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ECONOMICS OF CACHING VERSUS IMMEDIATE CONSUMPTION BY WHITE-BREASTED NUTHATCHES: THE EFFECT OF HANDLING TIME[1]

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Abstract. The effects of handling time on the caching behavior of White-breasted Nuthatches (*Sitta carolinensis*) were studied in deciduous woods in central Ohio during the winters of 1987–1988 and 1988–1989. I asked whether White-breasted Nuthatches differed in their treatment of food items with different handling times. During four alternating hour-long time intervals, free-ranging nuthatches were offered sunflower seeds (*Helianthus* sp.) either with the shell removed or with the shell intact. Handling time was significantly shorter for the seeds with the shell removed. Male and female nuthatches cached a significantly greater proportion of seeds with the shell removed. Whereas males took significantly more seeds with the shell removed than seed with the shells intact, females took a significantly greater number of seeds of both types than did males. Female nuthatches transported seeds with the shells removed significantly farther to their cache sites than did male nuthatches. These results suggest that handling time is an important factor used by White-breasted Nuthatches in their decision to cache or immediately consume a food item. Differences between the males and females may be related to interference competition by the socially dominant males. Female nuthatches appear to behave in a manner which compensates for this foraging disadvantage.

Key words: Caching; consumption; handling time; hoarding; sex-specific foraging; Sitta carolinensis; *White-breasted Nuthatch.*

INTRODUCTION

Animals that cache food confront many foraging-related decisions during their daily activities, one of which is whether or not to cache or to consume immediately any particular food item. Factors that may affect this decision include the need to minimize (1) the energetic costs of caching and (2) the cache loss to competitors (Jacobs 1987).

There are several factors which may affect the costs and benefits of caching, including (1) the energetic content of the food item, (2) the time and energy spent handling the food item, (3) the time and energy spent transporting the food item to the cache site, and (4) the time and energy spent relocating cached food. The time and energy spent transporting the food item to the cache site may be indexed by determining the handling time and the transportation distance for a food item.

In the deciduous forests of North America, White-breasted Nuthatches (*Sitta carolinensis*) forage in mated pairs (Grubb 1982) and maintain year-round territories (pers. observ.). During the nonbreeding season, male nuthatches are socially dominant to conspecific females (Waite 1987). Previous studies have shown that White-breasted Nuthatches scatterhoard surplus food intensively (Waite and Grubb 1988a).

If one of the functions of caching by nuthatches is to minimize the risk of procuring inadequate energy for the coming night, then when a nuthatch encounters surplus food items with a high energy content and low handling time (i.e., high net benefit), the bird should cache a high proportion of such items for use later in the day. However, if food items have a long handling time, their net benefit is lower and the proportion of such items cached rather than consumed should be low. Sunflower (*Helianthus* sp.) seeds with shells require a considerably longer handling time before being consumed by a nuthatch than those lacking shells. I examined whether caching by White-breasted Nuthatches is a function of food-handling time and energy. Specifically, I tested the prediction that nuthatches would cache a considerably smaller proportion of sunflower seeds with shells than seeds without shells.

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METHODS

This study was conducted during the winters (December–March) of 1987–1988 and 1988–1989 in 10 woodlots in Morrow County, Ohio (40°20′N, 82°50′W), located about 50 km northeast of Columbus. The area consists of large tracts of farmland interspersed with small deciduous woodlots (15–20 ha).

I tested six male and six female color-marked free-ranging White-breasted Nuthatches in eight woodlots. Each bird was a member of the socially dominant pair of nuthatches using a particular feeding site but none of the birds were from the same pair. I tested only the alpha birds to control for between-pair dominance effects on caching (Woodrey, unpubl.). Each nuthatch was offered an ad libitum supply of either sunflower seeds without or with the shells intact during four alternating hour-long sessions. I removed the shells from the sunflower seeds by hand. I controlled for the effects of caloric value by using the same type of sunflower seed for both treatments, the only difference being that one group had the shell removed while in the second group the shell was left intact. Another incidental control was provided by the birds themselves. When a nuthatch would remove the shell from a seed, the bird would discard the shell fragments and eat only the embryo of the sunflower seed. I randomized the order of presentation such that both treatments (with and without shells) were presented first an equal number of times. To avoid the confounding factor of diurnal caching rhythms in White-breasted Nuthatches (Waite and Grubb 1988a), I conducted this experiment from 07:00 to 11:00.

Nuthatches were observed from a blind 15 to 20 m from a feeder where the birds were offered seeds. The blind allowed for sufficient movement of the observer inside to observe all outcomes of seeds removed from the feeders. Data collected for each visit by a nuthatch to the feeder included the identity and sex of the bird, the treatment (seed with or without a shell), the handling time and the fate of the seed taken (i.e., cached or consumed), and the transportation distance for each item taken. I defined handling time as the interval between the time when a nuthatch picked up a seed from the feeder until the time when the bird either cached or consumed the seed. I also recorded the outcome of all intraspecific dominance interactions to determine the position of each nuthatch in the dominance hierarchy at each feeding site.

To eliminate sex differences in caching behavior, I analyzed records separately for males and females using two-tailed Wilcoxon's matched pairs signed rank tests (Hollander and Wolfe 1973). Significance was set at $P < 0.05$.

RESULTS

TREATMENT EFFECTS

Handling time for seeds without shells was significantly shorter for both males ($Z = 2.08$, $P = 0.0051$; Table 1) and females ($Z = 2.08$, $P = 0.0051$; Table 1). Both male ($Z = 2.84$, $P = 0.0045$) and female ($Z = 2.83$, $P = 0.0047$) nuthatches cached a significantly higher proportion of sunflower seeds without shells than with shells (Table 1). Whereas males took significantly more seeds without shells per hour than seeds with shells ($Z = 2.17$, $P = 0.029$), females removed equal numbers of the two types of seed ($Z = 1.05$, $P = 0.293$; Table 1). Neither males ($Z = 1.37$, $P = 0.17$) nor females ($Z = 0.57$, $P = 0.57$) showed any difference in the distance that they transported seeds with or without shells before consuming or caching them (Table 1).

SEX DIFFERENCES

While male and female nuthatches did not differ in handling time of sunflower seeds without shells ($Z = 1.53$, $P = 0.12$), handling time for seeds with shells was significantly shorter for females ($Z = -2.08$, $P = 0.04$; Table 1). Female nuthatches took significantly more seeds per hour than did males, regardless of whether the shell had been removed ($Z = 2.80$, $P = 0.005$) or was still intact ($Z = 2.81$, $P = 0.004$; Table 1). Females transported seeds without shells a significantly greater distance than did males ($Z = 2.49$, $P = 0.01$), but for seeds with shells, males and females showed no difference in transportation distance ($Z = 0.73$, $P = 0.47$; Table 1).

DISCUSSION

TREATMENT EFFECTS

The difference in behavior towards the different types of seeds may be understood in terms of a food item's net energy benefit to the individual nuthatch. When taking a seed with the shell intact, a bird would transport the item to a tree and proceed to remove completely the shell from

TABLE 1. Means ± standard errors for handling time, proportion of seeds cached, number of seeds taken/hour and distance transported by White-breasted Nuthatches for sunflower seeds with and without shells.

	Males		Females	
	Shelled seeds (n = 82)	Unshelled seeds (n = 48)	Shelled seeds (n = 138)	Unshelled seeds (n = 132)
Handling time (sec)	22.0 ± 1.4	52.0 ± 2.9	27.0 ± 3.3	44.0 ± 1.7
Proportion of seeds cached	0.96 ± 0.02	0.06 ± 0.03	0.95 ± 0.02	0.07 ± 0.03
Number of seeds taken/hr	12.7 ± 0.9	8.5 ± 1.1	22.2 ± 1.5	19.8 ± 1.6
Distance transported (m)	15.0 ± 1.4	21.0 ± 0.9	21.0 ± 0.8	20.0 ± 0.9

the seed. Such a procedure involved a significant investment of time and energy (Table 1). By caching the item after removing the shell, the bird would incur the risk of losing the cached item and its energy to a competitor. The cost of cache loss includes the time and energy lost while shelling the seed, the time and energy lost while caching, and the energetic content of the food item. If, however, the nuthatch consumed the remaining portion of the seed, that individual would recoup at least some of the energy spent shelling the sunflower seed. By immediately eating items with long handling times, the nuthatches may maximize the net benefit from sunflower seeds with shells.

White-breasted Nuthatches cached rather than consumed sunflower seeds from which I had removed the shell (Table 1). Because the birds invested no time and energy in shelling, the only potential cost associated with caching such sunflower seeds with the shell removed was transportation time or the possible energy loss if the cache were pilfered by a competitor. Thus, nuthatches may maximize the net benefit of sunflower seeds with the shell removed by eating very few and caching the rest.

An alternative explanation for the observed behavior is that nuthatches may want to get the valuable, shelled seeds away from the feeding tray and to a protected cache site as soon as possible. They may be more willing to leave behind on the tray seeds with shells than those without, while they spent time to shell and eat seeds. Data concerning seed loss would be critical in evaluating this hypothesis.

In a similar study, Jacobs (1987) found that gray squirrel caching behavior was affected by handling and travel time. Jacobs (1987) also showed that gray squirrels preferred to cache seeds from a source closer to the cache site. These results indicated that a squirrel's decision to cache was based on the rule "eat the best and cache the rest."

The disparity between my study and that of Jacobs (1987) may relate to differences in the social systems of White-breasted Nuthatches and gray squirrels. Gray squirrels scatter caches over their home range, which overlaps with those of other individuals (Thompson 1978), suggesting that intraspecific food competition may be high. White-breasted Nuthatches forage in mated pairs (Grubb 1982) and defend year-round territories against conspecifics. Therefore, birds of a pair probably do not experience high levels of competition from other nuthatches at natural food sources. In my study, conspecifics from adjacent territories were only occasionally observed intruding and taking sunflower seeds from the feeder.

It is likely that nuthatches experience some level of cache pilferage from such other species in the bark-foraging guild as the Downy Woodpecker (*Picoides pubescens*), Tufted Titmouse (*Parus bicolor*), and Carolina Chickadee (*Parus carolinensis*). While all of these species certainly rob nuthatch caches, only the Downy Woodpecker is dominant to the White-breasted Nuthatch at a feeder (Waite and Grubb 1988b). Hence, most of the interspecific competition occurs after the nuthatches have decided to cache a food item. Because of fundamental differences in the two systems, and because the squirrel study was conducted in a confined, laboratory setting, direct comparisons may yield little insight into the effects of handling time on caching behavior in general.

Based on differences in handling times for the two types of sunflower seeds, one might expect a nuthatch to make more trips per hour when presented with seeds with the shells removed. This prediction held for males, but not for females, a disparity possibly related to the fact that

females transported seeds with the shells removed a greater distance than did the males or perhaps an artifact of the small number of nuthatches tested.

SEX DIFFERENCES

Female White-breasted Nuthatches handled seeds with the shell intact for a significantly shorter time than males (Table 1). This result may be due to the fact that, although the difference was not significant, females tended to transport seeds with shells a shorter distance than did males (Table 1).

Because female White-breasted Nuthatches are socially subordinate to males, a female's access to resources may be limited through interference competition from the male. The fact that female nuthatches took a significantly greater number of both types of seeds per hour than did males (Table 1) suggests that females took more items to offset the foraging disadvantage of interference competition by male nuthatches. Enoksson (1988) found that male European Nuthatches (*Sitta europaea*) in Sweden took more seeds per visit and spent a longer time at the feeder, while females collected more seeds per unit time spent at the feeder. She also concluded that social dominance by male nuthatches was the main cause of sex differences in nuthatch foraging.

Male White-breasted Nuthatches have been observed stealing food items recently cached by females (pers. observ.). By transporting sunflower seeds with the shells removed farther than males did, female nuthatches may have reduced their risk of kleptoparasitism by the male.

These data indicate that nuthatches do treat shelled and unshelled seeds differently. To distinguish between the alternative hypotheses explaining this behavior, one would need to know the relative importance of loss of cached seeds vs. loss of shelled seeds at the feeding tray. Further research addressing the relative importance of cache and seed loss should provide further insight into the factors that affect the caching behavior of animals.

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