ORNIS SVECICA 3:49-58, 1993 https://doi.org/10.34080/os.v3.23043

Food caching in the European Nuthatch *Sitta europaea*

HANS KÄLLANDER

Abstract

The behaviour and cache sites of European Nuthatches storing naturally occurring beech *Fagus sylvatica* and hazel *Corylus avellana* nuts in a South Swedish wood are described. Data are also given on the retrieval of cached nuts in winter and on recaching. On average it took a Nuthatch about 1 min to cache a beech nut. A third of all caches were below 1 m, 20% in the ground. Of those in trees, most were at heights between 5 and 15 m and less than 20% on branches thinner than 4 cm; of caches made above ground, 43% were in dead, often rotten wood. The choice of cache site was related to the kind of item to be cached: a higher proportion of hazel than beech nuts was cached in the ground. Oak was used proportionally more, and other species of tree proportionally less for caching than suggested by their abundance, perhaps because oak presented much dead wood which was extensively used for caching. More than 80% of all caches were covered with material from the immediate surroundings of the cache site. The Nuthatches removed the seed coat from a high proportion of the beech nuts before caching them; however, none of those cached in the ground and similar sites were shelled. During the coldest part of the winter, 1.1 nut per hour was retrieved in a winter following a poor mast crop vs 4.6 in a winter following a rich one. Re-caching was common at all times but less so in winter.

Hans Källander, Dept of Ecology (Animal Ecology), Lund University, Ecology Building, S-223 62 Lund, Sweden.

Received 29 March 1993, Accepted 2 May 1993, Edited by M. Grahn

Introduction

Nuthatches (Sittidae) are among those avian taxa in which food storing is most wide-spread (Löhrl 1988), suggesting that the behaviour evolved early in the evolutionary history of this family.

For the European Nuthatch *Sitta europaea* there exists an early published record of food storing. Thus, already about a century ago the Swedish geologist and naturalist A.G. Nathorst described this behaviour in a paper entitled "The Nuthatch's planting of cereal grains in the trees" (Nathorst 1897; author's translation of the Swedish title). However, although food caching has been described for both the European Nuthatch (Löhrl 1958, Moreno et al. 1981) and several Asian (Löhrl 1988) and North American species (references in Vander Wall 1990), these studies have used artificial foods (sunflower seeds) normally not available in the habitats that nuthatches inhabit. The provision of artificial food such as sunflower seed no doubt is a valid method for answering certain specific questions relating to food storing. However, one must be aware of the fact that the pattern of storing that the birds employ may differ from the one they use when storing naturally occurring food, e.g. storing niches may differ.

The present paper aims at giving a descriptive account of the storing behaviour and cache sites used by European Nuthatches in natural conditions.

Study area and methods

Observations were carried out in Dalby Söderskog National Park, a 36 ha mixed deciduous wood 10 km east of Lund, southernmost Sweden (55°40'N, 15°20'E). This wood has been left largely unmanaged and contains numerous fallen trees and much dead

wood. Although in a process of natural change, with the oldest tree generation gradually becoming replaced by younger trees, the wood still contains plenty of old oak *Quercus robur,* beech *Fagus sylvatica* and elm *Ulmus glabra* trees. Some dryer areas are dominated by beech, but most of the wood is truly mixed. Most often there is a predominance of elm, but with a high proportion of oak and beech and also with scattered ash *Fraxinus excelsior* trees. Beech-dominated and many elm-dominated parts are rather open whereas richer areas with more oak have an understorey of hazel *Corylus avellana;* other areas have regenerating very young ash. In mast years, solitary beech trees scattered throughout the wood, some of them very old, produce heavy crops and these trees tend to produce some mast also in less good years. Because of airborn pollutants, lichens are scarce on trunks and branches contrasting with the situation elsewhere in Sweden. In general the wood is fairly open thus facilitating observations of bird behaviour. Most observations of food storing by Nuthatches were made in its mixed, central parts in which the proportion of oak is relatively high.

During 1977-1991, the spring population of Nuthatches in Dalby Söderskog has varied between 4 and 20 pairs, in relation to the severity of the preceding winter (unpubl. data); the autumn population, although not censused, no doubt has been considerably larger on average (cf. Matthysen 1989, Enoksson 1990). The caching behaviour of Nuthatches exploiting natural foods was studied from autumn 1979 onwards, with more systematic observations in 1979, 1980, 1986 and 1992. Observations of retrieval and use of stored food were made in six winters during 1979/80 to 1986/87. In addition, a very limited experiment in which sunflower seeds and commercial hazel nut kernels were provided, was carried out in early spring 1980.

To characterize the kind of sites used for caching, I located Nuthatches either when they were actively storing food or followed them until they started doing so. I then recorded the kind of food stored and of cache site used (ground, fallen log, tree, or other), estimated height above ground and, for trees, species, diameter of trunk or branch used. I also noted other characteristics of the cache site, such as whether in moss or rotten wood. In some data sets I also recorded whether beech nuts were shelled or not before being cached, and whether or not caches were covered. On a number of occasions I also recorded the time taken to store an item (and the time taken to find a new one). All observations were continuously talked into a small, portable tape recorder.

Nuthatches live in permanent pair territories (e.g. Löhrl 1958, Matthysen 1986, 1987), and even though birds sometimes flew considerable distances intruding into the territory of another pair in order to exploit a particularly rich source of food (as below an old beech), this meant that I usually recorded the caching activity of just one pair at a time. However, data were collected from many pairs over several years and I have been unable to find any significant differences in the kind of sites used by different pairs, so I am confident that the data presented below give an adequate description of the caching behaviour of Nuthatches in old, mixed deciduous forest.

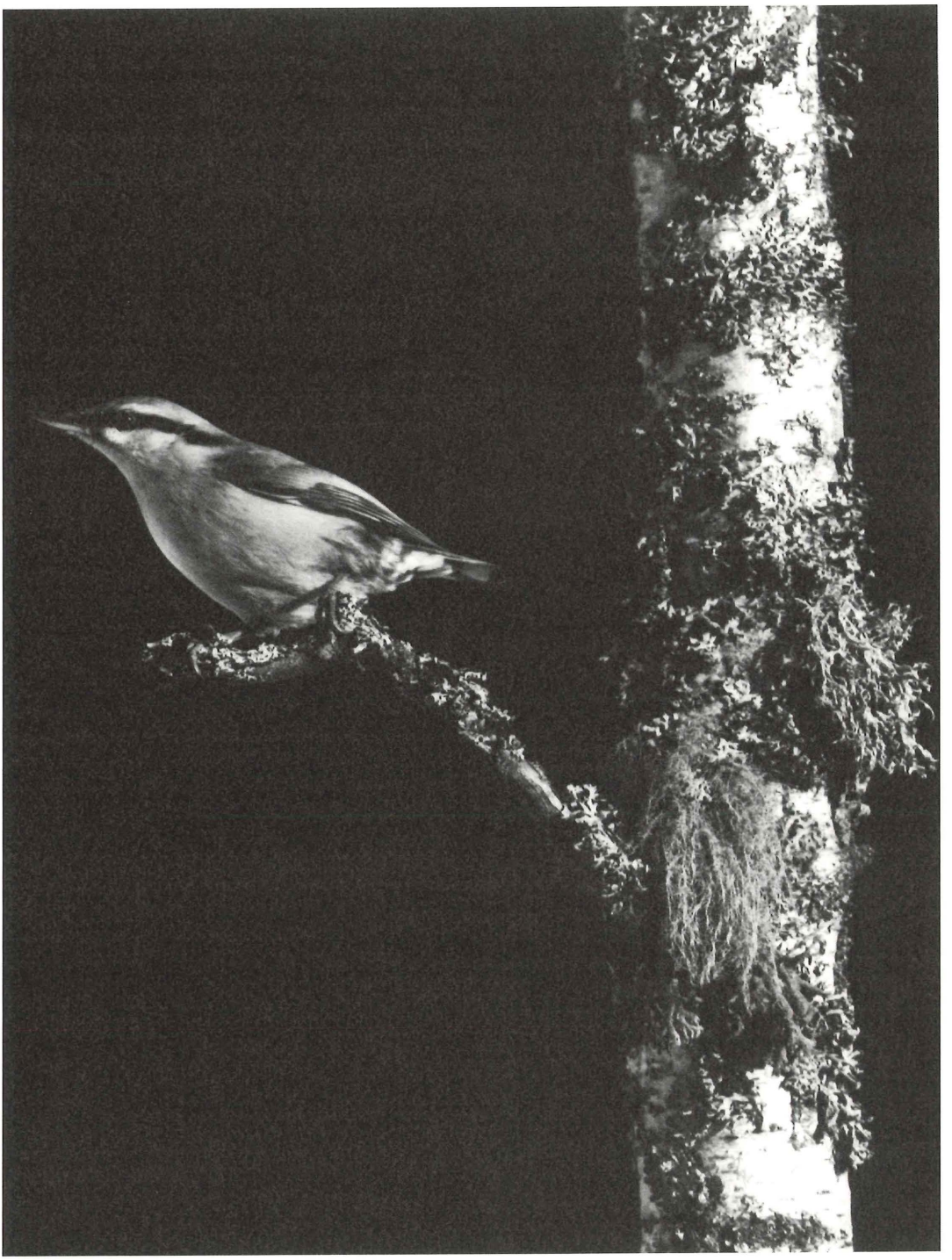
In five winters I followed the foraging activities of Nuthatches in mid-winter in order to estimate how often they retrieved, and used, cached beech or hazel nuts. After locating a Nuthatch or, usually, a pair of Nuthatches, I tried to keep one or both birds under continuous surveillance for as long a period as possible (up to 46 min) recording each time they recovered a nut. Nuthatches are easier to find when they hammer a nut open than when they forage; when Nuthatches were found in this way, observations were not started until normal foraging had been resumed for a couple of minutes.

Caching behaviour

Seasonal occurrence and kinds of food cached

Nuthatches cache food year-round. Although my observations between late April and mid-October are only casual, I could demonstrate caching on 21 May 1980, i.e. when Nuthatches in South Sweden have young in the nest, by providing mealworms to one pair; the male took 3-4 mealworms at a time and cached them singly in trees. I have also seen a male Nuthatch cache some kind of nut in early June and a female cache a large larva in late summer. In early August 1988, when ants were swarming in a small village, I observed a pair of Nuthatches catching them on the wing, eating some and caching others in fruit trees (cf. Dorka 1980). Also in winter and early spring have I seen Nuthatches cache insects (a larva, a moth and a carabid beetle, respectively). However, no doubt caching activity peaks in autumn when first hazel and later beech nuts become available.

Hazel nuts seem to be collected and cached from August onwards as long as they remain available, but, at least in Dalby Söderskog, caching birds are extremely difficult to observe in early autumn because of the dense vegetation in parts with hazel. Beech nuts are taken as soon as they can be extracted from



The food caching European Nuthatch *Den födohamstrande nötväckan.* Foto: Jan Schutzer

the cupulae. After a long drought in summer 1983, a heavy mast year, branches on a beech tree had partly wilted making the cupulae open earlier than normal. Thus already on 19 August a pair of Nuthatches were busy caching beech nuts. Usually, however, the caching of beech nuts started in late September. At this time the Nuthatches either ran outwards on the finer twigs or hovered in front of them inserting their long bills into the cupulae and extracting a nut. As more mast fell to the ground later in the season, Nuthatches spent increasingly more time searching for seeds there.

General behaviour during caching

Nuthatches are scatter-hoarders, i.e. cache items singly scattered over the territory (Löhrl 1958, Persson et al. submitted). Löhrl (1958) has provided a detailed description of the caching act of Nuthatches. In short, a beech nut is usually carried to a tree and either shelled or cached with the shell intact (see below). Whether shelled or not, it is inserted deep into a crevice, moss or rotten wood. Especially when placed in rotten wood or a crack in a dry branch, the nut is often hammered in place. In most instances, the cache is then covered with a tuft of moss, dead wood, or some other material available within the nearest few decimetres of the bird. After a quick inspection the bird leaves the site or, occasionally, removes the nut and tries to store it in another place. Sometimes as many as 4-5 sites are tried before an item is finally cached.

As described by Löhrl (1958), when smaller seeds are taken (such as sunflower seeds provided by man), Nuthatches usually take two or three seeds at a time, depositing them on a horizontal branch while caching the first one; remaining seeds are then cached within a few decimetres to a couple of metres from the first one.

The covering of caches

In the material collected in 1980-86, I had explicitly stated that the Nuthatch covered its cache in 101 out of 111 cases (91%), but no mention of whether the cache was covered or not had been made in another 115 cases. In a material collected in late autumn 1992, the cache was covered in 49 of 60 cases (82%). However, this material included seven instances when only pieces of beech and hazel nuts were cached (after partial comsumption); in four of these the cache was left without cover. Of the remaining instances when caches were not covered, two were very deep behind loose bark and in a crack in a dry branch, respectively; in one, the bird seemed to search for something to cover the cache with but found nothing; in one, it made covering movements without any material in its bill. From these data, it seems safe to conclude that European Nuthatches cover at least 80%, and probably more, of their caches of naturally occurring seeds.

Shelling of beech nuts

Often Nuthatches shell a beech nut before caching it, usually by sitting upside down on the trunk hammering on the nut, after having inserted it in a bark crevice. The frequency with which the shell is removed from beech nuts before caching clearly depends on the future cache site. Thus, whereas 74 out of 106 beech nuts cached in trees were shelled, this was the case for none of 55 nuts cached in rotten logs on the ground, in bare soil among the roots of up-rooted trees, or in the ground itself ($\chi^2 = 68.3$, d.f. = 1, $P < 0.001$). I have no data to show whether the proportion of nuts cached with the shell removed changes during the course of the autumn.

Time taken to create a cache

The mean time taken a Nuthatch to store a beech nut from leaving the source until returning to it was 65 s (SD 68 s, N = 90), with a range from 13 to 485 s. The longest caching times reflect the shelling of the nut and the trying of a large number of sites in succession. Caching in the ground was faster than caching in trees as indicated by the fact that all of nine timed caching events there involving naturally occurring food items took less than 29 s (mean 22.0 s, SD 6.26; $t = 1.89$, $P < 0.1$).

In an experiment in which sunflower seeds and hazelnut kernels were provided, hazelnut kernels took 34.2 s (SD 13.2 s, N = 11) to cache in trees and 23.9 s (SD 12.3 s, N = 16) to cache in the ground ($t = 2.08$, $P<0.05$). A caching trip with sunflower seeds took 43.9 s (SD 19.4 s, N = 45) reflecting the fact that Nuthatches normally take two or three such seeds at a time.

The time it took a Nuthatch to find a beech nut after returning to the source of course varied with the size of the beech mast crop. In 1980 it took 26 s (N=30) and in 1983, a mast peak year, 10 s (N=66). However, one must keep in mind that these figures were obtained at beech trees during peak availability of nuts.

Cache sites

Cache site characteristics

The height distribution of 206 caches for which height was recorded, is shown in Table 1. About a third of the caches were below 1 m, most of them in the ground or on fallen logs but some were in moss at the base of thick trunks. Almost half were between 5 and 15 m high up in trees (most mature trees in Dalby Söderskog approach 20 m and some exceed this height), a height distribution similar to that reported by Moreno et al. (1981) for Nuthatches caching sunflower seeds in winter.

Of a total of 348 cache sites recorded, 19.8% were in the ground, including in the soil among the roots of up-rooted trees, and another 10.6% were on fallen, usually rotten and moss-covered logs; the remaining 69.5% were in trees, including a few in hazel. More than half of those in trees (57.9%) were on either main or secondary, more or less vertical trunks, and of the 102 caches made on branches, only 18.6% were on branches less than 4 cm thick. Thus, Nuthatches mainly used trunks and thick branches for caching.

Table 2 gives a more detailed presentation of the kinds of sites used by the Nuthatches when caching in trees. Sometimes a cache site would show more than one of the characteristics listed in the table, such as moss covering rough bark. In those cases, caches were listed under the most prominent feature of the site. Most caches in holes were where small branches had fallen off but sometimes Nuthatches entered cavities and cached inside them.

Table 1. Height distribution of Nuthatch caches in Dalby Söderskog (beech nuts, N = 191; hazel nuts, N = 15).

Höjdfördelningen för 191 bokollon och 15 hasselnötter gömda av nötväckor i Dalby Söderskog.

Height (m) *Höjd (m)*	Beech nuts *Bokollon*	% %	Hazel nuts *Hasselnötter*	% %
>20	1	0.5	1	6.7
15 - 20	12	6.3	-	-
10 - 15	46	24.1	-	-
5 - 10	51	26.7	-	-
2 - 5	22	11.5	2	13.3
1 - 2	7	3.7	-	-
0 - 1	36	18.8	1	6.7
Ground (0) *Marken*	16	8.4	11	73.3

Tree species used for caching

To obtain an estimate of the species composition among trees available for caching, I counted all trees more than 20 cm in diameter at breast height within 5 m on either side of a number of random transects through those parts of the wood in which caching observations had been carried out. This distribution was then compared with that for trees used for caching, the two being significantly different (χ^2 = 91.1, d.f. = 3, P < 0.001). Nuthatches showed a clear preference for caching in oak which was used twice as frequently as expected from its abundance. Elm was used slightly less, and beech and ash much less than expected. However, there has been no regeneration of oak in Dalby Söderskog for a very long time and so oaks are on average older and thicker than the other tree species. As elm may not be suitable as a cache substrate until mature, I made a new estimate counting only trees more than 45 cm in diameter (b.h.). Although less pronounced, the preference for oak, and the difference between observed and expected values, still remained (χ^2 = 19.4, d.f. = 3, P < 0.001). A similar preference for caching in oak was also found by Moreno et al. (1981).

Table 2. Characteristics of Nuthatch caches in Dalby Söderskog (caches in the ground, among the roots of fallen trees, etc. excluded; N = 226 beech nuts).

Egenskaper hos 226 gömmor för bokollon (gömmor i marken, rotvältor och likn. uteslutna).

Cache characteristics *Gömmors egenskaper*	N	%
Behind loose bark *Bakom lös bark*	58	25.7
In rotten wood *I murken ved*	47	21.0
In (rough) bark *I (grov) bark*	44	19.5
In small holes *I små hål*	21	9.3
In cracks in (usually dry) wood *I sprickor i (oftast torr) ved*	20	8.8
In moss *I mossa*	15	6.6
"Dry branch", unspecified *"Torrgren", ospecificerat*	12	5.3
In fork *I grenklyka*	7	3.1
Others *Övrigt*	2	0.9

Table 3. Consumption and recaching of beech nuts retrieved during late autumn and winter, respectively.

Antal bokollon som ätits hela, delvis eller omhamstrats under senhöst respektive vinter.

Period	Eaten whole *Äts hela*	Cached after partial consumption *Äts delvis, hamstras*	Recached whole *Omhamstras hela*
Oct - Nov	2	1	8
Dec - Feb	32	6	8

One reason why Nuthatches preferred to cache in oak trees probably is that most of the oaks had plenty of dead wood (cf. Table 2). Some oaks were more or less dead while also relatively healthy ones had dead branches or stumps of branches. Although this was also true of the majority of old elm trees (and of some very old beech trees), it is probably safe to say that oaks presented more dead wood than the other species of tree. Nuthatches used dry or rotten wood extensively as caching sites. Thus, combining all kinds of dead wood, from dry branches with longitudinal cracks to rottening logs, but excluding caches made in the ground, 42.8 % (98 out of 229) of caches were in such sites.

Cache sites in relation to kind of item stored

The position of caches was dependent on the kind of item stored. While only a fifth of beech nuts were cached in the ground, 60% of whole hazel nuts were so ($\chi^2 = 16.7$, d.f. = 1, $P < 0.001$). Similarly, only three out of 57 caches of sunflower seeds were in the ground versus 13 out of 27 commercial hazelnut kernels ($\chi^2 = 24.7$, d.f. = 1, $P < 0.001$).

Use of stores

Retrieval behaviour

Nuthatches occasionally retrieved a beech nut or a piece of hazel nut during normal foraging in a way suggesting that the item was found by chance. However, when Nuthatches were observed in winter, the usual pattern was uninterrupted 'normal' foraging for tens of minutes, i.e. the chiselling off of flakes of bark, moss, etc. and the inspection of bark crevices. The focal bird would then suddenly fly directly to a particular site, for instance a rotten branch, often 10-20 m away, and start hammering. After a while it would extract a beech or hazel nut which was then either consumed partly or in its entirety. In the former case, the remains were most often cached, normally close to the place of consumption.

Frequency of retrieval

During the coldest period (Dec - Feb) in each of five winters between 1980/81 and 1986/87 I followed foraging Nuthatches and recorded each time they retrieved and consumed a nut. In total 29.9 'Nuthatch hours' and the retrieval of 73 nuts were recorded, giving an overall retrieval frequency of 2.4 nuts/h. There were, however, considerable differences between years. After the poor mast autumn of 1981, only eight retrievals were seen in 455 min (1.1 nut/h), whereas after the very rich mast in autumn 1983 five retrievals were recorded in 66 min (4.6 nuts/h).

Recaching

Retrieval of cached nuts was also commonly observed during periods when beech nuts were still available for caching (and were being cached). In such situations retrieved nuts were either eaten or recached. Recaching of stored food items occurred at all times but seemed to be more frequent in late autumn than in winter (Table 3). As during the winter observations, it was sometimes difficult to decide if a cache was found by chance during normal foraging. Mostly, however, the bird would fly to a particular site and start hammering only to retrieve a beech nut that was later cached in a new site, sometimes after first having been shelled (cf. Persson et al. submitted).

Discussion

Traditionally one distinguishes between short-term and long-term hoarding (Källander & Smith 1990, Vander Wall 1990). In the former, the stored food is used within hours or days, whereas long-term hoarding means the storing of food over longer periods of time, such as from one season to another. This distinction has, however, been criticized recently (Stanback 1991), mainly on the grounds that storage times may show continuous variation and that the two categories thus may represent only the ends of a continuum. Where then does the European Nuthatch's food caching fall?

Both this study and a previous one using artificial food (Nilsson et al. 1993) have conclusively shown that Nuthatches use hoarded food long after it was stored (also see Löhrl 1988). In the study of Nilsson et al., Nuthatches still retrieved cached sunflower seeds in late winter 98 days after the feeders had been removed, and in the present study cached beech and hazel nuts were used long after these nuts had become unavailable to non-hoarders. Thus, there is no doubt that the Nuthatch must be considered a long-term hoarder. However, long-term and short-term use of hoarded food may not be mutually exclusive even though the "goals" may differ. Thus, if short-term use is a means of avoiding carrying fat and of achieving an optimal allocation of resource intake during the course of the day (McNamara et al. 1990), the same pattern of exploitation could well apply to food stored over long periods of time. Interestingly, Nilsson et al. (1993) demonstrated that the rate at which Nuthatches retrieved and consumed cached seeds was linearly related to ambient temperature: more cached seeds were used on cold than mild days.

Do Nuthatches remember their caches?

If Nuthatches use the stores they create in autumn all through winter, how then do they relocate their caches? Some species, notably the nutcrackers *Nucifraga* spp., have been shown to possess a remarkable capacity to remember their stores (for data and references, see Vander Wall 1990). Do Nuthatches have a similar capacity? Unfortunately this question cannot yet be answered. During the winter observations of retrieval of cached food in the present study, Nuthatches were often seen to interrupt their normal foraging and fly directly to a particular spot and retrieve a nut, and similar observations were made by Persson et al. (submitted). However, as shown above, recaching of nuts was common and it is therefore impossible to say for how long a particular cache had remained unexploited. In some cases snow or ice had covered the cache for about a week, the Nuthatch removing it to reach the cache. However, conclusive evidence that Nuthatches can remember their stores over longer periods of time are lacking.

Persson et al. (submitted) speculated that by re-caching the bird refreshes its memory, thereby extending the period over which stored food can be used. Another explanation of this behaviour is that the bird recaches for its own use those items cached by its mate which it happens to come across. Although this may sometimes be the case, the fact that a bird would often fly directly to a site, retrieve a nut and then recache it, speaks against this explanation. In the study of Persson et al. (submitted), recaching took significantly longer than the original caching, implying that recached seeds were more carefully hidden; no such data are available from the present study. However, on one occasion (26 October 1980, not included in the data presented above) a pair of Nuthatches were extremely busy extracting nuts from the cupulae of a beech tree. Apparently the cupulae had just opened, possibly in response to the weather conditions, and the birds only quickly inserted the nuts in the rough bark of some nearby oaks before returning to the beech canopy. It is possible that they used the oaks as a temporary storage place enabling them to secure as many of the nuts as possible before these were discovered by competitors (cf. discussion in Källander & Smith 1990, Persson et al., submitted).

Cache protection, cache sites and preparation of food to be stored

Normally the Nuthatches hid nuts carefully, indicating that they were valuable to them. Thus, more than 80% of all caches were covered with material from the immediate surroundings of the cache, and those that were not covered were usually in well-protected sites such as deep cracks in dry branches, etc. Nearly 70% of all cache-sites recorded were in trees and of these more than 40% were in dead, often rotten wood. The latter kind of substrate is probably important also in other areas (pers. obs.), but may have been more so in Dalby Söderskog where there is very little lichen growth on trunks and branches.

The kind of item to be cached influenced the choice of storing site, as shown by the fact that a significantly higher proportion of hazel than beech nuts was cached in the ground (and of commercial hazel nut kernels than sunflower seeds). Apparently the Nuthatches assessed how difficult an item was to cache - or, perhaps, how valuable it was. This observation has implications for studies of the caching niches of small birds: the use of sunflower seeds may give a picture differing from that of foods cached naturally. That is not to say that studies using sunflower seeds cannot provide interesting insights, only that some caution is necessary when interpreting the results.

The seed coat was removed from a large proportion of the beech nuts before they were cached. Thus,

the birds incurred a handling cost at the time of caching (cf. Woodrey 1990) and made a similar benefit (in time saved) at the time of exploitation (when time may be more important). For this to be the explanation for shelling, then a large proportion of the nuts cached must survive until exploited by the hoarder, or the time-saving benefit must be great, or both. One might think that removal of the seed coat would reduce the nuts' resistance to fungal attack but this still remains to be tested. It is interesting to note, however, that none of the beech nuts seen to be cached in the ground, or in rotten logs on the ground, were shelled prior to caching, i.e. in places where nuts seem likely to deteriorate more rapidly than in trees. An alternative explanation for the shelling of nuts would be that shelled nuts are for short-term use whereas those cached intact are for long-term use.

The adaptive value of food caching in the Nuthatch

As indicated in this study, Nuthatches scatterhoard food year-round but do so particularly in autumn when suitable seeds such as hazel and beech nuts are available. Although estimates of the amounts stored are still lacking, the amounts are clearly impressive, especially in mast years. In the present study it took a Nuthatch on average slightly more than a minute to cache a beech nut, and observations of mine indicate that a bird may cache up to 20-30 beech nuts per hour. Hoarding may go on for much of the day in autumn, only interrupted by foraging bouts and interactions with neighbouring pairs. As beech mast may be available from the end of September well into December (unless covered with snow), these figures give a rough indication of the amounts of food stored; to these should be added hazel nuts stored from August onwards.

If Nuthatches store such large quatitites of food as suggested above and use the stores throughout winter, is this reflected in their winter survival? Or, to express the question in a more precise way: Is there a positive correlation between the amounts of food stored and winter survival in European Nuthatches? Do nuthatches that are able to store much food have better survival than those that are not? Is winter survival better after mast autumns than after autumns poor in nuts? The unexpected answer to these questions seems to be 'no'. In several studies (e.g. Nilsson 1987, Matthysen 1989, Enoksson 1990), late autumn populations of Nuthatches have been found to be higher in mast years, reflecting higher recruitment (Nilsson 1987, Enoksson 1990) or better autumn survival of juveniles (Matthysen 1989). Although spring populations were higher after autumns rich in beech mast, winter survival was uncorrelated with beech mast abundance (Nilsson 1987) or was even lower among adults after mast autumns (Matthysen 1989). Enoksson (1990) experimentally supplied sunflower seeds from summer to the beginning of December in two years with few hazel nuts. In both years, the autumn density of Nuthatches increased in her plot but winter survival was unaffected. These results may appear especially intriguing as Nilsson et al. (1993) in a study somewhat similar to that of Enoksson found a clear effect of stored food on the nutritional status of Nuthatches in winter. The most likely explanation seems to be that mortality over winter is density-dependent and masks the positive influence of stored food. However, an experimental study of the effects of food caching on Nuthatch winter survival is called for.

Acknowledgements

I thank Bodil Enoksson, Jan-Åke Nilsson and Henrik G. Smith for comments on the manuscript.

References

Dorka, V. 1980. Insektenspeichernde Kleiber *Sitta europaea.* Unterscheidung von langfristigem und kurzfristigem Nahrungsspeicher-Verhalten. *Ökol. Vögel* 2: 145-150.

Enoksson, B. 1990. Autumn territories and population regulation in the nuthatch *Sitta europaea*: an experimental study. *J. Anim. Ecol.* 59: 1047-1062.

Källander, H. & Smith, H.G. 1990. Food storing in birds: an evolutionary perspective. *Current Ornithol.* 7: 147-207.

Löhrl, H. 1958. Das Verhalten des Kleibers (*Sitta europaea caesia* Wolf). *Z. Tierpsychol.* 15: 191-252.

Löhrl, H. 1988. Etho-ökologische Untersuchungen an verschiedenen Kleiberarten (Sittidae). *Bonn. zool. Monogr.* 26.

McNamara, J.M., Houston, A.I. & Krebs, J.R. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behav. Ecol.* 1: 12-23.

Matthysen, E. 1986. Some observations on sex-specific territoriality in the Nuthatch. *Ardea* 74: 177-183.

Matthysen, E. 1987. Territory establishment of juvenile Nuthatches *Sitta europaea* after fledging. *Ardea* 75: 53-57.

Matthysen, E. 1989. Nuthatch *Sitta europaea* demography, beech mast, and territoriality. *Ornis Scand.* 20: 278-282.

Moreno, J., Lundberg, A. & Carlson, A. 1981. Hoarding of individual nuthatches *Sitta europaea* and marsh tits *Parus palustris. Holarct. Ecol.* 4: 263-269.

Nathorst, A.G.1897. Nötväckans sädesplanteringar i träden. *Öfversikt Kongl. Vet.-Akad. Förhandl.* 1897: 103-113. (In Swedish.)
Nilsson, J.-Å., Källander, H. & Persson, O. 1993. A prudent hoarder: effects of long-term hoarding in the European nuthatch. *Behav. Ecol.* 4: in press.
Nilsson, S.G. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *J. Anim. Ecol.* 56: 921-937.
Persson, O., Källander, H. & Nilsson, J.-Å. Submitted. Rehoarding and the order of retrieval of stored seeds in the European nuthatch.
Stanback, M. 1991. A reassessment of avian food caching. *Bird Behav.*9: 1-6.
Vander Wall, S.B. 1990. *Food hoarding in animals.* Univ. Chicago Press, Chicago & London.
Woodrey, M.S. 1990. Economics of caching versus immediate consumption by white-breasted nuthatches: the effect of handling time. *Condor* 92: 621-624.

Sammanfattning

Nötväckans Sitta europaea *födohamstring*

År 1897 publicerade geologen och naturforskaren A.G. Nathorst en kort uppsats kallad "Nötväckans sädesplanteringar i träden" (Nathorst 1897). Från iakttagelser av havreplantor uppe i träden och hur sädeskornen placerats drog han slutsatsen att det var nötväckor, som åstadkommit fenomenet, och han drog också den likaledes korrekta slutsatsen att de gömt kornen för kommande behov, dvs hamstrat. Nötväckans hamstringsbeteende har sedermera beskrivits av Löhrl (1958). Hans studier, liksom senare studier av asiatiska och nordamerikanska nötväckearter (Löhrl 1988, Vander Wall 1990) har emellertid använt solrosfrön som hamstringsobjekt (vissa arter har därtill endast studerats i voljär). Föreliggande arbete beskriver nötväckans hamstring av naturligt förekommande föda, främst bokollon, under naturliga betingelser.

Studieområde, metod

Studien, som varit ganska extensiv, genomfördes i Dalby Söderskog nationalpark 10 km öster om Lund, Skåne, under åren 1979-1992, med mera intensiva insatser under vissa av åren. Vårpopulationen av nötväcka i Dalby Söderskog varierade under denna tid mellan 4 och 20 par (egna opubl. data). Höstpopulationens storlek är okänd men torde samtliga år ha varit högre, ibland mycket högre.

Även om Dalby Söderskog inte gått fri från ingrepp, har skogen ändå fått utvecklas förhållandevis fritt och det är gott om delvis döda träd, liksom av omkullblåsta träd i olika stadier av förmultning. På grund av regionens höga halter av luftföroreningar saknar träden emellertid i stort sett lavar, något som sannolikt påverkar nötväckornas val av hamstringsplatser. Skogen, som är ganska öppen, domineras av alm i de flesta områden men av bok i torrare delar. Gamla ekar är vanliga i nästan hela skogen och speciellt i dess centrala delar, där hassel utgör buskskikt. Åtminstone enstaka bokar finns inom flertalet nötväckerevir (inom samtliga studerade).

För att beskriva det slags platser nötväckorna använde som gömställen för framför allt bokollon, men även för hasselnötter, lokaliserade jag hamstrande nötväckor eller följde nötväckor tills de började göra hamstringsturer. I en kasettbandspelare talade jag in uppgifter om typ av gömställe (mark, rotvälta, liggande stock, träd, osv.), gömmans höjd över marken, och för gömmor i stammar och grenar, deras diameter. Vidare noterades detaljer som huruvida gömman var i lös ved, i mossa, grova barkspringor etc. samt, för ett stort antal gömmor, huruvida fågeln täckte över gömman innan den lämnade platsen. I samband med vissa observationer noterades också om nötväckan skalade bokollonet innan detta gömdes.

Under den kallaste delen av fem vintrar följde jag också nötväckor kontinuerligt under deras födosök under så långa sammanhängande perioder som möjligt och noterade deras utnyttjande av gömd föda.

Nötväckor håller par-revir året runt och fåglarna är oftast trogna reviret under hela sin livstid (Löhrl 1958, Matthysen 1986, 1987), men genom att studierna utfördes under åtskilliga år och i olika delar av skogen torde de insamlade data vara representativa åtminstone för nötväckor i sydsvenska lövskogar.

Resultat

Nötväckor gömmer föda året runt (egna iakttagelser), men den viktigaste hamstringsperioden infaller på hösten då först hasselnötter och sedan bokollon blir tillgängliga. De är "gleshamstrare", dvs placerar endast en födopartikel i var och en av glest utspridda gömmor. Vanligen täcks det gömda över med material från den närmaste omgivningen - i föreliggande studie täcktes 82-91% av alla gömmor; i de fall så inte skedde var födan (vanligen ett bokollon) placerad djupt bakom lös bark eller i djupa sprickor i ved.

Mycket ofta skalades bokollon innan de hamstrades. Intressant att notera är, att 74 av 106 bokollon som gömdes i träd skalades, till skillnad från inget enda av 55 som placerades i marken eller i ruttnande stockar.

Det tog i medeltal nötväckorna 65 s (13 - 485 s, N = 90) att gömma ett bokollon och återvända till

källan. De längsta tiderna uppstod när fågeln prövade ett stort antal ställen innan den slutligen gömde. Tiden att finna ett bokollon varierade naturligtvis med tillgången och var under den rika bokollonhösten 1983 endast 10 s (N = 66), uppmätt under bokar när tillgången var som högst.

De flesta gömningar skedde på 5-15 m höjd och endast drygt 1/10 i marken (Tabell 1). I träd var mindre än en femtedel i grenar av mindre än 4 cm tjocklek, dvs nötväckorna visade en förkärlek för stammar och grova grenar. Av trädslagen, som utnyttjades för gömning, visade nötväckorna en klar (och statistiskt säkerställd, $P < 0,001$) preferens för ek, möjligen därför att ekarna i Dalby Söderskog har rikligt med döda, torra eller murkna grenar. Nästan 40% av alla gömmor i träd skedde nämligen i olika typer av död ved, följd av "lös bark", vilken också oftast är förbunden med död ved (Tabell 2). Valet av hamstringsplats var också beroende av födoslag: en signifikant ($P < 0,001$) högre andel hasselnötter än bokollon hamstrades i marken.

Under den kallaste delen av fem vintrar följde jag nötväckor och registrerade när de plockade fram hamstrad föda. Oftast skedde detta genom att de avbröt sitt normala sökande (under vilket de med näbben fläker bort mossa och lös bark, inspekterar sprickor och håligheter, osv.), flög iväg till en bestämd punkt, stundom flera tiotal meter bort, där de sedan hamrade med näbben för att efter en stund hala fram ett bokollon eller en hasselnöt. I medeltal under knappt 30 "nötväcketimmar" registrerades 2.4 sådana framplockningar av hamstrade bokollon/nötter i timmen; efter den usla bokollonhösten 1981 endast 1,1 nöt/h och efter den mycket rika hösten 1983 4,6 nötter/h.

Såväl under hamstringsperioder som under vintern omhamstrades en del av den framplockade födan, dock tydligen en mindre del under högvintern än under hösten (Tabell 3).

Diskussion

Såväl föreliggande studie som en experimentell studie av Nilsson et al. (1993) visar att nötväckan är en långtidshamstrare, dvs att den utnyttjar föda lång tid efter det att denna lagrats. Frågan är hur nötväckan återfinner sina gömmor, i synnerhet som mängden bokollon och hasselnötter som hamstras under loppet av en höst torde uppgå till åtskilliga tusen. Ännu saknas studier av nötväckans minneskapacitet, men kan den vara i närheten av nötkråkornas (se Vander Wall 1990 för data och referenser)? Persson et al.(submitted) spekulerar i att omhamstring kan vara en metod att "fräscha upp minnet".

Nötväckorna i föreliggande studie gömde bokollon och hasselnötter noggrant - mer än 80% av alla gömmor täcktes noga och dessutom var många ollon djupt inkörda i murken ved, djupa sprickor och liknande, något som antyder att den gömda födan var värdefull.

Det faktum att en högre andel hasselnötter än bokollon gömdes i marken visar att hamstringsplatserna anpassas till födoslaget. Denna iakttagelse har en viss betydelse: försiktighet är påkallad när det gäller vissa slutsatser baserade på experiment med solrosfrö.

En hög andel av bokollonen skalades innan de gömdes, vilket innebär att fågeln ådrog sig en (tids)kostnad i samband med gömningen. Sannolikt mer än kompenseras denna av den tidsvinst fågeln gör vid utnyttjandet (då tid kan vara än viktigare än vid hamstringstillfället). Man tycker dock att skalade bokollon skulle vara mer utsatta för svampangrepp än oskalade, men detta återstår att undersöka. Intressant är dock att konstatera att bokollon som gömdes i mark och liknande ställen, där risken för svampangrepp förefaller vara högre än uppe träden, aldrig skalades.

Om nu nötväckan är en långtidshamstrare som lägger upp stora förråd, avspeglas detta i högre vinteröverlevnad? Eller riktigare uttryckt, står vinteröverlevnaden i relation till mängden hamstrad föda? Trots att Nilsson et al. (1993) fann att nötväckepar, som gavs möjlighet att hamstra stora mängder solrosfrön, var i bättre kondition under senvintern än kontrollfåglar som inte utfodrades, har hittills utförda studier inte visat några effekter på vinteröverlevnaden (Nilsson 1987, Matthysen 1989, Enoksson 1990). Sannolikt beror detta på att nötväckepopulationerna under höstar med rik bokollontillgång är mycket höga och att täthetsberoende vinterdödlighet maskerar de positiva effekterna av hamstring.