FOOD CACHING VERSUS IMMEDIATE CONSUMPTION IN THE NUTHATCH: THE EFFECT OF SOCIAL CONTEXT

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ABSTRACT   We studied the hoarding behaviour of the Nuthatch *Sitta europaea* in wild during winter, and examined whether or not the trade-off between caching (external reserves) and consumption (internal reserves, fat deposit) in this species is a function of the social context in which the individual forages. We compared the caching behaviour of birds foraging solitary or with another bird (conspecific or heterospecific). When solitary, the Nuthatch hoarded in a higher proportion than when in the presence of another individual. The time feeding was significantly longer when in social than when solitary. The efficiency of caching (loss of the cache due to robbery or disturbance) also decreased when another individual was present. The results of this study undertaken in natural condition demonstrated that the presence of another individual was perceived by the Nuthatch as a source of potential cache loss. In a social context Nuthatches tended to increase internal reserves (fat deposits), also benefiting from the potential robber by sharing vigilance (conversion of scanning time into feeding time). If solitary, Nuthatches maximized external reserves (caches) for later consumption. We conclude that the decision about the way energy reserves are generated by the species studied is dependent on the social context in which the individual is involved.

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INTRODUCTION

In order to survive during prolonged periods of food scarcity or unpredictability, birds store energy reserves. Accumulation of energy stores increases the probability of survival under environmental harshness (Brittingham & Temple 1988, McNamara & Houston 1990). Small passerines wintering in temperate areas may generate internal food reserves (fat deposits) and/or external larders (Blem 1990, Vander Wall 1990, Haftorn 1992). For these small birds, fat reserves provide a solution to face short-term food deprivation (e.g. fasting at night, unpredictable food availability; Haftorn 1992). Acquisition and maintenance of such internal reserves bears the cost of increased energy expenditure while foraging, and a higher predation risk associated with a decreased maneuverability (Lima 1986, Rogers 1987). On the other hand, food hoarding provides a way for storing larger amounts of food, usually for longer periods. This behaviour requires much time and energy devoted to find, store,

and secure food caches during periods of low energetic requirements or high food availability, for a later consumption when energy demands increase (e.g. earlier morning hours, snowstorms; Källander & Smith 1990).

Several studies have demonstrated the marked influence of other individuals on the survival of previously stored food caches (see Vander Wall 1990, and references therein; but see Baker *et al.* 1988, 1990). If other individuals present may reduce the profitability of larders by robbing food caches, food hoarding individuals should develop behavioural strategies to reduce this cache loss.

Different patterns of acquisition and allocation of energy to internal (i.e. eating) and external (i.e. caching) stores have been analyzed in relation to both starvation risk (Hurly 1992) and handling time (Woodrey 1990, Jacobs 1992). To our knowledge, there is no information under natural conditions about the trade-off between generating external larders and internal reserves (fat deposits) considering the presence of potential robbers gathered in

the same flock. The behavioural strategies performed by the cacher to minimize the robbing risk remain also unknown. Only studies made with captive birds have partially analyzed the problem (Stone & Baker 1989, Baker *et al.* 1988, 1990).

Hoarders can minimize the risk of cache loss to robbers either by decreasing the profitability of the cache for the robber (diminished pilfering probability and/or increased pursuing travel cost; Waite 1992), or converting storing time in feeding time (thus, generating internal energy reserves instead of external energy reserves), or both. If this hypothesis is correct, two predictions could be made: (1) solitary foraging birds will store food in a higher proportion than when foraging with some other birds (see also Stone & Baker 1989); (2) the hoarder will consume more food items at the food patch in the presence of another individual.

In this paper we study the hoarding behaviour and the responses to potential robbers of the Nuthatch *Sitta europaea*. This is a regular winter hoarder that maintains year-round territories where mated pairs forage together, although it is also frequently found foraging in mixed species flocks during winter (Cramp & Perrins 1993). We examine whether caching behaviour by Nuthatches is a function of the social context, our main objectives being:
(1) to show under natural conditions how important is robbery in the interaction hoarder-robber, considering the magnitude of the interference and its frequency of occurrence (Vander Wall 1990);
(2) to test in nature if Nuthatches modify their food hoarding behaviour in an attempt to minimize cache loss due to robbers (increasing both cache protection and travel distance to cache site), and
(3) to investigate whether or not the trade-off between food intake (i.e. fat deposits) and caching rate is actively managed in relation to the social context in which the Nuthatch forages.

MATERIAL AND METHODS

The field study was carried out with a population of Nuthatch inhabiting a 6 ha mixed forest of *Pinus*

sylvestris, *Castanea sativa*, *Acer* spp. and *Populus* sp. (El Ventorrillo, 1500 m above sea level, 40°45'N 04°01'W, Sierra de Guadarrama, Madrid) from October 1991 to January 1992. Birds were netted and colour banded before starting the field work for an accurate identification of each individual, thereby avoiding pseudoreplication.

We designed two different types of feeders (wooden boxes) differing in their accessibility to food. A "closed feeder" was made with one side (20x11 cm) covered by a 4.8 mm mesh plastic net allowing birds access to food (husked peanuts). This feeder type forced birds to handle peanuts through the plastic net in order to obtain small pieces of food (approx. 2-4 mm average diameter) for immediate consumption or caching. Feeders were suspended in pairs from pine branches ca. 50 cm below the canopy and 3 m above the ground, and spaced 0.5-0.75 m apart. This arrangement of closed feeders let the focal bird forage on one feeder while the other could be used by another bird. An "open feeder" was also designed, consisting of a wooden box with one side uncovered to allow Nuthatches to take food, mainly for caching (in few occasions Nuthatches carried a seed to a branch located 1-3 m around feeder for consumption). The open feeders were filled with unshelled sunflower seeds, and were erected on the tree trunk 3 m above the ground. "Closed feeders" were designed to study the decision made by the focal bird between eating at the foraging patch or caching; "open feeders" were used to study the caching behaviour of focal Nuthatches and the robbing pressure by other individuals.

Five feeding points were established in the study area, spaced 75-150 m apart. Prior to sampling, birds were allowed to familiarize themselves with feeders for two weeks. We assume, therefore, that all birds had experience of the two types of feeders. Data were recorded during the morning and central hours of the day (9:00 - 14:00 h GMT) to avoid the effect of circadian rhythms on hoarding and eating, and to record behaviour when caching intensity is higher (pers. obs., Waite & Grubb 1988, Lucas & Walter 1992).

Behaviour of Nuthatches at closed feeders was recorded at each feeding station for sampling peri-

ods of 40-60 minutes. Sampling began when one individual came into the feeder and began to pick the peanuts either to eat or to remove them for caching. For each focal individually marked bird we noted (1) whether it was solitary (no other bird in the same tree containing feeders) or with another bird within a radius of 1.5 m around the feeders (1.5 m was the distance at which birds actively responded to the presence of other individuals, pers. obs.), (2) whether the bird abandoned the feeder with a piece of peanut for caching, and (3) we timed, with the aid of a stopwatch with lap memories, how long the focal bird stayed on the feeders, as well as the time spent vigilant while foraging. Birds were considered to be vigilant when the tip of the beak was raised to eye level or higher (Lendrem 1983, Hogstad 1988).

Parus caeruleus, P. cristatus, P. ater, P. major and *Dendrocopos major* were the usual species forming mixed-species flocks with Nuthatch in our study area. Only records lasting more than 15 s were used for statistical analyses. The average flock size outside the feeding points was small and aggregations were in loose social units. A pair of individuals (including the focal Nuthatch) was the modal size of bird groups at feeding points (Carrascal & Moreno 1992).

At open feeders only caching events were recorded by following, without disturbance, the marked birds (sunflower seeds eaten in situ were anecdotal, and not considered in data analyses). When a Nuthatch made a cache we recorded: (1) the number of trees visited before caching, (2) total flying time from the feeder to the cache site, and (3) caching time, which results from the addition of the time spent on a tree looking for the cache site, plus the time spent preparing (partially shelling) and hiding the seed into a bark crevice, plus the time spent covering (usually with a piece of lichen or moss) the cache. All times were recorded with the aid of a stopwatch with lap memories. We also noted whether or not a caching Nuthatch was followed by another bird (conspecific or heterospecific), as well as the success of the follower in pilfering the seed after the Nuthatch left the cache site. Average distance flown by Nuthatches from the feeding point to the cache site was similar to that reported by Moreno *et al.* (1981), i.e. 25.5 m ($SD = 12.8, n = 10$).

The energetic balance of the caching of an average sun-flower seed was estimated considering both weight and caloric content of sunflower seeds (1941 J/seed; the fresh weight of a shelled seed is 0.076 g, $SD = 0.024$, $n = 20$; energy content obtained from Cummings & Wuycheck 1971), the cost of short flights between trunks (9.1 BMR-day; Carlson & Moreno 1992), the cost of activity on trunks (i.e. hopping, handling seeds and crevices; 2.3 BMR-day; Weathers *et al.* 1984, Bryant *et al.* 1985), and the time devoted to these two activities. The energetic balance of a caching event was calculated as the difference between the energy content of a sun-flower seed and the energy invested in hoarding (flying, searching for a cache site, preparing and hiding the seed), divided by the energy content of the seed (expressed in %).

Behavioural sample records at feeders obtained per individual were averaged for the 10 sedentary Nuthatches present in the study area. Two individually marked Nuthatches were never seen followed by another individual. Mann-Witney U-tests (two-tailed) were used for all comparisons. The relatively low number of persecution events recorded did not allow division of data into different social contexts (e.g. heterospecific, conspecifics). Nevertheless, marginal analyses with the pooled data (not distinguishing between marked Nuthatches) showed no statistically significant results when comparing the Nuthatch foraging with a conspecific versus with a subordinate species (the four *Parus* species; Carrascal & Moreno 1992).

RESULTS

Robbing rate and caching behaviour (Open feeders)

Along the study period, the number of followers pursuing a hoarding Nuthatch was at most one. The potential robber individual attempting the theft pursued the hoarder flying between trees directly to the immediate vicinity of the cache site,

Table 1. Mean ($\bar{x}$) and standard error (*se*) of caching time and flying time of individual Nuthatches followed and not followed by another individual (conspecific or heterospecific). Sample sizes (*n*, number of individuals) are different because two individual Nuthatches were never followed during observations. Total sample size for the 10 individually marked Nuthatches was 96 records when they were not followed, and 27 records when they were followed by another bird.

	Not followed			Followed		
	$\bar{x}$	*se*	*n*	$\bar{x}$	*se*	*n*
Caching time	66.4	5.4	10	77.9	13.3	8
Flying time	3.6	0.5	10	5.5	0.6	8

and hopping concealed in branches at 1-3 m of distance while the hoarding Nuthatch was trying to make the cache.

Persecution frequency of Nuthatches while caching was 24.1% (*s* = 14.1, 119 food caching events made by 10 individuals). In three of the 27 persecution events observed (11.1%) the follower (another Nuthatch, a Crested Tit, and a Great Spotted Woodpecker) stole the food cache made by the Nuthatch immediately. Robbery affected 2.5% of the 119 food caching events made by the 10 individual Nuthatches. Besides the loss of caches due to robbery, followers disturbed Nuthatches with their presence and provoked the loss of food items while they were being handled or hidden: Nuthatches lost the sunflower seed in 14.8% of the

times they were followed (*n* = 27), whereas this frequency was 3.7% when they hoarded solitary ($\chi^2_1 = 4.21, P = 0.040, n = 92$). Total losses of food caches due to disturbance or robbery reached up to 25.9% of the times Nuthatches were persecuted, and 5.9% of all hoarding events observed (percentages obtained with the pooled sample for the 10 individual Nuthatches). Therefore, the presence of another individual while Nuthatches were hoarding affected the efficiency of caching.

Total caching time of food items did not differ between caching solitary or caching followed by another individual ($Z = 0.22$, $P = 0.82$; Table 1). Nevertheless, when followed while hoarding, Nuthatches spent more time flying looking for a cache tree than when they hoarded solitary ($Z = 2.18$, $P = 0.029$; Table 1).

An estimation of the energetic balance of caching an average sun-flower seed (conversion of foraging time in energy without including the future probability of loss), showed that the instantaneous energy intake of a caching event was a 96% when Nuthatches were not followed, and 95% when they were followed by another individual. Therefore, the increase in time spent flying did not seem to markedly affect caching efficiency (the action of getting and storing a seed).

Immediate consumption versus caching (Closed feeders)

When Nuthatches visited the feeders solitary they left them with a piece of peanut more often than when they foraged at feeders with another bird

Table 2. Caching frequency (% of times each individual Nuthatch abandoned the box feeder with a piece of peanut for caching), time spent at feeders, and vigilance rate when Nuthatches were feeding solitary or in the presence of another individual at box-feeders covered with a mesh plastic net. Acronyms as in Table 1. Total sample size for the 10 individually marked Nuthatches was 149 records when solitary, and 64 with another bird at the feeding point.

	Solitary			With another bird		
	$\bar{x}$	*se*	*n*	$\bar{x}$	*se*	*n*
Caching frequency (%)	44.3	3.8	10	25.2	5.5	10
Time spent at feeder (seg)	36.7	3.7	10	66.9	8.6	10
Vigilance rate (seg/min)	16.1	1.2	10	8.8	1.5	10

$(Z = 2.50, P = 0.013)$. Time at feeders did not significantly differ when birds left with or without food for caching: 30 s (3.5) versus 43 s (5.7) respectively (standard errors in brackets; $Z = 1.55$, $P = 0.121$; test performed with data of birds feeding solitary see Table 2).

Time feeding at boxes was significantly longer when Nuthatches were foraging with other birds than when they were alone in feeding sites ($Z = 2.76, P = 0.006$). The vigilance proportion (seconds vigilant per minute feeding on feeders) was higher when Nuthatches were feeding solitary than when another individual of the same or another species was present ($Z = 2.84$, $P = 0.005$; Table 2).

DISCUSSION

Cache defence against followers

Under the natural conditions of this study, followers were perceived as sources of potential cache loss by Nuthatches, due to the high persecution pressure and the immediate losses suffered by robbing or distraction (e.g., Waite 1992 and Zamora et al. 1992 for other social and foraging contexts). This kleptoparasitic interaction between members of natural flocks (monospecific or heterospecific) is also common in free-ranging passerines (see review by Brockmann & Barnard 1979).

To increase travel time while foraging has the associated foraging cost of increased energy expenditure. The relative cost of increasing travel time could be different for the hoarder and the follower. The relative cost for a follower would be very high, as it would fly farther behind the hoarder with a low success of immediate pilfering the food cache (11%; see Results). The lengthening in travel time observed in the Nuthatch might, therefore, represent a discouraging behaviour of persecution pressure (see Waite 1992 and Zamora et al. 1992 for similar results in hoarding-cheating and area-copying interactions). Moreover, the observation of other individuals hoarding, without immediate pilfering of their caches, does not provide future benefit to the observer, as potential cheaters have a low recovery rate for caches made by another (Vander Wall 1982, Baker et al. 1988, 1990). Due to the high energetic content of a sunflower seed, the relative energetic cost of lengthening travel time per seed cached was very low, causing only a slight decrease (1%; see Results) in the potential profitability of the caches (if retrieved).

Time devoted to cache site selection and cache preparation did not increase in the presence of a potential robber when a potential robber is present. This suggests that cache site selection and preparation are not associated with the expectancy of future survival of stored food. If cache loss due to pilferers in the subsequent days after hoarding is very high relative to immediate robbing (compare results in Sherry et al. 1982 and Brodin 1992 with our data of 11% of immediate pilfering), hoarding individuals should always cache food items with the same investment in security.

Trade-off between generating internal and external reserves

Hurly's (1992) model on hoarding decisions assumes that hoards represent a form of alternative external energetic reserves equivalent to internal fat reserves, which implies that hoards and fat reserves can be actively managed (McNamara et al. 1990). Hurly's results demonstrated that such management is indeed dynamic, and dependent on the predictability of the food source. Lucas & Walter (1991) suggested that, for a survival-rate maximizer, fat levels and caching decisions are not associated in a linear way, because hoarding increases foraging time and reduces time available for alternative behaviours. Other trade-offs between eating and hoarding have been found considering handling cost of food items (Woodrey 1990, Jacobs 1992), environmental factors, and time of the day (see review by Vander Wall 1990).

If foraging strategies tend to maximize survival of the individual (McNamara & Houston 1986), we would expect such strategies to take into account the presence of potential robbers in the surroundings while hoarding. Nuthatches hoarded less and spent more time feeding in the presence of another bird. Therefore, policies of acquiring fat deposits may have evolved as a response to the possibility of

cache loss due to robbers. If hoarders devote their foraging time to eat, they develop a short-term control of energy reserves, securing energy (in the form of fat deposits) for periods of food shortage or increased energy requirements. Blem (1990) pointed out that the surplus energy stored as fat reserves may be enough for small birds to survive as much as 4 days of typical winter weather. Solitary Nuthatches would tend to increase external reserves, whereas in the presence of another bird, Nuthatches would tend to increase internal ones. In the presence of potential cache robbers Nuthatches foraged safer, as potential pilferers acted as early warners of predation attacks, and shared vigilance time (Carrascal & Moreno 1992; see also Metcalfe 1984). In addition, Nuthatches benefited by conversion of vigilance time into feeding time. Therefore, the disadvantage of social foraging that causes a reduction of optimal larder size is balanced by obtaining secure internal reserves under safer conditions.

The results of this study show how the presence of other individuals has an important effect in determining the caching behaviour in a scatter-hoarder species, and the way energy reserves (external reserves versus fat deposits) are generated. The presence of potential robbers decreased cached intensity and success, but enhanced feeding under safer conditions. Social influence on hoarding behaviour should receive more attention in order to explain the caching behaviour of wild populations that usually interact with other flock members, and to show the relative importance of robbery for the understanding of the adaptiveness of hoarding.

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SAMENVATTING

De auteurs bestudeerden het 'hamster'-gedrag van de (Europese) Boomklever in het veld gedurende de winter. Zij onderzochten of de keuze tussen het verbergen van voedsel ('hamsteren' i.e. aanleg externe reserves) en onmiddellijke consumptie (interne reserve, opvetten) samenhangt met de omstandigheid dat de Boomklever alleen fourageert of in een groep.

Het voedsel (pinda's en zonnepitten) werd aangeboden op enkele vaste voederplekken. Als de vogel in zijn eentje de voederplaats verliet, besteedde hij evenveel tijd aan het verstoppen van voedsel als wanneer hij door andere vogels werd gevolgd. Maar in het eerste geval vlogen ze minder lang (Tabel 1) en werden ze minder dikwijls verstoord en beroofd. Vogels die de voedselplaats in hun eentje bezochten, 'hamsterden' vaker dan Boomklevers die samen met soortgenoten of andere vogelsoorten aanwezig waren. Daar stond tegenover dat Boomklevers in een groep meer tijd konden besteden aan foerageren en minder tijd aan waakzaam zijn kwijt waren.

Uit deze studie in het veld blijkt dat de Boomklever de aanwezigheid van een andere vogel ervaarde als een bron van mogelijk verlies van het verborgen voedsel. In een groep neigen Boomklevers ertoe de interne reserve (vet aanleg) te verhogen en profijt te trekken van de waakzaamheid van potentiële belagers, immers tijd voor waken tegen gevaar ('scannning') kan worden besteed aan foerageren.

Als ze alleen zijn, maximaliseren Boomklevers hun externe reserves door te 'hamsteren'. De onderzoekers concluderen dat de manier waarop energie reserves worden aangelegd afhankelijk is van de sociale context waarin het individu zich bevindt.- HdN/JvR