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MEMORY FOR HOARDED FOOD: AN AVIARY STUDY OF THE EUROPEAN NUTHATCH[1]

ROGER HÄRDLING, HANS KÄLLANDER AND JAN-ÅKE NILSSON[2]
Department of Animal Ecology, University of Lund, S-223 62 Lund, Sweden

Abstract. In an aviary study, each of six male European Nuthatches *Sitta europaea* was allowed to hoard 30 sunflower seeds in natural hoarding substrates. After eight days, each bird was allowed to search for its cached seeds and its performance compared with that of a bird without previous experience of the specific aviary. In all but one case, the hoarder found significantly more seeds than did the naive bird and the hoarder also found the first seed significantly sooner. Furthermore, hoarders found a fixed number of seeds more quickly than did naive birds. These results suggest memory of cache sites.

Key words: hoarding, retrieval, memory, Nuthatch, Sitta europaea.

Hoarding of food for future use is important in many bird species (Roberts 1979, Källander and Smith 1990, Vander Wall 1990). In Nuthatches (*Sitta* spp.), the behavior has been described in all species studied (Löhrl 1988). North European Nuthatches (*Sitta europaea*) hoard large numbers of seeds (Källander 1993) and have been seen retrieving cached food after several months (Nilsson et al. 1993).

For hoarding to be adaptive, the hoarder must be sufficiently better at relocating its caches than are other individuals (Andersson and Krebs 1978). Both niche separation and memory have been proposed as methods for accurate relocation of caches. Although there is evidence for niche differences in hoarding birds (e.g., Moreno et al. 1981, Brodin 1994a), in the species most thoroughly studied, niche separation is not believed to be the major means of securing hoarded food from competitors (Stevens and Krebs 1985, Brodin 1994b). Aviary studies of Marsh Tits *Parus palustris* (Cowie et al. 1981, Sherry 1981, Sherry et al. 1981, Shettleworth and Krebs 1982), Clark's Nutcrackers *Nucifraga columbiana* (Vander Wall 1982, Balda and Kamil 1992, Kamil et al. 1993), and Black-capped Chickadees *Parus atricapillus* (Sherry 1984, Hitchcock and Sherry 1990) have all supported the memory hypothesis. The evidence for this hypothesis, however, must be treated with some caution because most results, at least from non-Corvid passerines, come from aviary studies using very small numbers of seeds (Table 1). This contrasts strongly with the natural situation in which a bird must remember very large numbers of caches (Grubb and Pravosudov 1994). Furthermore, most aviary studies have used artificial caching sites, such as drilled holes, which also may have influenced recovery accuracy. Probably, relocating a cache in a natural, structurally complex environment will require the remembering of much more information than finding cached seeds in a simple, artificial one.

The aim of the present study was to establish the role of memory as a possible mechanism for the relocation of caches in the European Nuthatch. In an aviary study we used natural hoarding substrates, higher numbers of cached seeds, and longer retention intervals than have been used in most previous aviary studies (Table 1).

METHODS

The experiment was conducted during the period 10 January to 28 February 1994 in eight outdoor aviaries near Lund, South Sweden. The aviaries had net roofs, semi-transparent walls on three sides, a wooden wall on one side, and measured 3.5 × 3.5 × 2 m. The birds could hear but not see each other. To supply the experimental birds with hoarding substrates similar to the ones normally used in the field (Källander 1993), each aviary was furnished with stumps of rotten wood, thick branches with loose bark, and sides of whole oak logs with fresh bark and lichens on them.

Eight male Nuthatches were caught with mist-nets at feeders baited with sunflower seeds. All birds were banded with an aluminium ring and an individual combination of color rings. To accustom them to the aviary conditions, they were kept in the aviaries for about a week (mean ± SD = 7.5 ± 2.7 days) before the experiment started. During this time they were fed mealworms and had access to water with a vitamin additive.

Each bird was allowed to hoard 30 dark sunflower seeds. However, two of the eight birds only hoarded 16 and 18 seeds, respectively, and were excluded from the analyses. It took the birds from 20–160 min (mean = 92 ± 59 min) to cache 30 seeds. In no case was a seed hoarded outside the provided hoarding substrates. After the hoarding session, the bird was captured and put in a small cage indoors where it was given mealworms and water with vitamin additive. On the ninth day after hoarding, it was brought back to the aviary and allowed to retrieve seeds for two hours. To obtain a baseline estimate with which to compare each hoarder's performance, we also let each bird search a different aviary during two hours for the seeds cached by one of the other Nuthatches. Thus birds were consid-

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[2] Corresponding author: Jan-Åke Nilsson, e-mail: jan-ake.nilsson@zooekol.lu.se

TABLE 1. Summary of published aviary studies investigating the accuracy of memory in small (non-Corvid) passerine birds. Given are means, or in cases where this could not be extracted from the original papers, ranges of number of birds, number of seeds hoarded and retention intervals.

Species	*n* birds	*n* seeds	Retention interval	Hoarding substrate[1]	Source
Black-capped Chickadee	9	8	2 hr	A	Baker et al. 1988
(*Parus atricapillus*)	6–8	5	1–84 days	A	Hitchcock and Sherry 1990
	4–7	2–12	24–48 hr	A	Sherry 1984
	9	5	3 hr	A	Sherry and Vaccarino 1989
	8	2–7	4 hr	A	Herz et al. 1994
	9	15	3 hr	A	Hitchcock and Sherry 1995
Marsh Tit	3	6	3 hr	A	Sherry et al. 1981
(*Parus palustris*)	4	9	3–24 hr	A	Sherry 1981
	3–4	8–12	2–3 hr	A	Shettleworth and Krebs 1982
Willow Tit (*Parus montanus*)	11	2	24 hr	N	Suhonen and Inki 1992
European Nuthatch (*Sitta europaea*)	6	30	9 days	N	This study

[1] Hoarding substrate is divided into two categories: A = artificial, with only one substrate and often with drilled holes as cache sites; N = natural, structurally complex substrates.

ered naive when searching a different aviary other than their own.

All search sessions took place between 09:00 and 11:00 after overnight deprivation of food. With the aid of photographs of the aviary on which the exact location of all caches were marked, seeds removed by the naive bird were replaced before the hoarder was allowed to search the aviary. Efforts were made to mimic the original caches. This was achieved by covering the seeds with lichens or dead wood in the same way as Nuthatches normally do (Källander 1993) and as they did when caching in the aviary. Every time a bird found a seed, the time was recorded to the nearest minute. All parametric tests follow Sokal and Rohlf (1981) and nonparametric tests follow Siegel and Castellan (1988).

RESULTS

The naive birds found on average (± SD) 10.8 ± 6.7 seeds during the 2-hr trials, whereas those that had originally hoarded the seeds found an average of 17.2 ± 4.4 seeds. In all but one aviary, the hoarder found more seeds than the naive bird resulting in significantly more seeds being consumed by the hoarders than by naive birds (Fig.1; Wilcoxon signed-ranks test, $n = 6$, $T = 20$, $P < 0.05$, two-tailed). Furthermore, the time until the first seed was found was significantly shorter for hoarders ($\bar{x} = 4.3 \pm 5.0$ min) than for controls ($\bar{x} = 13.5 \pm 12.1$ min) (Wilcoxon, $n = 6$, $T = 21$, $P < 0.05$, two-tailed).

For each pair of search sessions (naive and hoarder searching the same aviary), the smallest number of seeds found was determined; in all but one case this was the number found by the naive bird ($\bar{x} = 10.7 \pm 6.3$ seeds). Starting with the first encountered seed, the time intervals between subsequent retrievals up to this number were used as a measure of search time. Hoarding individuals retrieved a seed on average every 5.7 ± 7.3 min (median = 3 min) vs. 9.0 ± 8.7 min (median = 6 min) for naive birds (Mann-Whitney *U*-test, $n_1 = 35$, $n_2 = 35$, $W_x = 1{,}400.5$, $P < 0.01$, two-tailed).

Our replacement of seeds found by the naive bird could potentially have introduced a bias if the replaced seeds were either easier or more difficult to find than the original caches. Replaced seeds were, however, not found significantly more or less often than expected by chance in any replicate (binomial tests); the total number of replaced seeds found by the hoarders did not differ from that expected ($G_{adj} = 0.37$, df = 2, ns) and hoarding individuals found replaced seeds neither earlier nor later than other seeds in the retrieval sequence (Mann-Whitney *U*-test, $n_1 = 35$, $n_2 = 70$, $W_x = 1{,}084$, ns, two-tailed).

DISCUSSION

Our aviary experiment demonstrated that birds that cached seeds retrieved more of them than naive birds allowed to search the same aviary. Hoarders also found seeds sooner and with shorter intervals than did naive birds. Because the birds were food-deprived before all retrieval sessions, they should have had the same motivation to search for food in both situations. The potential possibility that our results were influenced by differences in familiarity with the particular aviary between the naive and the hoarding bird is probably not important because all eight aviaries were very similar in design and in the location and structure of hoarding substrates, and all individuals had spent one week in such an aviary prior to the experiment.

A preference for specific types of caching sites cannot be excluded as the explanation for the higher retrieval accuracy of the hoarding birds. However, this seems less likely because the naive birds were allowed to search for quite a long time in a very restricted area (12.2 m^2) and every cache substrate available should have been searched by the time the session ended if finding a seed was just a matter of looking in the right places. Direct observations also confirmed that the naive bird visited all parts of the aviary during its search session. In aviary 5 (Fig.1), the naive bird found more seeds than the hoarder. Interestingly, the bird that hoarded in that aviary was the fastest one to hoard 30

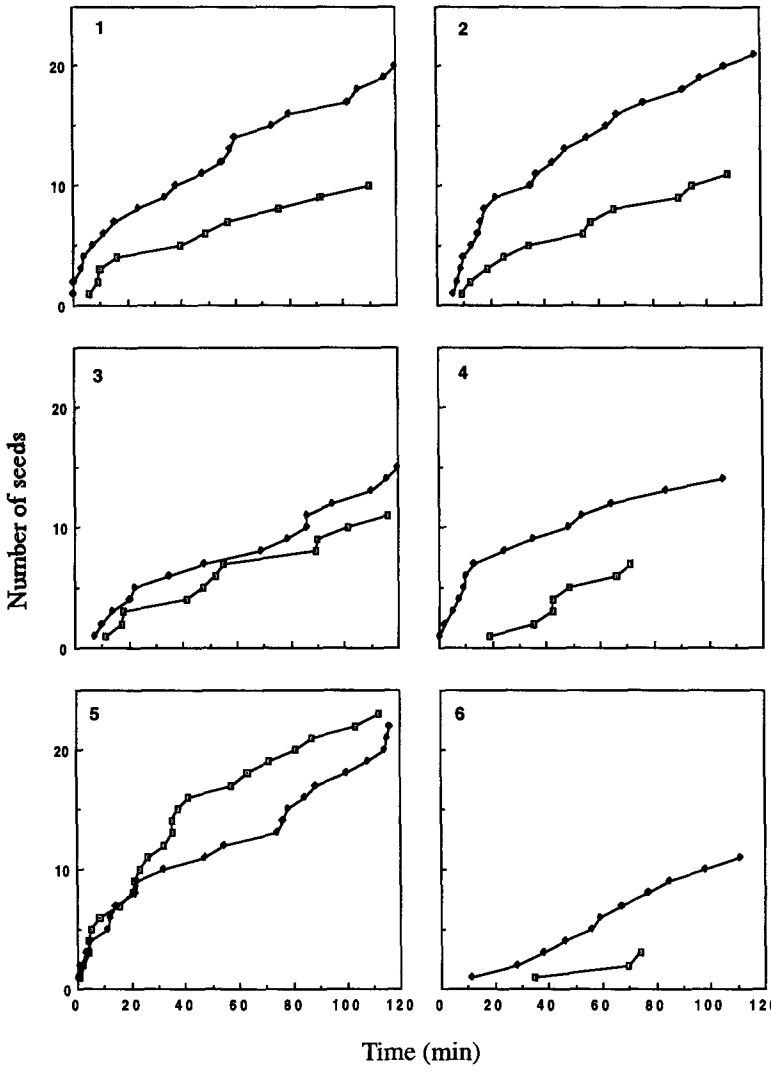

FIGURE 1. Cumulative numbers of seeds found by the hoarder and the naive bird in each aviary. Filled squares = the hoarder; open squares = the naive bird. (The results for two birds that failed to hoard 30 seeds are not shown.)

seeds (in 20 min) and eight of the seeds were easily found when the aviary was inspected afterwards. In contrast, seeds cached by the other birds were very carefully hidden and very difficult to see.

Seeds we had replaced were not over-represented among those later found by the hoarder. Thus, replacement of seeds does not seem to have introduced any bias. The other measure of accuracy of retrieval, mean time until the first seed was recovered, does not suffer from this potential bias, because only one out of six first-found seeds was a replaced one.

Hoarding birds not only found more seeds but also found the same number of seeds faster than did naive birds, suggesting that this was not simply because naive birds stopped searching after a while. The explanation for these differences probably is that the positions of at least some of the hoarded seeds were still remembered by the hoarder after eight days. The pattern of retrieval seems to differ between hoarders and naive birds: most of the hoarders first rapidly retrieved a few seeds and then retrieved seeds at longer intervals, whereas the naive birds did not show this pattern (Fig.1).

The fact that the naive birds in this study discovered a relatively high proportion of the caches suggests that intraspecific cache pilfering could be potentially important in the natural situation. European Nuthatches live year-round in permanent pair-territories vigorously

defended against other Nuthatches (Matthysen 1985). Therefore, most pilfering should be within the pair. However, a recent experimental study showed that such pilfering amounted to less than 5% (Härdling et al. 1995). The success of naive birds to relocate caches in the present study therefore most likely was an effect of the restricted number of potential cache sites that the aviary offered and the relatively high density of caches compared with the situation in nature.

Our study suggests that the Nuthatches most probably used memory to retrieve the seeds as has been concluded from aviary studies of other hoarding birds (see references in Table 1). Many of the previous studies, however, have been criticized for using simple and artificial hoarding substrates as well as low numbers of hoarded seeds (usually less than 10 seeds; Table 1) and short retention intervals (Grubb and Pravosudov 1994). By using artificial hoarding substrates such as drilled holes, the complexity of the environment is reduced considerably. In such environments, a memory that is not sophisticated enough to be used in natural conditions may be sufficient for accurate retrieval. A low density of hoarded food also means a low probability that naive birds should find food items by chance and so may discourage them from continuing to search for food. Our study has shown that even under somewhat more natural conditions, a memory for each cache site seems to be the most important mechanism by which a hoarder retrieves its hoarded food.

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