Grey squirrels remember the locations of buried nuts

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Abstract. It has previously been assumed that grey squirrels, *Sciurus carolinensis*, cannot remember the locations of nuts they have buried, and hence must relocate nuts by their odour. This assumption was tested by measuring the accuracy of cache retrieval of captive squirrels. Each squirrel was released alone into an outdoor arena, where it cached 10 hazelnuts. After a delay of 2, 4 or 12 days, each squirrel was returned to the arena and tested for its ability to retrieve nuts from its own cache sites and from 10 cache sites used by other squirrels. Although each squirrel's own caches were close to the caches of other squirrels, the squirrels retrieved significantly more nuts from their own sites than from sites used by other squirrels, after all delays. The retrieval accuracy of the squirrels under these conditions indicates that while grey squirrels can locate buried nuts by their odour, they can also remember the individual locations of nuts they have buried.

'Squirrels have been criticized for hiding nuts in various places for future use and then forgetting the places. Well, Squirrels do not bother with minor details like that. They have other things on their mind, such as hiding more nuts where they can't find them' (Cuppy 1949).

That food-storing birds can remember the locations of their food caches is now firmly established (marsh tits, *Parus palustris*: Sherry et al. 1981; Shettleworth & Krebs 1982; black-capped chickadees, *P. atricapillus*: Sherry 1984; Clark's nutcrackers, *Nucifraga columbiana*: Vander Wall 1982; Kamil & Balda 1985). Surprisingly, there is only limited evidence that a mammal can remember the locations of its caches (Macdonald 1976), despite the wide occurrence of food-storing in mammals (Smith & Reichman 1984; Sherry 1985); instead, mammals are assumed to find a cache by the odour of its contents (Cahalane 1942; Tinbergen 1965; Howard et al. 1968; Murie 1977).

One type of spatial memory has been studied in detail in food-storing mammals: memory for the location of food sources (laboratory rat, *Rattus norvegicus*: Olton & Samuelson 1976; Mongolian gerbil, *Meriones unguiculatus*: Collett et al. 1986; grey suirrel, *Sciurus carolinensis*: McQuade et al.

1986). Remembering the location of food sources, however, may be easier than remembering cache locations. The food-storer must not only learn the location of many more cache sites than food source sites, but it must learn them in one trial, when the food item is hidden, and it may have little opportunity to rehearse its memory. In this study we examine the role of spatial memory in cache retrieval by a food-storing mammal.

Whether grey squirrels remember where they have buried their nuts has long been debated (Merriam 1884; Stapanian & Smith 1984; Gurnell 1987). Like the seed-eating birds mentioned earlier, grey squirrels scatter-hoard (Morris 1962), placing individual seeds, such as acorns (Fagaceae) or hickory nuts (Juglandaceae), in separate cache sites and retrieving them months later (Thompson & Thompson 1980). Grey squirrels frequently cache nuts in areas adjacent to or overlapping the caching areas of other squirrels (Jacobs 1987) and are capable of detecting caches by their odour (Thompson & Thompson 1980). Thus, under natural conditions, grey squirrels may search for buried seeds they have cached and those cached by other squirrels. If a squirrel remembers the locations of its caches, it should be more likely to find its own caches than to find another squirrel's caches. We tested this hypothesis by observing captive grey squirrels retrieving nuts from two types of cache sites: sites they had chosen and sites other squirrels had chosen.

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METHODS

Experimental Design

To measure the accuracy of cache retrieval, captive grey squirrels were individually released into a large outdoor arena and allowed to cache hazelnuts. After a delay of 2–12 days, fresh nuts were buried in the squirrel's cache sites and in an equal number of additional sites that had previously been chosen by other squirrels. If squirrels remember the sites of individual caches, they should retrieve a greater proportion of their own caches than those of other squirrels.

Subjects

Eight hand-raised male grey squirrels, between the ages of 7 months and 2 years, served as subjects. Squirrels were kept in individual wire cages measuring $61 \times 61 \times 122$ cm, which contained heavy wooden nestboxes filled with straw. The cages stood under a tarpaulin next to the outdoor experimental arena; the squirrels were exposed to natural light and temperature conditions during the period of the study (October to December 1984). Squirrels were fed commercial hamster chow and given water ad libitum. They were also occasionally fed apples, unshelled peanuts, hazelnuts and black walnuts; squirrels often cached nuts and hamster chow in their cages.

Apparatus

The experimental arena was situated in an open field belonging to Stony Ford Biological Station of Princeton University. The arena was a greenhouse skeleton covered with 2·5-cm wire mesh and a commercial shade-cloth; since the covering was not waterproof, trials were not generally run during heavy rain. The surface area of the caching arena measured $4·6 \times 9·8$ m and was covered with a matrix of concrete blocks measuring 20×40 cm, which formed a grid, 19 blocks wide by 23 blocks long. The blocks were separated by grass-covered interstices about 4 cm wide. Partway through the study, however, the grass was covered with a layer of small pebbles, as it had become sparse in areas where the squirrels had cached repeatedly. Data from each of these arena substrate conditions were first analysed separately, but because the results from the two arena conditions were similar (as described later), these data were combined.

The rows and columns of concrete blocks were painted with black numbers and letters measuring approximately 25×15 cm to facilitate description of the squirrels' movements. Six cinder blocks, painted either yellow, blue or red, were placed at regular intervals around the arena, to serve as prominent visual landmarks. Squirrels were released into the arena through a small door at one end of the arena; the observer sat on a small raised platform on one side of the arena.

Procedure

Caching phase

The squirrel was first released into the arena and given 10–15 shelled hazelnuts to eat, since squirrels do not cache until satiated; shelling the nuts reduced the squirrel's eating time. Squirrels spent an average ($\pm$SE) of 23 ± 2 min eating hazelnuts. Once a squirrel appeared satiated, which we assessed by criteria such as a decrease in feeding rate, it was given unshelled hazelnuts, one at a time, from the front of the arena. It usually ate some of these hazelnuts and then began caching them. Squirrels would often cache several nuts, then eat one or two nuts before continuing to cache the rest. We continued this procedure until the squirrel had cached 10 hazelnuts; on average, the squirrels spent $2·3 \pm 0·3$ min caching each nut, and cached 9–11 nuts in $22·1 \pm 1·3$ min. Squirrels generally cached 10 nuts ($10·0 \pm 0·1$); 9 or 11 cached nuts occurred when a squirrel either refused to cache more than nine nuts or ate a nut previously cached or was inadvertantly given an extra nut. The observer described the squirrel's movements on a portable tape-recorder; cache locations were marked on a map of the arena. When the squirrel had finished caching, it was returned to its home cage.

Preparation for retrieval

The buried nuts were removed by the observer, and the hole left by the removal was filled in and smoothed over. Latex gloves were worn during this procedure to minimize the addition of odour cues to the cache sites and all efforts were made to minimize disturbance of the sites. Extensive digging, however, was occasionally required to find a nut. The exact location of a buried nut was marked on a map and also a distinctive mark was placed on the closest concrete block with a waterproof ink marker. This mark ensured that the replacement

nut would be placed in the same site as the original nut. Because several squirrels were tested each day and cache sites were rarely reused, many such marks accumulated over the course of the trials. These small marks could not have served as landmarks for retrieval of a squirrel's own caches, since all nuts were buried next to such marks.

Retrieval phase

The retrieval phase occurred 2, 4 or 12 days after the caching phase. During the intervening period the squirrels were fed sparingly; they were given no food for 24 h prior to the retrieval phase. Immediately preceding the retrieval trial, fresh nuts (not handled previously by squirrel or observer) were buried in the locations previously chosen by the squirrel. An equal number of fresh nuts were buried in 'other' locations. The sites for these other caches were chosen randomly from a list of caches made that week by squirrels other than the subject. If a chosen site was less than 10 cm from the subject's site or from a previously chosen other site, it was disqualified and a new other site was chosen. The nuts were handled with latex gloves and were buried about 2 cm beneath the surface, a depth similar to that of the original caches. Refilling of cache sites was done blind: the experimenter burying the nuts did not know which of the caches belonged to the subject and which to other squirrels.

The squirrel was allowed to retrieve the same number of nuts that it had buried. Once again, the squirrel's movements and the time at which a nut was retrieved were noted on a portable tape-recorder. The squirrels spent a similar length of time retrieving and eating a nut as they had spent caching it: 2.5 ± 0.1 min. The squirrel was then returned to its home cage and not used in another trial for at least 24 h.

We tested squirrels after three delay periods (2, 4 and 12 days). Because the arena was outside, bad weather forced us to cancel several trials and thus equal numbers of trials per delay were not obtained. We completed the following trials: 2-day delay, 2·4 trials/squirrel ($N=7$); 4-day delay, 1·0 trial/squirrel ($N=5$); 12-day delay, 1·1 trials/squirrel ($N=6$). Because of the small sample size, we decided to combine the 4- and 12-day delays into one category, '4 or more' days. As discussed below, there were no significant differences between data from trials with 4- and 12-day delays.

Satiation appeared to affect retrieval behaviour in several trials: after some squirrels had retrieved and eaten a number of nuts, they re-cached subsequently retrieved nuts. Because their retrieval scores might have been affected by their search for new cache sites, such retrievals could not be used to calculate retrieval accuracy, and several such retrievals were excluded from a few trials. Thus, although in each trial the squirrel was allowed to retrieve as many nuts as it had previously cached (mean 10.0 ± 0.1 nuts; range 9–11 nuts), the mean number of retrievals per trial that contributed to the analysis was 9.1 ± 0.3 (range 5–10) nuts.

RESULTS

Figure 1 shows a representative trial by one squirrel (Alvin; 2-day delay); the subject retrieved caches with a typical degree of accuracy in this trial.

Cache Placement

An important assumption of our experimental design was that all squirrels distributed their caches about the arena in a similar manner. If this had not been the case, we would not have been able to distinguish between the squirrel's preference for a particular part of the arena and its memory of individual cache sites.

To compare cache distributions between squirrels, the arena was divided into six equal-sized areas. The mean number of caches each squirrel placed in each of the six areas, combining all delay periods is shown in Fig. 2. By comparing the inset schematic representation of the arena to the cache distribution data, it can be seen that the squirrels cached more nuts in some areas than others. Overall, the pattern may be described as a strong preference for caching near the back and side walls of the arena. This was not a simple preference for edges, because the squirrels did not cache nuts near the front edge. Instead, the squirrels were probably placing caches far from the food source. They also could have been avoiding the observer who sat at the food source. However, as the squirrels were tame, having been hand-raised by one of us (L.F.J.), this seems unlikely. In pilot trials, when the observer was in the enclosure, squirrels cached nuts around the observer's feet. However, preferences for certain caching areas varied little between individuals; there was no significant difference between individuals in the percentage of caches placed in each area ($\chi^2=1.403$, $df=5$, $P=0.946$, Friedman's method for randomized blocks).
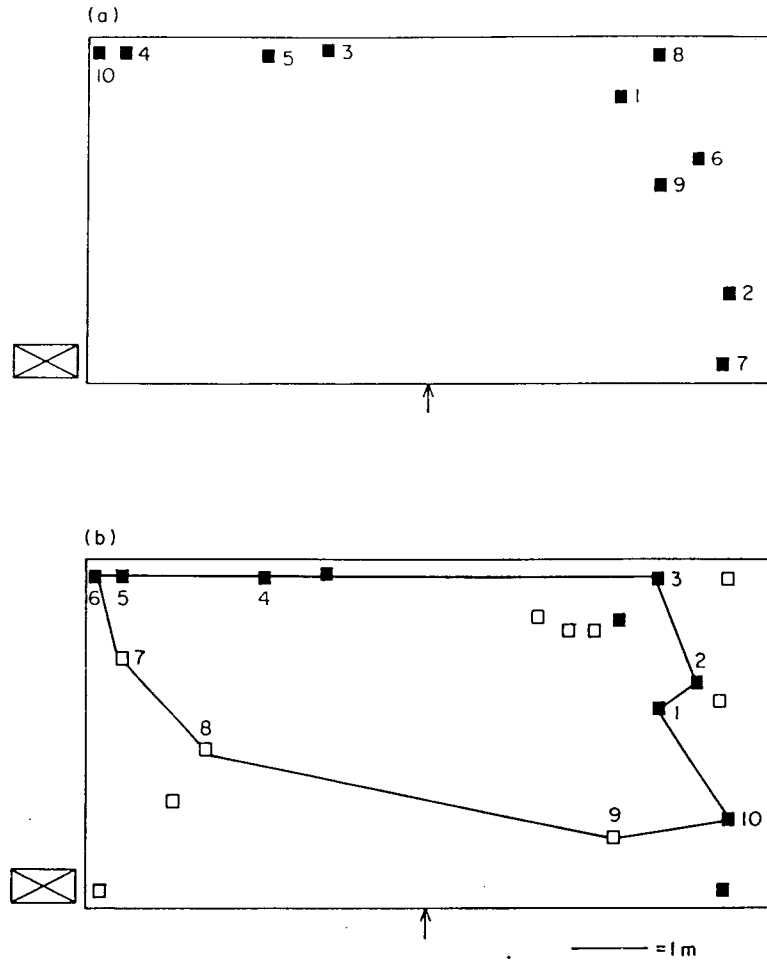
Figure 1. Schematic representation of (a) caching and (b) retrieval by the squirrel, Alvin (2-day delay). ■: Alvin's caches; □: caches of other squirrels. Numbers refer to the sequence in which nuts were cached or retrieved, the arrow indicates the location of the observer and the source of hazelnuts, and the rectangle in lower left indicates the squirels' place of entry into the arena. The polygon in (b) defines those caches considered, for the analysis, to be available during retrieval.
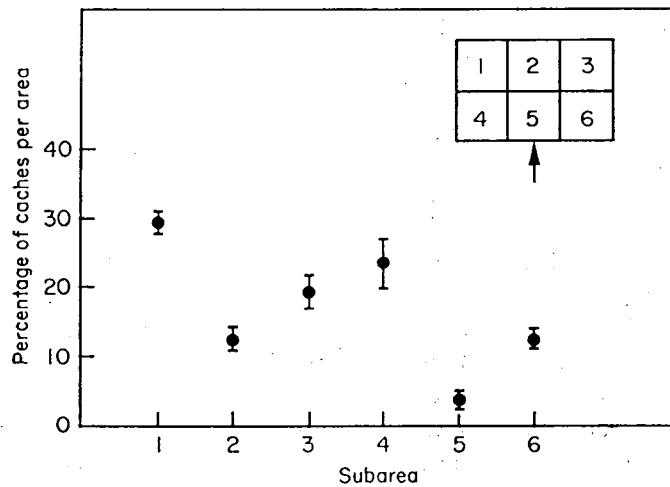

Figure 2. Summary of cache placement in the experimental arena by all squirrels ($N = 8$), combining all delay periods. Points indicate the mean ($\pm$ SE) percentage of all caches placed in each subarea by each squirrel. Inset diagram shows the relative positions of the subareas; the arrow indicates the observer's position, which was also the source of the nuts to be cached.
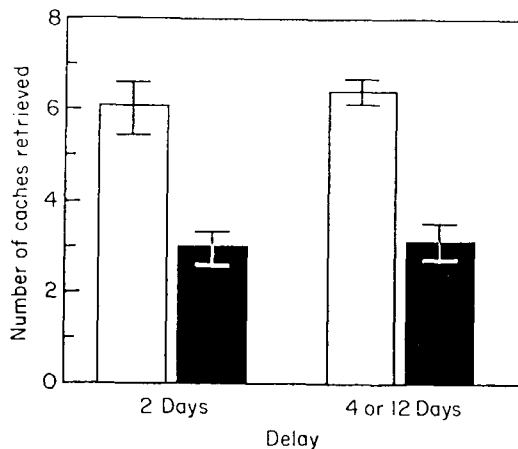
Figure 3. Number of caches retrieved after delays of 2 days and 4 or 12 days. Bar heights indicate the mean ($\pm$SE) number of caches retrieved; $\square$: own caches, $\blacksquare$: other caches.

Despite repeated use of the same areas, squirrels rarely cached more than once in the same cache site. When 'same site' is defined as two sites less than 10 cm apart, only 45 of 266 cache sites chosen over a 4-month period (including caches made in aborted trials) were ever used more than once; in only nine of these cases was a site reused by the same squirrel.

Memory for Cache Locations

A greater number of a squirrel's own caches ('own') retrieved than caches of other squirrels ('other') relative to the numbers of each cache type available, was taken as positive evidence for memory of cache location. For clarity, we first present the mean number of each type of cache retrieved after delays of 2 and 4 or 12 days (Fig. 3). Overall, squirrels retrieved more of their own caches than other caches, regardless of the length of delay (2-day delay: $P<0.009$; 4- or 12-day delay: $P<0.006$, Wilcoxon's signed-ranks test).

A more precise comparison, however, is that of the number of each type retrieved to the number of each type available. The number of available caches of each type was determined by counting only those caches that lay within the area searched by the squirrel, rather than counting all caches in the arena. This was done such that an individual squirrel's preference for a particular part of the arena would not bias the analysis towards a higher recovery of own caches. The search area for each trial was defined as the minimum polygon that encompassed all the retrieved caches, as seen in Fig. 1.

Within this area, the numbers of own caches retrieved, other caches retrieved, own caches available and other caches available were counted. For each trial, the ratio of own caches retrieved to other caches retrieved was compared with the ratio of own caches available to other caches available. For example Alvin's retrieval, illustrated in Fig. 1, was analysed as follows: he retrieved seven of his own caches and three other caches, yielding a ratio of 7:3, or 2·3:1 in caches retrieved. This ratio is greater than the ratio of cache types that were available in the polygonal area defined above as the search area; which, in this case, was 9:6 or 1·5:1. Data were analysed separately for trials with a 2-day delay and for those with a 4- or 12-day delay.

In the majority of the 2-day delay trials (15 of 17), the ratio of own to other retrieved was greater than the ratio of own to other available; on average, $2·7\pm0·7$ own:other were retrieved, compared with $1·3\pm0·1$ own:other available. In 12 of 13 trials at a longer delay (4 or 12 days) the same was true; on average, $2·3\pm0·3$ own to other were retrieved, compared with $1·6\pm0·2$ own:other available. These differences were statistically significant (2-day delay: $P<0·009$; 4- or 12-day delay: $P<0·013$, Wilcoxon's signed-ranks test). Furthermore, there was no difference between the scores after 4- and after 12-day delays ($P=0·186$, Mann–Whitney U-test), justifying their being combined for the previous analysis. There was also no difference in the scores obtained for 2-day trials in the grass-covered arena and the gravel-covered arena; these trials were also combined in the previous analysis.

To examine the strength of the squirrels' preferential retrieval of their own caches in more detail, we reanalysed some of the data using transcripts of the squirrels' behaviour during cache retrieval (10 trials, from all delays). The location where a squirrel ate each retrieved nut was ascertained from the transcripts. Assuming that this location was also the starting point of the squirrel's next search, we then measured the distance from this location to the two closest caches. In some cases, the two closest caches were one own cache and one other cache; moreover, one of these caches was closer to the squirrel than the other. A squirrel, facing such a choice between two close caches, could simply retrieve the closest cache, regardless of whether it was its own cache or that of another squirrel, or it could preferentially retrieve its own cache, even if the other cache was closer, or it could disregard both closest caches and retrieve a more distant
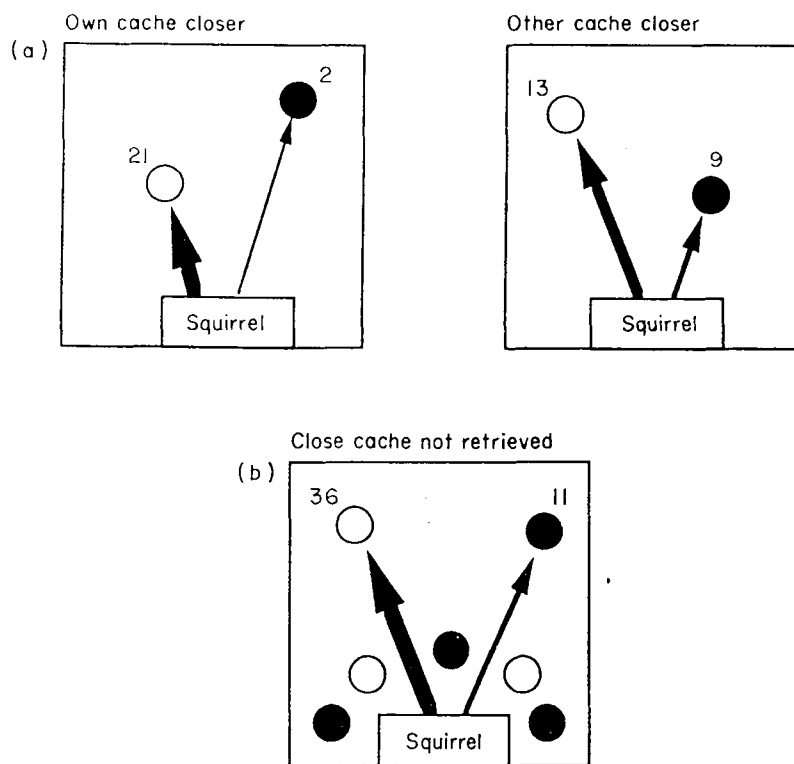
Figure 4. Retrieval of cache types (own or other) under different retrieval conditions. O: own caches; ●: other caches. The arrow from the squirrel to the cache represents the squirrel's retrieval decision; the thickness of the line indicates the frequency at which squirrels chose to retrieve their own caches or other caches. (a) An adjacent cache was retrieved, and either the squirrel's own cache was closer or the other cache was closer ($N = 45$). (b) A distant cache, not one of the two closest caches, is retrieved ($N = 47$).

cache, either one of its own or that of another squirrel. Su :h cases where a choice was presented were then analysed further. If the difference in distance from the squirrel to each of the two closest caches was less than 0·5 m, the retrieval was put into the 'own cache closer' category. In the sample analysed, retrievals of distant caches were as frequently observed ($N = 47$) as retrievals of closest caches ($N = 45$). The number of own caches retrieved was compared with the number of other caches retrieved for each of the three types of retrieval: (1) own cache is closer and a close cache is taken, (2) other cache is closer and a close cache is taken, and (3) a close cache is not taken. The observed number of retrievals was then compared with the expected number of retrievals of each type. The expected number of close retrievals was estimated as two-thirds, because of the observation that when one of the two closest caches were taken, 30 of the 45 caches retrieved were closer than the cache not retrieved. Thus, it appears that the overall probability of a close cache being retrieved (regardless of cache type) is 30/45 or two-thirds. When squirrels

chose to retrieve caches from further away, we expected them to retrieve equal numbers of own and other.

Regardless of the position of the cache relative to the squirrel, squirrels always retrieved more of their own caches than other caches, as shown in Fig. 4. The bias towards retrieving own is significant under both conditions: own cache closer ($\chi^2 = 15·7$, $df = 1$, $P < 0·001$) and other cache closer ($\chi^2 = 6·18$, $df = 1$, $P < 0·05$). Even when retrieving further caches, squirrels retrieved more nuts from their own cache sites than from other sites ($\chi^2 = 13·30$, $df = 1$, $P < 0·001$).

DISCUSSION

Although squirrels buried nuts in areas where other squirrels had also buried nuts, they retrieved significantly more nuts from their own cache sites than from the cache sites of other squirrels, even after delays of 4 or 12 days. This retrieval accuracy could not be explained by the squirrels' habitual use of the

same areas: the ratio of own caches to other caches retrieved was greater than expected based on the availability of caches in the area searched during retrieval. A squirrel was also more likely to retrieve its own cache even when another squirrel's cache was closer to it or when a squirrel neglected to retrieve the cache closest to itself and instead dug up a more distant nut.

These results support our hypothesis that grey squirrels can remember where they bury nuts. Clearly, however, squirrels use other methods, in addition to their memory of specific locations, to find buried nuts. Because the squirrel always retrieved at least one nut from another squirrel's cache, our results confirm earlier observations that grey squirrels can locate a cache by the odour of its contents (Thompson & Thompson 1980).

That squirrels find caches using odour cues has been well-established; that they are also capable of remembering cache locations is a novel result. An interesting implication of these results is that the squirrels employed two methods to find caches: they returned to sites where they had buried nuts and they searched for the odour of buried nuts. Under the conditions of this experiment, either the first method was used more often than the second, or it succeeded more often. Perhaps these methods are used simultaneously: squirrels might sniff the ground for odour cues while they are orienting to the locations of remembered caches. Evidence from a study of grey squirrels searching for hidden seeds suggests that squirrels place different weights upon the cues associated with a remembered food source (McQuade et al. 1986). Captive grey squirrels were trained to look for seeds in covered dishes, which differed in their location, their colour and their odour. The cues were then disassociated, and the analysis of the squirrel's orientation errors led to the conclusion that the most important cue was the location of the food dish, followed by its colour and odour. If squirrels use the same methods to find their caches as to find food sources, then the most important feature remembered about a cache may be its location as well. Grey squirrels, like black-capped chickadees, may also remember the type of seed in a cache (Sherry 1984); their memory of the colour and odour of food dishes, in the above study, suggests that they can.

Our experiment, however, does not address the question of the capacity of a squirrel's memory for cache locations. Under natural conditions, grey squirrels may cache thousands of nuts, over areas a hundred times as large as the experimental arena used here (Jacobs 1987). The maximum length of time between caching and retrieval in the field has not been determined, but it is probably 8–9 months (Cahalane 1942; Thompson & Thompson 1980). Finally, such factors as the number of caches, the size of the caching area and the length of time before retrieval may interact and thereby increase the difficulty of the squirrel's task.

Regardless of its capacity, a grey squirrel's memory for cache locations may have significant adaptive value. When caches are covered with snow, as is the case for much of this species' range and for much of the retrieval season, a squirrel's survival may depend on its accurate memory of some cache locations. Even in the absence of snow cover, the use of memory may be critical to a food-storer's survival. Fox squirrels, *Sciurus niger*, prefer to cache in open fields. This behaviour has been hypothesized to decrease cache pilfering by increasing the predation risk faced by would-be cache pilferers, who must forage more slowly than owners, who can move efficiently to and from remembered sites in exposed areas (Stapanian & Smith 1986).

Memory of cache locations, even in the absence of competitors or predators, may have additional adaptive value if it increases a squirrel's retrieval efficiency. The squirrels in this study appeared to minimize their retrieval search paths by running directly from one patch of two or three caches to the next, harvesting the caches with little re-tracing of their path; this can be seen in the sequence of retrievals illustrated in Fig. 1. If so, this would indicate that grey squirrels, like chimpanzees *Pan troglodytes* (Menzel, 1973), can remember a series of locations in relation to each other and use this information to form a cognitive map, where information about cache sites may be encoded.

Such cognitive processing would be adaptive in an animal that manages an inventory of thousands of items, over many months. Grey squirrels are active all winter, even at the northern limit of their range (Thompson 1977), and during this period they spend much time on the ground, apparently searching for caches and occasionally digging up and reburying a nut or acorn (Jacobs, unpublished observations). In the present study, squirrels also dug up and reburied nuts, though not until they had first eaten several nuts. These observations suggest that grey squirrels may redistribute their caches. Such behaviour could be advantageous: squirrels could rearrange caches that were hastily laid out

during the autumn harvest, and thus maintain an optimum dispersion of caches, which has been shown to reduce loss to pilferers (Stapanian & Smith 1984). As the year progressed and they emptied more caches, the remaining caches could again be rearranged. Such husbandry of caches would also refresh their memory of cache locations, and thus reduce the length of time they must remember the locations. More information on the natural history of cache retrieval by grey squirrels is needed before the capacity and adaptive value of their spatial memory for cache locations can be fully estimated.

ACKNOWLEDGMENTS

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