HOARDING NUTHATCHES SPEND MORE TIME HIDING A HUSKED SEED THAN AN UNHUSKED SEED

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ABSTRACT We examine how time investment in handling food items of similar energy content affects hoarding behaviour of wild Nuthatches *Sitta europaea* during autumn-winter in Central Spain. We test the possibility that Nuthatches invest more time caching husked than unhusked seeds as they will obtain a benefit from the lower expenditure of energy and time during future consumption of prepared caches. Sunflower seeds were husked in most of the observed caches (71.5%). In the study population individuals devoted over 27% of their hoarding time to handling the seed (removing the sunflower shell), which means an important proportion of the time budget of hoarding Nuthatches. Hiding time, and time and distance flying from feeders to cache sites were longer when Nuthatches hoarded husked than unhusked seeds. These results are consistent with the prediction that more valuable items will be spaced more widely together with more securely.

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INTRODUCTION

For scatter hoarding to be a stable strategy there must exist mechanisms leading to the avoidance of extensive loss of caches to pilferers, thereby increasing the hoarder's rate of cache retrieval (Andersson & Krebs 1978, Roberts 1979). Many hoarding bird species cover their caches with vegetation, which improves the probability that caches will be recoverable because they have not been pilfered (Bossema 1979, James & Verbeek 1983, Källander & Smith 1990). Spacing stored food items has also been shown to safeguard caches, as it reduces the probability that a robber which finds one cache by chance will find additional caches by conducting an area-restricted search (reviews by Vander Wall & Smith 1987, Källander & Smith 1990, Vander Wall 1990). Hiding and spacing food items are, however, energy and time consuming behaviours. Therefore, a hoarder's decision about how much to invest in these activities should take into account the energy value of caches. Waite & Reeve (1993) demonstrated in a field experiment that Gray Jays *Perisoreus canadensis* spaced large caches (*i.e.*, with higher energy content) more widely than small ones, a strategy that would tend to yield a high rate of storage of recoverable food energy over a long term. Nevertheless, little is known about how the relative value of food items determined by time investment in cache preparation (*e.g.*, for husking, placing seeds into crevices, reducing cache loss to decomposers, etc.) affects spacing of caches.

The Nuthatch *Sitta europaea* frequently hoards food and maintains year-round territories (Cramp & Perrins 1993). During autumn they store seeds that are used during the subsequent winter, thus enhancing the nutritional status of birds (Källander 1993, Nilsson *et al.* 1993). Although little is known about losses of caches to pilferers, Carrascal & Moreno (1993) have shown that Nuthatches apparently perceive other individuals (mainly conspecifics and tits) as sources of potential cache loss while hoarding, as indicated by adjustments in their hoarding behaviour

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when hoarding in the presence of other individuals. Nuthatches often husk seeds (*e.g.*, acorns, hazelnuts and beechnuts) before caching them, although the frequency of husking depends on seed size and features of the cache site (Cramp & Perrins 1993, Källander 1993). Here we examine how different amounts of handling food items of similar energy content (sunflower seeds) affects caching behaviour (time devoted to concealment and transport distance from food source) in wild birds during autumn and winter. By husking the seeds, birds incur a handling cost at the time of caching (Woodrey 1990), but obtain a benefit from the lower expenditure of energy and time during future consumption of prepared caches. The preference for husked seeds should cause an increase in the rate of pilferage, which will reduce the value of the cache. Consequently, Nuthatches should invest more time hiding husked than unhusked seeds and store them farther from the food source (*i.e.*, at lower densities).

MATERIAL AND METHODS

We conducted field work on 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) during November 1991 - January 1992 and November 1993 - January 1994. The length of the day during the study period was 8-10 hours. Ambient temperature during observations ranged between 0 and 15 °C. Birds were netted and colour-ringed before starting the field work for individual identification. We observed hoarding behaviour of eight individuals during the first study period and other six individuals during the second (n = 14 different individuals). All individuals occupied autumn-winter territories (1-2 ha) during the study period.

We used wooden boxes (20x11x11 cm) with one open side as feeders to study the caching behaviour of focal Nuthatches. These feeders were mounted on tree trunks 2 m above the ground and filled with unhusked sunflower seeds. Five feeding points spaced 75-150 m apart were permanently established (*i.e. ad libitum* food offer) during each study period. Nuthatches made an extensive use of feeders, hoarding an average of 132 seeds/day (SE = 13.7, n = 14; Carrascal *et al.* 1994).

Prior to sampling, birds were allowed to familiarize themselves with feeders for 2 weeks. We assume, therefore, that all birds had experienced feeders. Behaviour of Nuthatches was recorded only from 10:00 to 14:00 h GMT to avoid any possible effects of circadian rhythms on hoarding behaviour, and to record behaviour when caching intensity is higher (Löhrl 1958). Records for each individual were obtained during a sampling period no longer than one week. Caching events were recorded by following the marked birds without disturbing them (the amount of sunflower seeds eaten *in situ* were negligible, and were excluded from data analyses). When a Nuthatch made a cache we recorded: (1) flying time from the feeder to the cache site, (2) estimated distance from the feeder to the cache site, (3) time spent husking the seed (usually by wedging the seed into a bark furrow and hammering it with 10-15 blows), and (4) time spent hiding the seed (time spent on a tree looking for a cache site, time spent wedging the seed into a bark crevice, and time spent covering the seed, usually with a piece of lichen or moss). All times were determined with a stopwatch with lap memories. Data for each seed were grouped depending on whether or not the seed was husked by the Nuthatch.

For each individual sampled, records of husked as well as unhusked seeds were obtained during each sampling day. Average time in which seeds were cached did not differ between husked and unhusked (husked seeds: 12.25 h GMT, SE = 0.08, n = 200; unhusked seeds: 12.29 h GMT, SE = 0.09, n = 80; $F_{1,278} = 0.01$ in a tentative ANOVA test incurring in pseudoreplication). Time of day was not either correlated with any of the dependent variables (hiding time: $R^2 = 0.057$; flying time: $R^2 = 0.026$; flying distance: $R^2 = 0.047$).

The number of hoarding events ranged from 11 to 32 per individual Nuthatch ($\bar{X}$= 20, n = 14). Wilcoxon matched-pairs ranks tests were used for all comparisons.

RESULTS

Seeds were almost always taken singly (1.1 seeds per visit to feeders, SE = 0.03, n = 14). On average, Nuthatches husked 71.5% of the seeds they stored (SE = 5.3, n = 14). Average time invested on husking seeds was 31 seconds (Table 1).

When Nuthatches husked sunflower seeds they spent significantly more time flying to cache trees than when they hoarded unhusked seeds (Table 1). Accordingly, husked seeds were cached at significantly greater distances than unhusked seeds. Hiding time was significantly longer when Nuthatches hoarded husked than unhusked seeds. When husking occurred during a caching event, 32% of the time spent on that caching event was devoted to husking the seed. Considering the average time invested in husking seeds, the percentage of seeds that were husked, and the data in Table 1, the study population of Nuthatches devoted 27.7% of its hoarding time to handling sunflower seeds (*i.e.*, preparation of the seed by removing the shell).

DISCUSSION

Time spent handling sunflower seeds to remove the shell prior to storage had a considerable impact on the time budget of hoarding Nuthatches. The value of removing shells from the seeds may be related to a lower expenditure of energy and time during future consumption of prepared caches when energy requirements may be high (*e.g.*, increasing fat reserves late in the day before night, and avoiding the risk of starvation early in the morning; Carrascal *et al.* 1994). Thus, preparing a food cache for the occasion when food requirements are high may enhance the value of hoarding. If the relative value of food caches is influenced by the behaviour of the hoarder (cache preparation removing the shell), and this behaviour is adaptive, the hoarder should increase the probability of cache retrieval.

According to this, our results show longer hiding times for husked than for unhusked seeds. The greater the time investment in securing the cache (inserting it into a deep crevice and covering it with a tuft of moss, lichen or dead wood), the lower the probability of it being pilfered (Bossema 1979, James & Verbeek 1983). Another way of increasing the probability of cache retrieval may be to space the caches widely. According to the model of optimal cache dispersion (Vander Wall 1990, and references therein), closely-spaced caches suffer higher rates of pilfering than widely-spaced caches. Our results are consistent with the

Table 1. Mean of 14 individual Nuthatch means ($\bar{x}$) and standard error (SE) of husking time, hiding time, flying time, and flying distance from feeder to cache site for nuthatches hoarding sunflower seeds that they either husked or did not husk. Results of Wilcoxon matched-pairs signed-ranks tests are shown.

	Unhusked seeds		Husked seeds			Wilcoxon test	
	$\bar{x}$	SE	$\bar{x}$	SE	N	Z	P
Husking time (s)	-	-	31.0	3.2	14		
Hiding time (s)	34.4	4.5	61.1	8.4	14	2.92	0.004
Flying time (s)	2.9	0.3	4.8	0.5	14	2.98	0.003
Flying distance (m)	15.0	1.5	32.5	4.1	14	2.92	0.004

prediction that more valuable items will be spaced more widely (Waite & Reeve 1993), as husked seeds were stored further than unhusked seeds from the feeders. The increase in distance from the feeder of husked seeds probably increase their survival, as demonstrated by Brodin (1993) for the Willow Tit *Parus montanus* in a similar study.

From our results an obvious question emerges: if Nuthatches invest considerably in husked seeds (relative to unhusked seeds), why do they invest such time in husk removal before seeds are stored? It makes much more sense to pay the price of seed husking only after retrieving the cached (unhusked) seed. In this way, Nuthatches can completely avoid the problem of having high-investment caches pilfered by other birds. (In fact, the allocation of time to husking sunflower seeds in this study contrasts with data obtained by Moreno *et al.* (1981, and J. Moreno pers. comm.) in Southern Sweden using similar methods, where 94% of the sunflower seeds stored by Nuthatches were unhusked.) The most probable explanation for this paradox is that in our study area, where winter temperatures are relatively high (see above) and the period of snow cover is reduced to a few days in the whole winter, Nuthatches behave as short-term hoarders. Hoards likely represent easily accessible food sources to be used mostly during the course of the day when energy demands are higher (before roosting and/or early in the morning). In milder areas with relative long days may be more affordable to enhance cache retrieval by increasing the relative value of the cache (larder quality) than by increasing the amount of items cached (larder quality).

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SAMENVATTING

In Centraal-Spanje werd van een populatie Boomklevers met kleurringen het voedselverstopgedrag gedurende de herfst en winter bestudeerd. Boomklevers bleken verschillend om te gaan met gepelde en ongepelde zaden, in deze studie vooral zaden van zonnebloem. Als hypothese werd gesteld dat meer tijd gespendeerd zou worden in het verstoppen van gepelde zaden dan in het verstoppen van ongepelde zaden, omdat 's winters energie kan worden bespaard doordat de ongepelde zaden onmiddellijk kunnen worden gegeten.

De Boomklevers bleken bij de voedertafel een aanzienlijk deel van hun tijd te spenderen aan het openhakken van de zonnepitten. Ook werd meer aandacht besteed aan het verstoppen van de opengebroken zaden: de vogels waren langer afwezig na het openbreken van een zonnepit en er werd een grotere afstand afgelegd dan bij een ongepelde zonnepit. Dit bevestigt inderdaad de theorie dat waardevol voedsel beter en verder weg wordt verstopt, en er dus meer tijd aan wordt besteed, dan aan minder waardevol voedsel.

GOK