

Memory for cache locations in Merriam's kangaroo rats

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Abstract. The ability of Merriam's kangaroo rats, *Dipodomys merriami*, to remember the location of food caches and to relocate caches in the absence of the odour of buried seeds was examined. Eight wild-caught kangaroo rats cached seeds in an experimental arena, and retrieved them 24 h later. Before retrieval, all odours associated with the cache sites were removed and seeds were replaced in only half of the cache sites. During retrieval, kangaroo rats were significantly more likely to search cache sites, with or without seeds, than non-cache sites. Non-cache sites were primarily investigated after all cache sites had been searched, indicating that search of non-cache sites did not denote an error in cache retrieval. These results suggest that kangaroo rats can remember the locations of food caches, and can relocate cache sites even when there is no odour of buried seeds. To estimate the advantage enjoyed by the forager with greater information, a second experiment compared an owner's success in retrieving its caches with the success of naive kangaroo rats searching for these same caches. Nine wild-caught kangaroo rats were allowed to search for caches that were distributed in the same spatial pattern as that created by one kangaroo rat from the first experiment. The naive subjects found significantly fewer caches than had the cache owner in the same length of time. This suggests that the use of spatial memory by a Merriam's kangaroo rat to relocate its food caches gives it a competitive advantage over other kangaroo rats that may be searching for its caches.

Foragers commonly store surplus food for later consumption (Vander Wall 1990). Such behaviour should only be adaptive if animals that store food are more likely to retrieve the food caches than are their competitors (Andersson & Krebs 1978). When an animal scatter hoards, or places small surface caches in scattered locations (Morris 1962), such caches are usually not defended and appear vulnerable to competitors. Indeed, artificially created caches disappear rapidly (Stapanian & Smith 1978; Thompson & Thompson 1980; Sherry et al. 1982) and such disappearances have been attributed to cache pilfering, i.e. the removal of cache contents by individuals other than the owner.

In the face of competition from pilferers, a food-storer must somehow ensure that it will retrieve a sufficient number of its caches. It might do this by remembering the precise locations of its caches. The ability to remember cache locations has been demonstrated in some species of food-storing birds (marsh tit, *Parus palustris*, Sherry et al.

1981; Clark's nutcracker, *Nucifraga columbiana*, Vander Wall 1982) and mammals (red fox, *Vulpes vulpes*, Macdonald 1976; grey squirrel, *Sciurus carolinensis*, Jacobs & Liman 1991). In the grey squirrel study, squirrels preferentially retrieved nuts from their own cache sites rather than from the cache sites chosen by other squirrels. However, because each cache site contained a buried nut, it is not clear whether they could have found the precise location without the odour cues emanating from the cache (Jacobs & Liman 1991).

Whether a mammalian food-storer can find a cache location without the use of odour cues is not known. The present study addressed this question in Merriam's kangaroo rats, *Dipodomys merriami*. Merriam's kangaroo rat is a small (35 g) granivorous desert rodent that scatter hoards seeds over its home range (Daly, Jacobs & Wilson, in press); it is not known whether it can remember the locations of these caches. In experiment 1, kangaroo rats were allowed to search for caches they had made, only half of which contained seeds. If a kangaroo rat can remember the locations of its caches, it should be more likely to search sites where it had cached seeds than sites where it had not cached

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seeds. Moreover, if a kangaroo rat does not need odour cues to find its caches, it should be equally likely to search cache sites containing seeds and sites that did not contain seeds.

A second experiment addressed the question of whether a kangaroo rat's knowledge of its cache locations gives it a competitive advantage over other kangaroo rats searching for its caches. This advantage has been predicted (Andersson & Krebs 1978), but not empirically demonstrated.

GENERAL METHODS

Subjects

Adult kangaroo rats were live-trapped in the vicinity of Palm Desert, California and Tucson, Arizona, and transported to the laboratory 1–9 months before the experiment began; I assumed that such subjects would be experienced cachers, retrievers and pilferers. Kangaroo rats were housed singly in plastic cages measuring 48 × 27 × 20 cm, filled with a 3-cm layer of sand for bedding and dustbathing and containing a 15 × 9 × 6 cm brown glass jar as a nest chamber. They were fed a mixture of grains (millet, wheat and rolled oats) and fresh spinach, and had continual access to water. They were kept under a partially reversed 12:12 light:dark cycle, the lights being extinguished at 1200 hours. Because kangaroo rats are nocturnal, this increased their activity during a portion of normal daylight hours. Trials were run between 1200 and 2200 hours.

Apparatus

The test arena was a rectangular wooden enclosure (2 × 1 × 0.6 m), the floor of which was composed of eight galvanized steel plates (0.5 × 0.5 m each). Four of the eight plates were perforated with 16 holes, measuring 2.5 cm in diameter. A small plastic cup was placed into each hole for caching; these were termed the 'caching plates'. Six black plastic tunnels (plastic pipe, 5 cm in diameter, cut in half or plastic pipe elbows, 5 cm in diameter) were placed at regular intervals around the arena, against the wall and in the corners, to serve as hiding places. The cups were filled with white sand and capped with blue poker chips and served as discrete artificial cache sites, a design adapted from Kamil & Balda (1985). The caching cups will hereafter be referred to as 'cache sites'. A large number

of cache sites were used to increase the difficulty of orienting correctly to the cache sites during cache retrieval. The poker chips increased the conspicuousness of any caching or retrieval behaviour and facilitated the analysis of videotaped records. The arena was situated in a small room illuminated by low-intensity red lights which shed sufficient illumination for video-recording. Visual cues outside of the arena included the light source hanging above the arena, the video camera mounted on one wall and shelves on the opposite wall. Auditory cues by which the kangaroo rats could have oriented themselves, such as conversations occurring outside the experimental room were also available.

I cleaned the arena before each trial and between the caching and retrieval phase of each trial to remove any odours, such as scent marks near caches, by which a kangaroo rat could relocate caches without remembering cache locations. First, I washed the walls with a strong detergent, and then either replaced or turned over the steel plates which made up the floor. I sifted the sand used during the caching phase, mixed it in a large pan, replaced the sand into new plastic cups, and covered each cup with a washed and dried poker chip.

EXPERIMENT 1

Individual kangaroo rats were allowed to cache shelled sunflower seeds in the arena. After 24 h, the subject was allowed to search for its cache sites, only half of which contained seeds. If kangaroo rats remembered caches according to their location, then they should be equally likely to search filled or emptied cache sites, and they should only search sites where they had cached. A fourth category of site caches not made by the subject, was not included in this study. Although my hypothesis would predict that kangaroo rats would not search such sites, subjects would have been encouraged to search locations where they had not cached, which would have obscured estimates of their accuracy in returning only to places where they had cached.

Each subject received six trials; a trial consisted of a caching phase followed by a retrieval phase. Eight kangaroo rats (four males and four females) cached seeds regularly in the sand-filled cups, and data from these subjects were used to estimate the accuracy of their memory for specific locations. An additional six kangaroo rats (five males and one female) cached only on the surface of the arena, not

in the cups, and data from their trials were used to examine their choice of substrates searched during retrieval.

Methods

Caching phase

Each subject was partially food-deprived for 24 h, during which period its intake was reduced from an ad libitum supply of its normal diet to a smaller amount (2 g) of a less preferred food (rolled oats). I then released the kangaroo rat into the arena to eat and cache seeds from a dish of 100 shelled sunflower seeds, situated in the centre of the arena. I removed the subject from the arena after all the seeds had been taken, or after 2 h had elapsed, whichever came first. Subjects were then partially food deprived until the retrieval phase, 24 h later. I did not wash the plastic tunnels and the food dish, and in fact handled them minimally to avoid disturbing scent marks, replacing them in exactly the same positions as they had occupied during the caching phase. These tunnels thus served as a set of familiar olfactory and visual landmarks in the arena, so that the kangaroo rat would be more likely to recognize the arena as the same place it had cached the day before, despite the cleaning procedures.

To reduce the repeated use of the same sites, I systematically changed the configuration of available cache sites for each of six trials (Fig. 1). One subject (male 613) was mistakenly given the third configuration twice (third and sixth trials). However, despite experiencing the same environment twice, he cached in non-overlapping distributions during these two trials, and thus his earlier memories of the third trial could not have improved his retrieval accuracy in the sixth trial. The inter-trial interval was 10.2 ± 0.7 days (range = 4–25), excluding one long inter-trial interval for each of two subjects (132 and 178 days).

Retrieval phase

I replaced half of the caches (or the majority, in the case of an odd number of caches) in the cache sites for the retrieval. As satiation would reduce the motivation to search for food, only two seeds were replaced in each of the chosen cache sites. These seeds were taken from those originally cached at that site so that the kangaroo rat, encountering seeds that it had previously placed at that site,

would be more likely to recognize the cache as its own. This was important because kangaroo rats became reluctant to cache if they did not find any of their own caches during retrieval (personal observation). I placed the seeds at the bottom of the new cup, and covered them with sand and a clean poker chip.

I then released the subject into the arena for retrieval of its caches, only half of which actually contained seeds. Its retrieval behaviour was videotaped for 30 min, and then it was allowed to search the arena for an additional 30 min, to ensure it had had time to check each of its former cache sites. I used the videotaped record of the retrieval phase to calculate the percentage of each type of site (emptied cache site, refilled cache site and unused cache site) searched during the first 15 min of retrieval, although most caches were retrieved in the first few minutes of access to the arena. I defined a search as the first displacement of the poker chip by the kangaroo rat's head.

Results and Discussion

Kangaroo rats cached seeds in the sand-filled cups in 4.9 ± 0.3 ($\bar{X} \pm SE$) of six trials, yielding a total of 39 trials by eight subjects ($N=8$ for all results). In three of these trials, kangaroo rats placed only one cache in a cup. Because this disallowed partial replacement of caches, these trials were excluded from the analyses of retrieval accuracy. In an additional four trials, kangaroo rats only cached seeds on the surface of the steel plates, usually along the arena walls. Regardless of where seeds were cached, the subject was always allowed to retrieve its caches the next day. In the case of surface caches, some seeds were replaced for the retrieval phase, to encourage the subject to continue caching. Kangaroo rats cached in 5.4 ± 1.0 cups per trial (range = 1–14), placing 11.5 ± 0.9 seeds in each cache and 2.8 ± 0.3 caches on each caching plate. Thus, caches were typically distributed in clumps, each containing several caches, on some but not all of the four plates available for caching. This is illustrated in Fig. 1 by the cache distributions of three subjects.

To test the hypothesis that kangaroo rats can relocate caches without detecting the odour of buried seeds, the percentage of cups searched was compared among the three categories of cups: non-cache sites, emptied cache sites and refilled cache sites. As seen in Table I, kangaroo rats searched a

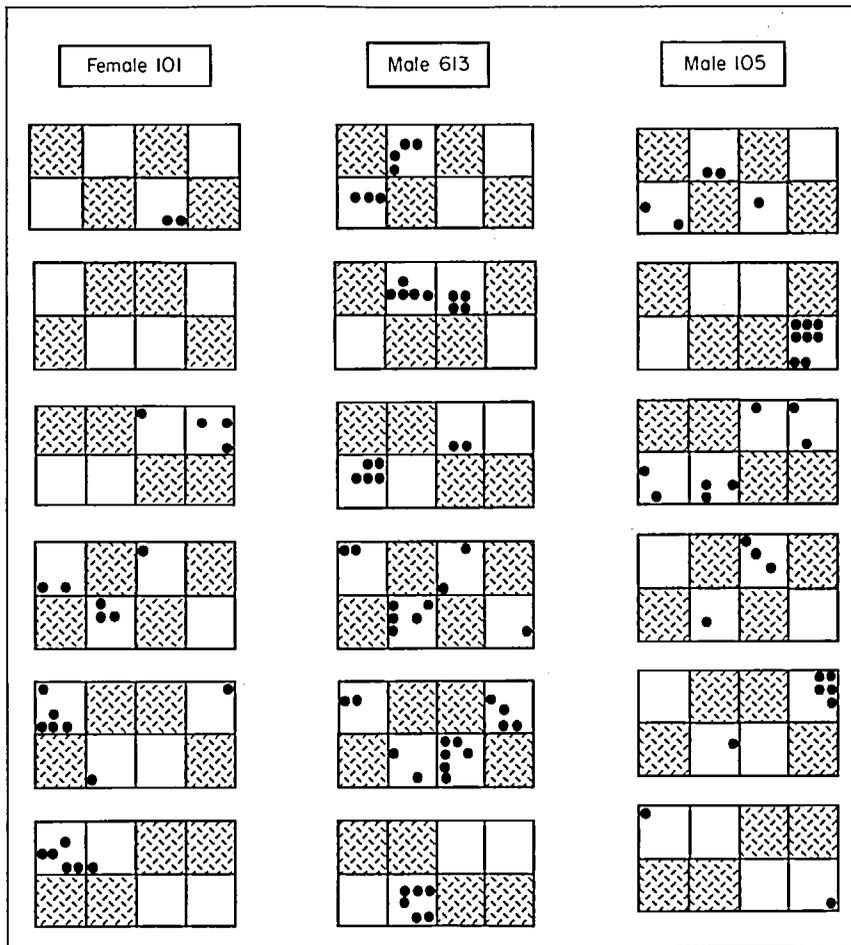


Figure 1. The distribution of caches produced by three kangaroo rats in experiment 1. The floor of the caching arena consisted of eight metal plates, four of which were unperforated (non-caching plates) and four of which were perforated and held 16 sand-filled cups for caching, evenly spaced in a 4×4 matrix. The spatial configuration of caching plates (\square) and non-caching plates (\blacksquare) was changed between trials, as shown. Cache sites (\bullet) were defined as cups in which the kangaroo rats buried seeds.

significantly greater percentage of sites in which they had cached seeds, than sites in which they had not cached seeds (two-tailed t -test: $t=11.15$, $df=14$, $P<0.0001$). They were not more likely to search cache sites with seeds; there was no significant difference between the percentage of filled and emptied cache sites that were searched (two-tailed t -test: $t=0.919$, $df=14$, $P=0.624$). Moreover, they searched a significantly greater percentage of emptied sites than unused sites (two-tailed t -test: $t=7.21$, $df=14$, $P<0.0001$). Because these sites were physically identical, it appears that kangaroo rats did not need to use olfaction to find caches.

Rather than olfaction, memory for cache locations appears to play an important role in cache retrieval. If a kangaroo rat can remember its cache locations, it should be more likely to search cache sites than unused sites. Because of the small number of caches made per trial, most sites (58.3 ± 1.0 of 64 sites, or 91.1%) were unused. However, on average $77.8 \pm 4.2\%$ of the first sites that a kangaroo rat searched (up to the number of caches it had made) were cache sites.

The probability that a subject's retrieval of its caches was greater than that predicted by cache availability can be calculated from the probability of a subject making the observed number of

Table I. Accuracy of cache retrieval, as estimated by the mean number and percentage of cache and non-cache sites searched, relative to the total number of that type of site available, during the first 15 min of retrieval ($N=8$)

Type of site	Number of sites searched		Percentage of sites searched	
	\bar{X}	SE	\bar{X}	SE
Refilled cache	3.0	0.5	93.3	3.0
Emptied cache	2.3	0.4	86.9	6.5
Unused (non-cache)	8.2	2.0	14.1	3.5

Percentage of sites is calculated as the number searched divided by the number available for searching at the beginning of the trial.

correct choices, given the availability of cache sites and non-cache sites (Polimeni & Straight 1985; see Appendix). Because the availability of cache sites and non-cache sites changes as more sites are searched, this method sums the changing probabilities of a cache site being chosen, given the availability of caches and non-cache sites at each point during retrieval. The process continues up to the maximum number of correct choices, which is the total number of caches available at the start.

This analysis yielded the following result: in 34 of 39 trials in which the subject cached in at least one cup, kangaroo rats were significantly more likely to search cache sites than predicted by the availability of cache sites ($P < 0.02$ for each trial). In four of the remaining five trials, retrieval of caches was not significantly different from that predicted by availability ($P = 0.062$ for each trial). In these four trials, each subject made two caches and searched one cache site and one non-cache site in the first two searches. In the fifth case, the kangaroo rat showed no evidence of searching cache sites before non-cache sites ($P = 1.0$). He had made six caches and all of his first six choices were non-cache sites (male 105, fifth trial, Fig. 1). This lack of accuracy was unique; it was the only trial in which such a pattern of retrieval occurred. The poor performance of this subject was especially striking, as in his four previous trials he had consistently retrieved all of his caches before investigating any non-cache sites. During this trial, this subject also searched a greater number of non-cache sites than had any other subject during any other trial (42, or 72.4% of those available, compared to the group mean of

14.1%) and he searched 20 of these non-cache sites before he found all of his six caches. It may be significant that the locations of his first six choices resembled a mirror image of his cache sites. This suggests that he might have remembered the spatial configuration of the caches but somehow became disoriented and hence searched the wrong end of the arena.

As mentioned earlier, in some trials the subjects did not cache in the cups but instead cached on the surface of the arena floor, and these trials were excluded from the previous analysis. These data were combined with data from cup-cache retrievals to test the following hypothesis: if kangaroo rats remember cache locations, then subjects who had not cached in the cache cups should not search cache cups during retrieval. Indeed, in 9 of 12 trials in which subjects had only cached on the surface, such subjects did not search any cups during retrieval; in the remaining three trials, subjects searched only one or two cups. When data from surface-cache trials and cup-cache trials were combined, there was a significant positive correlation between the number of cups used for caching (range=0-14) and the number of unused cups searched (range=0-42) during retrieval ($N=14$, $r=0.35$, $P=0.011$). Thus, kangaroo rats only searched cups when they previously had cached seeds in cups, again suggesting that memory plays an important role in cache retrieval.

If, in the course of retrieving its caches, a kangaroo rat searches an unused site before it has retrieved all of its caches, then this may be interpreted as an error in locating caches. However, if it only searches unused sites after it has found all of its caches, then such a search cannot be errors in retrieval but must be otherwise motivated, such as the need to explore. Similarly, if non-cache site searches represent errors, then one would predict that kangaroo rats would be more likely to search sites near caches than sites further away or in areas where no caches had been made. To test this hypothesis, searches of non-cache sites were categorized into those searched before and after all caches were retrieved, and by their location relative to the nearest cache (Table II). Searches of sites on plates that contained caches were defined as 'near cache' and searches of sites on plates without caches were defined as 'far from cache'.

Overall, kangaroo rats were more likely to search non-cache sites after they had retrieved all of their caches than before (two-tailed t -test: $t = 2.28$,

Table II. Searches of non-cache sites during the first 15 min of retrieval ($N=8$)

Location of non-cache site searches	Before retrievals		After retrievals	
	\bar{X}	SE	\bar{X}	SE
(1) All non-cache sites	2.3	0.6	6.4	1.7
(2) Plates with caches	1.3	0.2	4.3	1.1
(3) Plates without caches	1.0	0.5	2.1	0.7

Searches occurred either (1) before or after the kangaroo rat had retrieved all of its caches, (2) on plates that contained caches during that trial, or (3) on plates that did not contain caches.

$df=14$, $P=0.037$). When searches were divided into those near and far from caches, the same result was found: subjects searched more sites after retrieving all caches than before (two-tailed t -test: $t=2.65$, $df=14$, $P=0.018$). Despite a trend in the same direction, there was no significant difference in the number of 'far from cache' sites searched before and after all retrievals had been made (two-tailed t -test: $t=1.21$, $df=14$, $P=0.246$). These results imply that kangaroo rats retrieve all of their caches first and then search other non-cache sites nearby, particularly those near current cache sites; sites distant from any cache site may be searched either before or after all the caches have been retrieved. Because most searches of non-cache sites occurred after all retrievals had been made, these should not have interpreted as inaccurate retrieval attempts. This pattern of search may be an adaptive response to the heavy loss of caches induced by the experimental design (i.e. I removed half of the caches completely and reduced the remaining caches to two seeds each). Therefore, the kangaroo rats may simply have been rechecking the general area in which they had previously cached seeds.

EXPERIMENT 2

In this experiment, kangaroo rats were allowed to find and eat seeds cached by another kangaroo rat (the cache owner), and their foraging efficiency was then compared with the retrieval efficiency of the cache owner, as previously determined in experiment 1. I predicted that the cache owner, remembering the locations of its caches, would have found more caches in the same length of time than would a non-owner.

Methods

Subjects

Thirteen kangaroo rats (seven males and six females) served as non-owners. Five of these had completed the first experiment and the other eight, trapped at the same time and maintained under the same conditions, had only cached seeds a few times in the arena. There was no difference in the results between these two groups and their data were subsequently combined.

Procedure

After a 24-h period of limited food deprivation (up to 2 g rolled oats), each subject was allowed 15 min to find seeds buried in one of five cache distributions, on five consecutive days. Non-owners were thus given five opportunities to find the caches of one individual (male 613). The caches were placed in arrays of the first five distributions that this individual had produced during experiment 1, and were presented in the same order as shown in Fig. 1.

Before each trial the arena was cleaned in the manner described for experiment 1, and two shelled sunflower seeds were placed at the bottom of a sand-filled cup in the location of each cache made by male 613. The non-owner kangaroo rat was then released into the arena and allowed to search for and eat or remove seeds. After 15 min, the subject was removed, gently relieved of any seeds in its cheek pouches, and returned to its holding cage. The number of seeds it had eaten was calculated from the number of seeds still cached in the arena, and its ration of rolled oats for the intervening period before the next day's trial was adjusted accordingly. The total number of caches available ranged from six to nine; thus 12–18 seeds were available in the arena during each trial. This was usually in excess of what a kangaroo rat would eat; in some cases, kangaroo rats would re-bury excavated seeds at other sites.

Each trial was recorded on videotape and all cup searches, defined as the first displacement of the poker chip by the kangaroo rat's head, were scored to calculate the number and percentage of cache sites and non-cache sites that were searched.

Results and Discussion

Because the percentage of caches found in 15 min did not differ significantly between the inexperienced and experienced kangaroo rats (Mann-

Table III. The mean percentage of non-cache sites searched and cache sites found by non-owner kangaroo rats, one individual cache owner and all cache owners in experiment 1

Subject	Cache site			Non-cache site	
	<i>N</i>	\bar{X}	SE	\bar{X}	SE
Non-owners	9	68.7	10.3	13.6	3.2
Cache owner (male 613)	1	100.0	0	14.2	3.1
All owners	8	92.6	3.2	14.1	3.5

Whitney *U*-tests: $U=17.0$, $P=0.328$), these data were combined. Also, because 4 of the 13 subjects searched fewer than five cups during the five trials their search behaviour could not be interpreted and the data from these subjects were excluded.

Non-owner kangaroo rats found, on average, 3.8 ± 0.8 cache sites (Table III). This was 31.3% fewer cache sites containing seeds than the cache owner had found in experiment 1, a significant difference (one-sample *t*-test: $t=3.05$, $df=8$, $P<0.015$). The non-owners' success in finding caches can also be measured by restricting the analysis to the number of correct choices made, i.e. cache sites chosen up to the number of caches available. For example, seven caches were available in the arena on the first trial, and in her first seven searches, non-owner female 103 searched three cache sites and four non-cache sites, or 43% correct. Only those non-owners that had searched at least as many sites as there were caches available could be used in this analysis, reducing the sample from nine subjects to seven. The average scores of the non-owners were compared with the average score of the owner and with the average scores of all cache owners from experiment 1. This latter comparison gives a more conservative estimate of an owner's advantage relative to a cache owner, as the cache owner in this experiment (male 613) had displayed a higher than average retrieval accuracy in experiment 1.

Non-owners had significantly lower success searching for caches than the cache owner. Non-owners made 39.4% fewer correct choices than had the cache owner, a significant difference (one sample *t*-test: $t=23.5$, $df=6$, $P<0.0001$). Even when compared to the average owner in experiment 1, non-owners made 28.0% fewer correct choices, also a significant difference (two-tailed *t*-test:

$t=5.88$, $df=13$, $P<0.0001$). Thus, when searching the same number of sites, the average non-owner found significantly fewer caches than did the owner of the caches, and chose significantly fewer cache sites in the beginning of their searches than did the average cache owner.

GENERAL DISCUSSION

This study addresses the question of whether kangaroo rats can remember the spatial locations of their food caches. The first experiment demonstrates that kangaroo rats retrieve their caches based on the spatial locations of the caches and not by the odour of buried seeds, as they searched equal numbers of emptied and refilled cache sites during retrieval. Because they searched a lower percentage of unused sites than emptied caches, and because these sites differed only by their location, the kangaroo rats must have distinguished them, and hence remembered them, by their location. Furthermore, non-cache sites were usually searched after all cache sites had been searched. Thus, the search of non-cache sites might be interpreted as exploration or as additional attempts to find pilfered caches, and not as an inaccurate orientation to remembered cache locations.

The results of the second experiment indicate that detecting a cache by its odour, though effective, is not as efficient as remembering its location. The cache owner found 31% more caches than did the average non-owner, and searched fewer sites. Thus, the owner acquired more food for less effort than a non-owner. The owner strategy is not necessarily more efficient in total energy expenditure, however, because the owner had already invested energy by caching the seeds and by remembering their locations. The extra seeds discovered by the owner simply might have offset its previous expenditure of effort. On the other hand, the value of a cache is not only determined by its energetic content and the energy expended in caching and retrieval, but also by the availability of alternative food sources at the time of retrieval. Caches may increase in value as other foods become more scarce or when foraging is costly, such as during inclement weather or periods of high predation risk or intense competition from other foragers. Under these conditions, the cache owner strategy could be highly profitable.

This study presents the first evidence that memory for cache locations has immediate adaptive value for

a scatter hoarder such as the Merriam's kangaroo rat. The probability of pilfering may be particularly high for this species. The caches of Merriam's kangaroo rats are routinely pilfered by neighbouring kangaroo rats and other species of granivorous rodents (Daly, Jacobs & Wilson, in press). Competition for food between desert rodents may be a major determinant of the structure of desert rodent communities (Price & Brown 1983). A kangaroo rat's memory for its cache locations may serve several functions: if it can remember individual sites, then it can distribute caches in arrays that are unpredictable to its competitors, or change the location and density of its caches in response to pilfering. This latter response has been demonstrated in a scatter hoarding bird, the magpie, *Pica pica*, which spaces its caches more widely in higher risk habitats, i.e. where caches are pilfered more quickly (Clarkson et al. 1986). Other studies have also shown that the density of caches is a key factor in determining the rate of their disappearance (Stapanian & Smith 1978; Sherry et al. 1982).

A second ecological factor that may select for good spatial memory in Merriam's kangaroo rats is the reduced risk of predation, especially while retrieving caches. In the second experiment, owners

retrieved more caches than non-owners in the same length of time. The owner's advantage reported here may be a minimum estimate, because the arena was small and easily searched, and the seeds were larger, and perhaps more pungent, than those cached in the desert (Brown et al. 1979). Under natural conditions, where kangaroo rats range widely (Behrends et al. 1986) and scatter much smaller caches over large areas (Daly, Jacobs & Wilson, in press), owners who remember cache locations may significantly reduce their chance of predation while retrieving caches. Kangaroo rats forage, and perhaps retrieve caches, in open sites where they may be more vulnerable to predation than other granivorous rodents, such as pocket mice (e.g. *Perognathus*), which forage near and under shrubs (Brown & Lieberman 1973; Lemen & Rosenzweig 1978; Thompson 1982). If a kangaroo rat's memory of its cache locations allows it to retrieve caches more quickly, this should reduce its risk of predation, relative to the risk faced by a pilferer. Thus, kangaroo rats may have more than one reason to remember cache locations: to retrieve food from scattered locations before the cache is found by a pilferer or before the cacher is found by a predator.

APPENDIX

The following analysis is taken from Polimeni & Straight (1985). Let c = the number of caches and let r = the number of correct retrievals in the first c searches. The total number of available sites is 64, and the probability of making one correct retrieval from c caches is:

$$\frac{[c!/r!(c-r)!] \times \{(64-c)!/(c-r)![(64-c)-(c-r)]!\}}{[64!/c!(64-c)!]}$$

The probability of retrieving the observed number of caches is the sum of the above probability and the similarly computed probability for more caches retrieved, $r+1, r+2 \dots c$, which is the maximum number of correct choices. This technique yields the values reported in the text.

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