatial memory in *D. merriami* than in their larder-hoarding congeners, *D. spectabilis* (Jacobs & Spencer, 1994).

Many desert-dwelling rodents, including *D. merriami*, prefer seeds high in carbohydrates and low in protein (Lockard & Lockard, 1971; Price, 1983; Kelrick *et al.*, 1986; Frank, 1988). Such preferences appear to be related to a stringent water economy: protein exacerbates water loss (Frank, 1988), whereas carbohydrate metabolism generates a nontrivial amount of water as a byproduct (Schmidt-Nielsen & Schmidt-Nielsen, 1950). Accordingly, to test the effects of differential preference on caching behaviour, we provided kangaroo rats with two equally familiar foods, one relatively high in carbohydrate, the other in protein.

Experiment 1

Methods

The subjects were 24 Merriam's kangaroo rats, 10 males and 14 females, all over one year of age. Twelve of the subjects were laboratory-born animals (seven male, five female) and twelve (three male, nine female) had been wild-caught near the Boyd Deep Canyon Desert Research Station, Riverside County, California. The kangaroo rats were maintained on a 12:12 L:D schedule with lights off at 1400 hours and on at 0200 hours, and fed an *ad lib* mixture of rolled oats, wheat kernels and sunflower seeds, plus a leaf of spinach on most days.

The experiments were carried out in a room equipped with 4 plywood boxes, 100 × 100 × 62 cm. Each box had a removable, raised plywood floor with a 10 × 10 array of holes 4.5 cm in diameter. In each hole, a plastic cup, 3.5 cm deep and filled with sand, served as a potential cache site. Cups were fitted snugly into each hole, with their rims level with the plywood floor, and a thin layer of sand was sprinkled over the entire surface of the floor. One empty tin can was placed in each corner of each box to provide cover. The same L:D schedule was maintained in the experimental room as in the housing room.

Each box was provided with two petri dishes of novel food. One contained 12 g of mung beans, a relatively high protein, low carbohydrate food (24.2% protein, 60.3% carbohydrate, 1.3% fat — from: Price, 1983) and the other contained 12 g of rye, a relatively low protein, high carbohydrate food (11.5% protein, 69.5% carbohydrate, 1.7% fat — from: Kent-Jones & Amos, 1967). Preference for rye over mung had been established in previous trials with other subjects and was confirmed in the present experiment by measuring consumption. The average mung bean weighed 0.06 g with an average linear dimension of 4.3 mm (Price, 1983). The average rye grain weighed 0.05 g with an average linear dimension of 4.0 mm (calculations done as in Price, 1983). Placement of the two foods was counterbalanced. A leaf of spinach was also provided in each box.

A subject was placed in a box for 22 hours, entering at 1300 hours and exiting the following day at 1100 hours, thus allowing one full 12 hour 'night' for scatter-hoarding. All subjects were run for a single overnight session, four at a time, each in one of the four boxes, between October 3 and November 13, 1994.

Following the removal of a subject after a trial, the sand in each cup was sifted and the amount of food found in each spatially designated cup was recorded. A cup was considered to contain a cache if there was more than one rye grain or mung bean (or fragment thereof) buried in the cup, not visible on the sand's surface. This criterion excluded individual grains that may have accidentally been trodden into the sand by the rats. For each subject, the total amounts of rye and mung cached were weighed to the nearest 0.1 g on either an Ohaus triple beam balance or an electronic Mettler Basbal scale, as were the amounts left neither cached nor consumed. The amount eaten was computed as what was missing from the original 12 g. (Some rats crumbled some grains, causing very small particles to be lost in sifting; this loss was apparently minor since no rat 'consumed' more than 4.1 g in the 22 h test period. Loss was probably more substantial for the rye, because the grains are soft and easily crumbled, whereas mung beans typically only split into two halves.)

After the data were recorded, each box was swept out and the sifted sand was mixed and reused for the following rat. Any effects of conspecific odours on behaviour should have been felt by all subjects because the sand used for the first set of subjects had been used in previous pilot studies.

Statistical comparisons between the animals' responses to mung *versus* rye are one-tailed *t*-tests for paired samples, unless otherwise noted.

Results

As anticipated, rye was strongly preferred over mung. Mean consumption was 1.86 g (± 0.86 SD) of rye and 0.40 g (± 0.34 SD) of mung ($t_{23} = 7.72$, $p < 0.001$). Every kangaroo rat consumed more rye.

In addition to being preferentially eaten, rye was also preferentially cached: an average of 2.5 g (± 2.7 SD) of rye was cached compared to 1.2 g (± 2.3 SD) of mung ($t_{23} = 2.08$, $p < 0.05$). The two food species were rarely combined in a single cache: just 7% of 141 caches contained both foods, and these were treated for analytic purposes as one cache of each. The average numbers of caches were 4.4 (± 3.6 SD) of rye *vs* just

1.5 (\pm 2.1 SD) of mung ($t_{23} = 3.69$, $p < 0.001$). Thus, in accord with prediction 1, the more numerous caches of the preferred food were indeed smaller: the average rye cache contained 0.57 g and the average mung cache contained 0.81 g.

Four of the 24 subjects did not cache at all, and only nine cached both food species. Eleven animals cached only one food, ten of these caching rye and one mung; this difference represents a significant rye preference in itself (sign test: $p < 0.01$). If analysis is restricted to the nine subjects who cached both foods, the predicted differences are still apparent. These animals made a mean of 6.1 (\pm 3.3 SD) caches of rye and 3.4 (\pm 1.7 SD) caches of mung ($t_8 = 2.14$, $p < 0.05$). The smaller size of the more numerous rye caches did not quite reach significance, however: the means of the nine animals' individual mean cache sizes were 0.48 g (\pm 0.46 SD) for rye and 1.02 g (\pm 1.35 SD) for mung ($t_8 = 1.70$, $p < 0.1$).

Prediction 2, that caches of rye would be spatially more dispersed than caches of mung, was not supported. For the 9 animals who cached both foods, the mean dispersion of rye seeds was 18.2 cm and the mean dispersion of mung was 17.4 cm, where dispersion refers to the mean distance between any pair of individual seeds. This difference did not approach significance.

There were no significant differences in any recorded behaviour between females and males, between wild-caught and laboratory-born animals, or between groups of animals tested simultaneously.

Discussion

There was little evidence bearing on Prediction 2: the spatial dispersions of rye caches and mung caches were similar. However, Jenkins & Peters (1992) found that after initial rapid sequestering of food, *D. merriami* increased the dispersion of their caches over successive nights when given access to four linked arenas in a larger, more complex laboratory environment. This suggests that allowing the animals more time and a larger arena might permit a better test of Prediction 2, and that was the aim of experiment 2.

Experiment 2

Methods

Subjects were eight (four male, four female) of the nine *D. merriami* who had cached both species of food in experiment 1. Four (one male, three female) were wild-caught, and four (three male, one female) were laboratory-born. The ninth subject was no longer available.

Trials were carried out in the same plywood boxes used in experiment 1 but in this case adjacent boxes were joined by short tunnels of black plastic tubing, 13.5 cm long, allowing a subject access to all four boxes connected in series. Boxes were designated 1 through 4, such that boxes 1 and 4 were the ends of the linear series and each connected to only one other box, whereas boxes 2 and 3 each had two tunnel entrances/exits on opposite walls. One empty tin can was placed in a corner of each box.

Subjects were run individually. Each rat was introduced to a corner of box 3 between 1300 hours and 1345 hours, and removed 96 hours later. A petri dish containing 20 g of rye was placed in box 1, against the middle of the wall furthest from the tunnel to box 2, and a dish containing 20 g of mung was placed in the corresponding position at the opposite end of the series in box 4. This arrangement was reversed for half the subjects. A leaf of spinach was placed in each of the two middle boxes.

The lights were on the same cycle as in experiment 1. All subjects were run between January 25 and March 23, 1995. The method of data collection was the same as that used in experiment 1. An electronic Mettler BasBal scale was used to determine weights.

Results

Rye was again the preferred food (3.09 g consumed *vs* 1.34 g of mung; $t_7 = -3.70$, $p < 0.05$), but one of the eight animals, male 9205, actually ate more mung (1.44 g consumed *vs* 0.65 g rye). He also cached more mung by weight (7.57 g cached *vs* 0 g rye) and number of caches (15 *vs* 0 rye).

As predicted, the animals again made more caches of the preferred food, rye. Seven animals (all but male 9205) cached both foods, averaging 13.9 (± 14.3 SD) caches of rye and 8.9 (± 9.8 SD) caches of mung ($t_6 = 2.02$, $p < 0.05$). Moreover, as predicted, the average cache of rye was significantly smaller, at 0.16 g (± 0.11 SD), than the average cache of mung, at 0.27 g (± 0.15 SD; $t_6 = 2.25$, $p < 0.05$).

At the end of the four day trial, caches of rye were located farther from the source (183.14 cm \pm 115.3 SD) than caches of mung (98.93 cm \pm 106.1 SD; $t_6 = 1.51$, $p < 0.10$).

As predicted, cached rye was dispersed more widely than cached mung. For the seven subjects who cached both foods, the mean distance between pairs of rye seeds was 98.5 cm \pm 60.5 SD and for pairs of mung seeds it

was 51.3 cm \pm 41.6 SD ($t_6 = 2.36$, $p < 0.05$). For the six animals who made at least 2 caches of each food, mean distance between pairs of caches was 148.9 cm (\pm 68.2 SD) for rye, and 73.6 cm (\pm 61.4 SD) for mung ($t_5 = 1.96$, $p = 0.05$).

General discussion

The results from the two experiments indicate that Merriam's kangaroo rats regulate their caching behaviour in response to the value of available food. Caching a preferred food in a larger number of smaller caches that are spread over a greater distance than a less preferred food presumably entails more exposure to predation risk, as well as energy expenditure. The results of these experiments may reflect an adaptation that results in greater protection of caches of a preferred food against loss due to pilferage, since increased spacing of artificial caches made by the experimenter decreases risk of loss due to pilferage in a number of environments for a variety of caching species (Stapanian & Smith, 1978; Clarkson *et al.*, 1986; Daly *et al.*, 1992).

A number of studies have shown that the decision of whether to cache or consume a food is based on perishability. Many of these studies involve larder-hoarding species which are offered a choice between two foods that differ substantially in suitability for caching. Eastern woodrats (*Neotoma floridana*) preferentially consume a highly perishable food whereas they preferentially cache a less perishable food (Reichman, 1988; Post & Reichman, 1991). Grey squirrels (*Sciurus carolinensis*) prefer to cache acorns that will not germinate or rot quickly, while they consume acorns that have a higher likelihood of germinating or rotting if cached (Hadj-Chikh *et al.*, 1996; Steele *et al.*, 1996). In the present study neither of the foods had a high probability of rotting, nor did they differ in likelihood to germinate. Furthermore, the food that was preferentially consumed was also preferentially cached.

The preferences in this experiment were not absolute. Most animals ate some of both types of food and put some effort into sequestering the less preferred food. There is evidence from field studies that heteromyids will put less effort into foraging for less preferred foods (Bowers, 1988; Leaver, pers. obs.). Other researchers have shown that heteromyids also modulate

their foraging effort in response to food availability (Kotler, 1984; Price & Waser, 1985) and cues of predation risk (Kotler, 1984, Price *et al.*, 1984; Brown *et al.*, 1994; Bouskila, 1995). Since foraging and caching activities are carried out at some real risk to the animal, it makes adaptive sense that individuals are sensitive to the value of the food, among other things, and adjust their foraging and caching behaviours accordingly.

One potential problem in this and similar studies is that of finding an accurate measure of preferential caching between seeds that vary in caloric value, nutritional attributes, size and weight. Vander Wall's (1995) conclusion that yellow pine chipmunks cache Jeffrey pine seeds in smaller caches farther from the source than antelope bitterbrush seeds is based on seed number, but he points out that if one considers the actual food value of the caches then it is the more valuable Jeffrey pine caches which are larger. The problem with measuring cache size by number of seeds is that a cache with a small number of large seeds may be nutritionally equivalent to a cache with a larger number of small seeds. Comparing cache sizes by weight may thus be preferable.

In the present study, rye caches averaged smaller than mung caches regardless of whether one compared weight or number of seeds, and caches of both species were usually much smaller than cheek pouch capacity. Thus, differential cache size appears to reflect differential allocation of caching effort rather than limitations of what could be transported.

The laboratory allowed the animals freedom from conspecific and other competitors as well as from predators. The animals were not deprived of food or water and the arena was small (0.0004 ha) compared to the natural home range size of kangaroo rats. Behrends *et al.* (1986) found *D. merriami* home ranges to vary from 0.03 ha to 1.16 ha in the wild. Despite these factors the animals treated the two foods differently. One might expect these differences to be more pronounced in the wild where costs and benefits would be greater. We are currently investigating cache distribution in the field as well as the effects of pilferage cues on foraging and caching decisions.

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