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WINTER CACHING ECOLOGY OF DECIDUOUS WOODLAND BIRDS AND ADAPTATIONS FOR PROTECTION OF STORED FOOD[1]

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Abstract. We quantified cache-site selection by White-breasted Nuthatches (*Sitta carolinensis*), Tufted Titmice (*Parus bicolor*), and Black-capped (*P. atricapillus*) and Carolina (*P. carolinensis*) chickadees storing sunflower seeds in four deciduous woodlands during winter, 1983–1988. All species exhibited significant interpopulational variation in caching ecology. This may be related to, among other factors, differences in the floristic and physiognomic characteristics of vegetation on each site. Nuthatches, titmice, and chickadees each demonstrated a distinct pattern of seed storage that, in general, corresponded with published reports of foraging ecology. Those differences did not appear to be related to the need for protection of stored food from snow and ice cover, but rather for concealment from potential cache robbers. In protecting those cache sites, titmice and chickadees relied mainly upon inaccessibility by placing seeds on small branches and twigs, frequently in the outer portion of tree canopies. Nuthatches, on the other hand, used both difficult-to-reach (far under bark or deep in furrows) and cryptic (covered with bark or other material) locations to protect stored seeds. Disparity between parids and the nuthatch in caching ecology may be due to morphological differences and by the number of cache robbers likely to encounter each species' cache sites.

Key words: White-breasted Nuthatch; Sitta carolinensis; *Tufted Titmouse;* Parus bicolor; *Black-capped Chickadee;* P. atricapillus; *Carolina Chickadee;* P. carolinensis; *caching; winter.*

INTRODUCTION

Food-storing behavior of passerines has been examined in detail, especially aspects of spatial distribution (e.g., Cowie et al. 1981, Sherry et al. 1981, James and Verbeek 1985) and recovery (e.g., Tomback 1980, Sherry et al. 1981, Vander Wall 1982) of cached food in laboratory or controlled field situations. Relatively less detailed study has been made of the actual cache sites used by free-ranging populations and the factors that may affect cache-site selection. Given that stored food can potentially influence fitness of an individual (e.g., through improved reproductive success or through increased survival during periods of food shortage; Roberts 1979), ability to prevent cache loss is crucial to the evolution of food-storing behavior (Andersson and Krebs 1978, Smith and Reichman 1984). Vander Wall and Smith (1987) listed five sources of cache loss, three of which may be important to small passerines that store seeds during winter at northern latitudes: (1) cache robbers may steal food before an individual can relocate its stored food; (2) environmental factors, such as snow and ice, may prevent birds from retrieving their caches; and (3) an individual may lose a stored food item by forgetting its location.

Most studies of avian caching behavior have been conducted with parids in Europe and corvids in North America. Yet, food storing in winter bird assemblages in eastern North America is common and, surprisingly, no one to date has described in detail the caching ecology of many of those species. The purposes of this paper are to (1) describe quantitatively caching behavior of several winter populations of White-breasted Nuthatches (*Sitta carolinensis*), Tufted Titmice (*Parus bicolor*), and Black-capped (*P. atricapillus*) and Carolina (*P. carolinensis*) chickadees in Ohio and Arkansas, and (2) assess mechanisms by which those species protect stored seeds from potential cache robbers. Most parids and sittids are found in mixed-species flocks during winter, typically storing seeds in close proximity to other

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individuals. Consequently, we postulate that species should store food in locations that cannot be found easily by other flock members.

STUDY AREA AND METHODS

We observed caching behavior of nuthatches, titmice, and chickadees at four locations: (1) Darby Creek Metropolitan Park, Franklin County, Ohio (Darby); (2) Findley State Park, Lorain County, Ohio (Findley); (3) Kent State University campus, Portage County, Ohio (Kent); and (4) Lake Fayetteville Environmental Center, Washington County, Arkansas (Fayetteville). Each study area was part of a larger (>10 ha) woodland. White-breasted Nuthatches and Tufted Titmice were present on all study sites, but the species of chickadees differed between the two more northern sites (Black-capped Chickadee at Kent and Findley) and those to the south (Carolina Chickadee at Darby and Fayetteville). Because of the taxonomic, morphological, and ecological similarity between the two chickadee species, we grouped (a priori) both species together in some analyses. Birds were observed between 08:00 and 14:00 on 4–12 days during December–February 1983–1984 (Darby), 1985–1986 (Kent, Findley, and Fayetteville), and 1986–1988 (Fayetteville). We did not attempt to restrict weather conditions under which data were collected, but wind velocity was always low (Beaufort scale ≤ 2) and temperatures between $-4°$ and 15°C.

At each site, one 0.04-ha circular plot was randomly positioned (15–60 m from feeder) in each of four 90° arcs centered on the N, S, E, and W compass directions. All tree and shrub stems within each circle were identified to species and measured (diameter at breast height; dbh). This provided a measure of vegetation structure and composition on the four study areas.

We observed caching behavior within a 70-m radius (1.5 ha) circle centered on a single feeding station (1.5 m above ground on a pole) stocked with shelled ($\bar{x}$ length = 8.2 ± 1.7 mm SD; $\bar{x}$ maximum width = 4.4 ± 0.7 mm; n = 10) and unshelled ($\bar{x}$ length = 11.2 ± 0.7 mm; $\bar{x}$ = maximum width = 5.0 ± 0.3 mm; n = 10) sunflower (*Helianthus*) seeds (approximately 50% of each type). Rarely (<10% of observations for each species) did birds fly farther than 70 m when caching seeds and those observations were discarded from analyses. One to three observers positioned themselves at predetermined compass directions from the feeder, shifting their positions several times during each hour of observation. Because of the intense caching behavior exhibited by woodland birds (e.g., see Cowie et al. 1981), we could not monitor all birds at once, but rather randomly chose a focal individual when it flew to the feeder. For each case of food storage, we recorded 12 characteristics associated with the cache site: (1) distance from feeder; (2) substrate—substrate on which seed was cached (tree species, dead branch on ground, or grape vine); (3) height; (4) microsubstrate—if on tree, twig (≤1 cm diameter at cache site), branch (>1 cm at cache site), or trunk; (5) diameter of microsubstrate at cache site—≤1.0, >1.0–2.5, >2.5–8.0, >8.0–15.0, >15.0–23.0, >23.0–38.0, >38.0–53.0, or >53.0 cm; (6) horizontal position—inner 33%, middle 33%, or outer 33% of tree canopy; (7) tree diameter—diameter at breast height (same categories as [5]); (8) cache location—(a) furrow, crack, or rotted area; (b) under bark; (c) end of broken branch or in a bud; (d) between two branches; (e) leaf on tree; (f) other; (9) side of branch—top (25%), side (50%), or bottom (25%); (10) direction on tree trunk—if cached on trunk, the compass direction at the site of seed storage; (11) cover—whether an individual covered the cache with bark, lichens, snow, leaves, or other materials; and (12) shell—whether the seed was shelled or unshelled when cached. Variables (9) and (10) were not compared across populations because of small sample sizes at some locations. Instead, those two variables were used only in assessing nonrandom placement of seeds. Binoculars (7 × 42) were used to obtain details of cache sites.

Differences among populations and among species were assessed with log-likelihood ratio (G) tests for categorical variables and with one-way analysis of variance (ANOVA) for continuous data. Probability levels ≤0.05 indicated significant differences.

Because we dealt with small populations of unmarked individuals, we were compelled to record multiple observations for each individual and treat them as independent samples. If those observations are statistically dependent, however, then pseudoreplication has occurred and our reported α-levels are tenuous (Hurlbert 1984). However, in this study, we believe that multiple samples per individual were not necessarily correlated because, for every cache, birds flew back to the original point source of food to gather another seed. Thus, with each trip, birds initiated

TABLE 1. Characteristics of vegetation structure for each of the four deciduous woodlands in Ohio and Arkansas where caching behavior was observed.

	Site							
	Darby		Findley		Kent		Fayetteville	
Vegetation characteristic	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Stems/ha	4,800	934	8,119	2,138	5,606	1,493	4,050	679
Basal area (m^2)/ha	45	7	38	10	50	20	50	25
Canopy height (m)	19	2	13	1	19	2	23	1

a new caching bout, and there was no obvious constraint placed on birds due to their previous caching location. Limited observations on several color-marked titmice revealed no apparent dependence among cache sites chosen on 20–30 consecutive caching bouts.

RESULTS

COMPARISON OF VEGETATION ON STUDY SITES

All study sites were located in deciduous woodlands with canopies 13–23 m tall and well-developed understories (many saplings with trunks <2.5 cm dbh), but tree size class distributions and tree species composition varied among locations (Table 1, Fig. 1). Kent and Fayetteville were dominated by large (>38 cm dbh) trees, whereas Darby and Findley had a better representation of medium-sized (8–38 cm) trees.

When tree species composition was considered, even more striking site-specific differences became evident. On all sites stem densities were dominated by a miscellaneous collection of understory shrubs and saplings, and each area was unique in tree species composition when measured by basal area. Red (*Quercus rubra*) and white (*Q. alba*) oaks were the dominant canopy species at Fayetteville, while white oak and, to a lesser extent, red oak and white ash (*Fraxinus americana*) were well represented at Kent. (For this and all subsequent analyses, the "red oak" group may contain not only *Q. rubra,* but also a small [<5%] proportion each of post [*Q. stellata*], pin [*Q. palustris*], and black [*Q. velutina*] oaks.) Together, shagbark hickory (*Carya ovata*) and white ash comprised >60% of the basal area at Findley, while these same species, along with black walnut (*Juglans nigra*), were dominant overstory trees at Darby.

GENERAL CACHING ECOLOGY

We recorded 1,215 instances of caching by White-breasted Nuthatches (n = 403), Tufted Titmice (n = 300), and chickadees (n = 512). Most (60%) observations were collected at Fayetteville, while the remainder were approximately equally distributed among Darby (15%), Findley (13%), and Kent (12%). Numbers of caching observations (with sample sizes in parentheses) for each species (White-breasted Nuthatches, Tufted Titmice, and chickadees, respectively) at each location were: Darby (77, 83, 11), Findley (22, 23, 120), Kent (41, 36, 75), and Fayetteville (263, 158, 306). On all days at all feeders there were two to four nuthatches, two to six titmice, and four to eight chickadees. Figures 2–4 and Tables 2 and 3 summarize the caching ecology of nuthatches, titmice, and chickadees.

White-breasted Nuthatch. Nuthatches cached most seeds within 30 m of the feeding station ($\bar{x}$ = 20.3 ± 14.4 m SD). Seeds were always taken singly and, if not already shelled, usually wedged into a bark furrow on a tree trunk and hammered open with three to four blows. The entire seed then was carried to a large-diametered (usually >8 cm) trunk (69%) or branch (30%) and wedged under bark or in a furrow or crack in the bark. The seed was covered in about 50% of the observed caches with bark/rotted wood (81%), lichens (15%), snow (3%), or moss (1%). Cache sites averaged 8.0 (±5.6) m above ground, although height varied from 1 to 23 m. Large (>23 cm dbh) white, red, and post oaks comprised >75% of the substrates upon which seeds were stored. Nuthatches cached seeds on bottoms of branches more than would be expected by chance, but they used compass aspects on tree trunks randomly.

Tufted Titmouse. Titmice stored most seeds within 40 m of the feeding station ($\bar{x}$ = 27.3 ± 17.5 m). Only one seed was taken per trip and it was usually shelled before being stored (80% of the cases). When shelling seeds, titmice flew to a 1- to 2.5-cm branch, typically <20 m from the feeder, and placed the seed between both feet. After cracking open the shell with several strikes

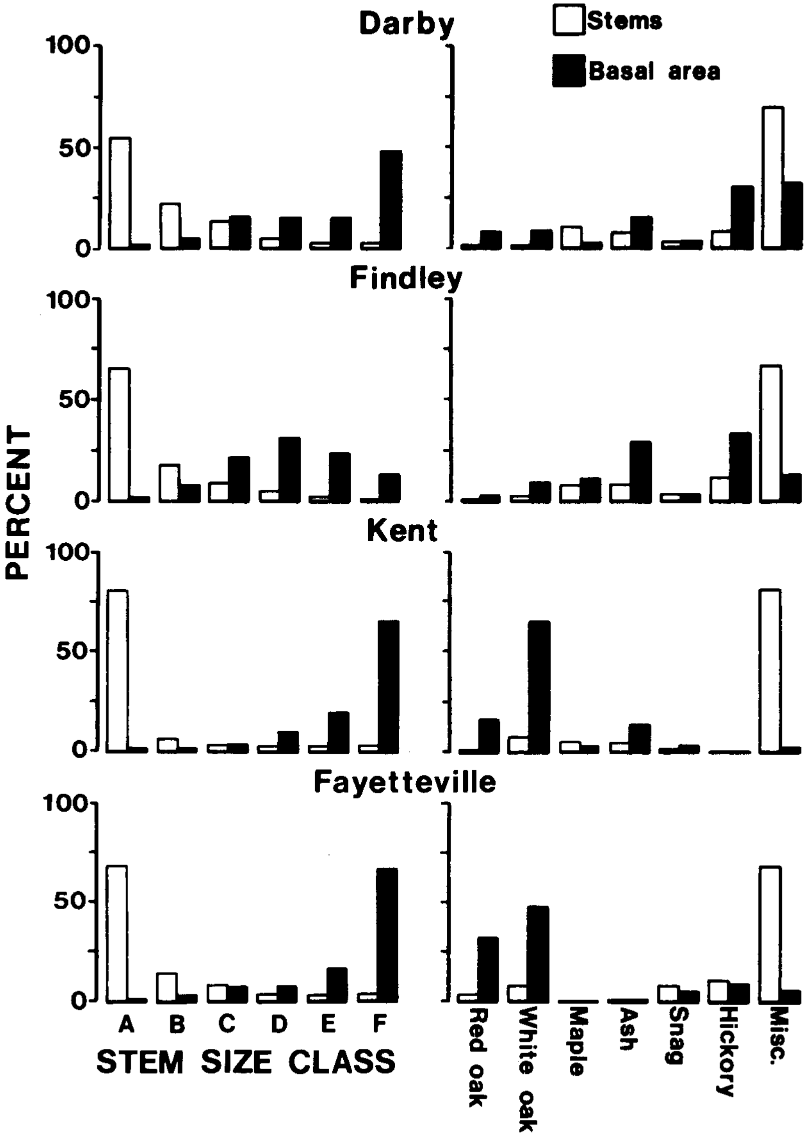

FIGURE 1. Comparison of vegetation structure and composition on the four study sites in Ohio and Arkansas. Stem size classes: A = ≤2.5, B = >2.5–8, C = >8–15, D = >15–23, E = >23–38, and F = >38 cm diameter at breast height.

of the bill, the entire seed was cached; only occasionally (approximately 15% of the cases) was the seed partially consumed before being stored. *Parus bicolor* stored seeds on small- to medium-sized (<8 cm) branches and twigs on medium- to large-diametered (>8 cm dbh) trees. As with nuthatches, titmice frequently were observed in oaks (40%), but they also cached seeds in grape vines (15%) and dead branches on the ground (10%). When caching in trees, titmice were seen equally in inner, middle, and outer portions of limbs, and seeds were positioned disproportionately on the top sides of branches. Titmice did not discriminate among different sides of tree trunks. Height of cache sites ranged from the ground to 25 m, but averaged 7.8 (±7.2) m. Tufted Titmice used a diversity of specific cache locations, but most often wedged seeds under loose bark (46%). Furrows, cracks, and rotted areas (15%), miscellaneous sites, such as the ground

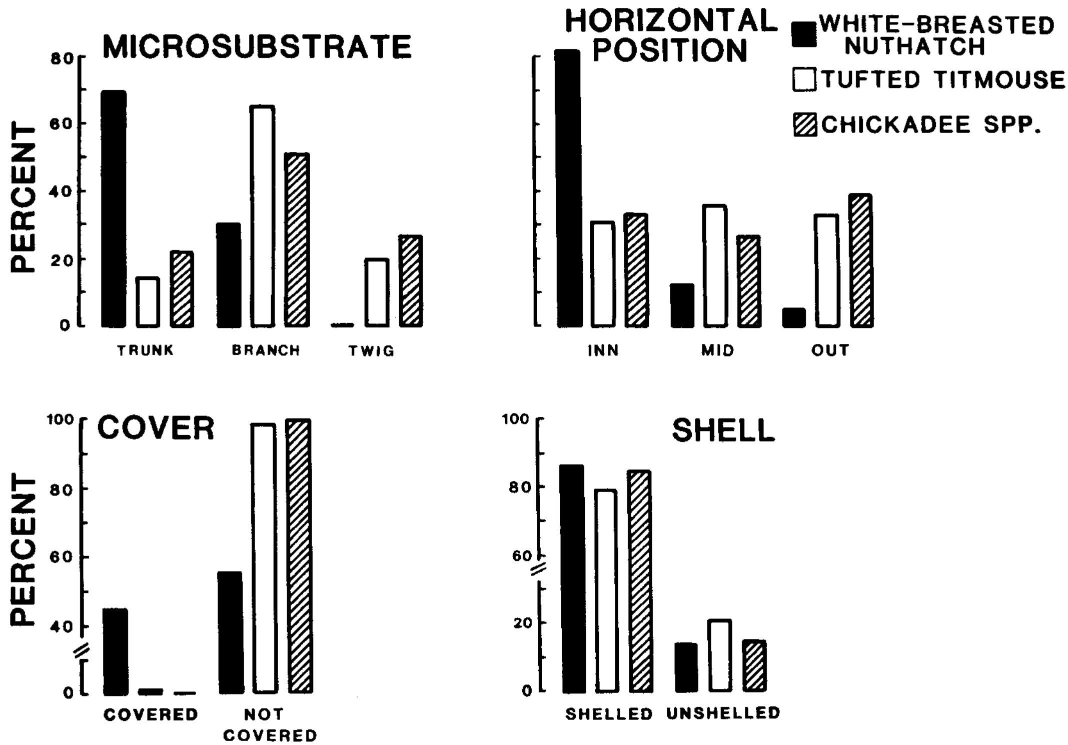

FIGURE 2. Comparison of the caching ecology of White-breasted Nuthatches, Tufted Titmice, and Carolina and Black-capped chickadees storing sunflower seeds in deciduous woodlands during winter.

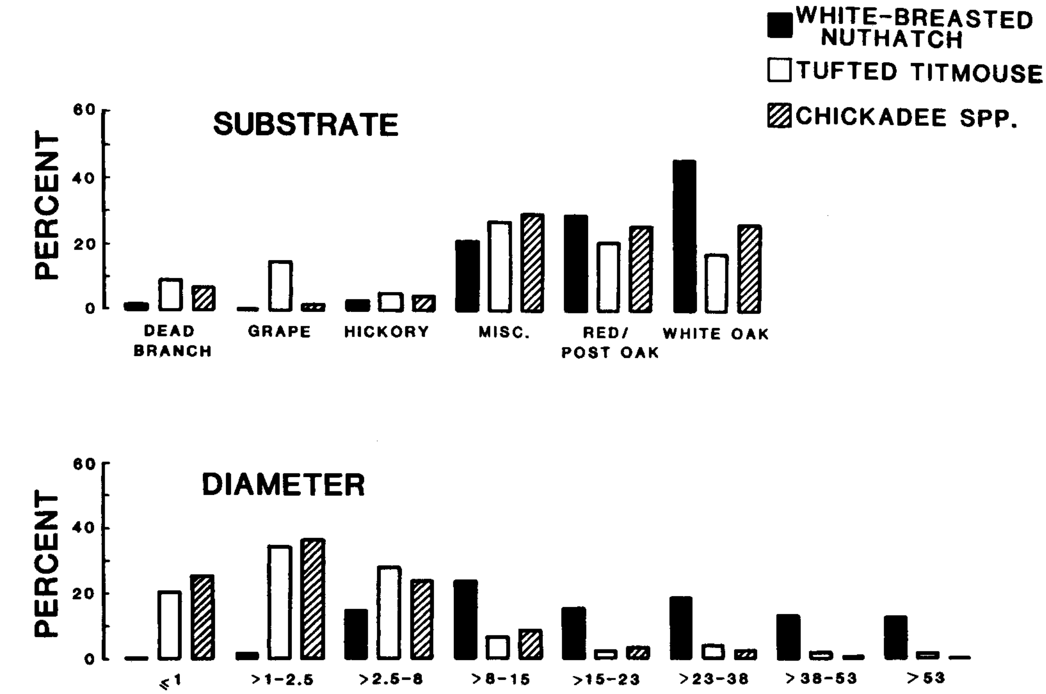

FIGURE 3. Comparison of the caching ecology of White-breasted Nuthatches, Tufted Titmice, and Carolina and Black-capped chickadees storing sunflower seeds in deciduous woodlands during winter.

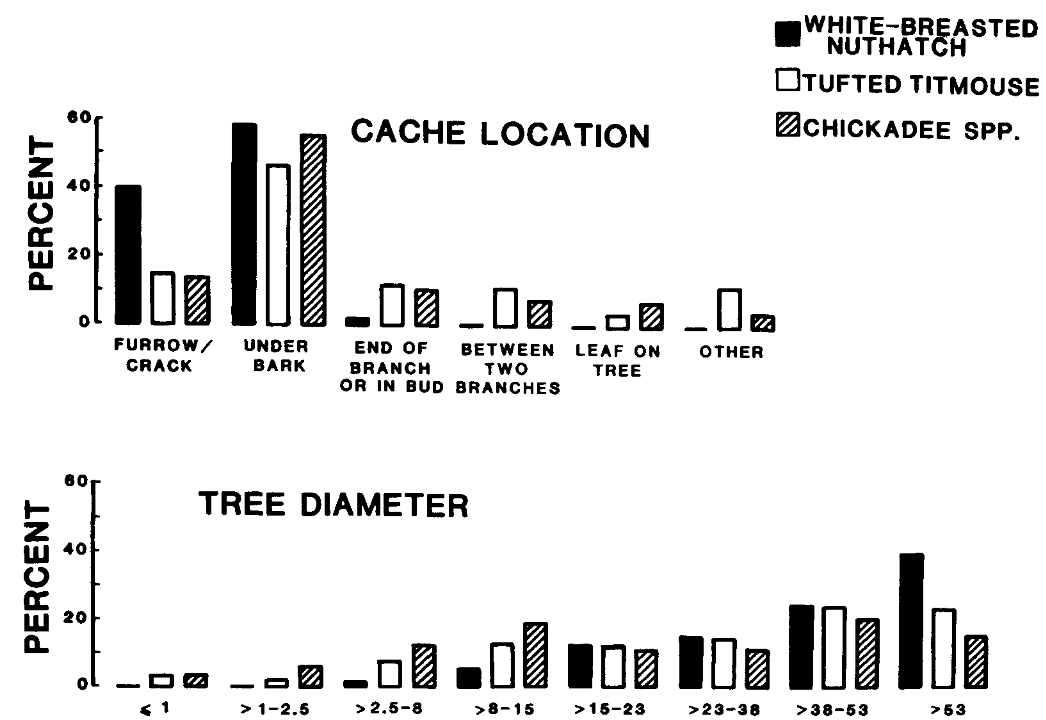

FIGURE 4. Comparison of the caching ecology of White-breasted Nuthatches, Tufted Titmice, and Carolina and Black-capped chickadees storing sunflower seeds in deciduous woodlands during winter.

(12%), between two branches (12%), and at the end of broken branches and twigs (12%) also were recorded regularly as cache sites. Titmice rarely covered stored food.

Black-capped and Carolina chickadees. Like titmice, chickadees cached seeds within 40 m of the feeder ($\bar{x} = 26.5 \pm 17.0$ m), opened unshelled seeds in a similar fashion, and shelled them before storing. In about 5% of visits to feeding stations, chickadees took two (always shelled) seeds. One of those seeds was placed on a branch (or occasionally on snow) and the other seed stored. The bird then would take the second seed and store it separately from the first. Also, in contrast to titmice and nuthatches, both species of chickadees often (approximately 50% of our observations) ate one-third to one-half of the seed before caching the remaining portion. Chickadees stored most seeds on branches (48%), twigs (25%), and small (<2.5 cm dbh) trunks (21%). More than 85% of those substrates were <8 cm in diameter and chickadees demonstrated a strong preference for caching on bottom sides of branches. Chickadees showed the same vertical

TABLE 2. Comparison of expected (random) use with observed use of sides of branches for White-breasted Nuthatches, Tufted Titmice, and chickadee species. Sample sizes in parentheses.

		Observed use (%)		
Branch side	Expected (%)	White-breasted Nuthatch (96)	Tufted Titmouse (85)	Chickadees (176)
Bottom	25.0	38.5	24.7	55.7
Sides	50.0	33.3	36.5	17.6
Top	25.0	28.1	38.8	26.7
	G	12.4	52.0	49.2
	P	<0.005	<0.001	<0.001

TABLE 3. Comparison of expected (random) use with observed use of trunk aspect (compass direction) for White-breasted Nuthatches, Tufted Titmice, and chickadees. Sample sizes in parentheses.

		Observed use (%)		
Aspect	Expected (%)	White-breasted Nuthatch (263)	Tufted Titmouse (33)	Chickadees (104)
316–45°	25.0	24.7	15.2	21.2
46–135°	25.0	19.8	24.2	23.0
136–225°	25.0	30.4	39.4	34.6
226–315°	25.0	25.1	21.2	21.2
	G	6.0	4.0	4.8
	P	>0.10	>0.10	>0.10

TABLE 4. Interpopulational differences in caching ecology of White-breasted Nuthatches, Tufted Titmice, and chickadee species across four locations in Ohio and Arkansas.

Variable	White-breasted Nuthatch	Tufted Titmouse	Chickadees
Distance	***[a]	***	***
Substrate	***	***	***
Height	***	ns	***
Microsubstrate	*	*	***
Microsubstrate diameter	***	**	***
Cover	***	ns	ns
Shell	***	***	***
Horizontal position	ns	ns	***
Tree diameter	***	***	***
Cache location	***	**	***

[a] *G*-test except for height and distance (ANOVA); * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, ns = not significant.

range in cache sites as titmice; on average those sites were at a similar height as those of congeners ($\bar{x}$ = 7.0 ± 6.2 m). Oak trees were used (53%) when storing sunflower seeds, but chickadees were observed on a wide variety of substrates. All size classes of trees were used and, like titmice, chickadees cached at all distances from the trunk. When on trunks, chickadees showed no preference for any compass direction. Most (56%) seeds were wedged under bark, but many of the same locations used by Tufted Titmice also were selected by chickadees. Carolina and Black-capped chickadees were unique, however, in their propensity to hide seeds in dead leaves still hanging from trees (8%). We never observed chickadees covering seeds after storage.

POPULATION COMPARISONS

White-breasted Nuthatch. Nine of 10 cache-site characteristics differed significantly across the four populations studied. Only horizontal position was similar among populations (Table 4).

Tufted Titmouse. Seven of 10 variables were significantly different among the four populations. Horizontal position, height, and covering of caches varied little among locations (Table 4).

Black-capped and Carolina chickadees. Nine of 10 comparisons showed statistical differences. Only cover was similar across study sites (Table 4). Differences were not attributable to our combining both species of chickadees for analysis because differences existed both within and between species when separate analyses were conducted.

SPECIES COMPARISONS

Distance from feeder. On average, White-breasted Nuthatches cached closer to the feeder than either titmice or chickadees; the latter two species were similar ($F = 21.8$; df = 2, 1,208; $P < 0.001$; Least Significant Difference [LSD] multiple comparison).

Substrate. Although oaks were used commonly by all three species, there was evidence for species-specific use of substrate types. Differences were due mainly to the relatively strict use of oaks by nuthatches, grape, and dead branches by titmice, and miscellaneous saplings by chickadees.

Height. White-breasted Nuthatches and Tufted Titmice cached seeds at similar heights, while nuthatches stored seeds higher in trees than did chickadees; titmice and chickadees did not differ ($F = 3.45$; df = 2, 1,207; $P = 0.032$; LSD test).

Microsubstrate. There was a strong preference for trunks by nuthatches, branches by titmice, and branches and twigs by chickadees. All species were statistically distinct in their use of microsubstrates.

Diameter of microsubstrate. Chickadees and titmice were statistically indistinguishable in selection of branch and trunk diameters, but both parids differed from White-breasted Nuthatches.

Cover. Only nuthatches covered their stored seeds.

Shell. All species stored shelled sunflower seeds 79–86% of the time, percentages that were not statistically heterogeneous.

Horizontal position. Whereas titmice and chickadees used all distances from the trunk when caching seeds, nuthatches concentrated on inner portions.

Tree diameter. Both Tufted Titmice and chickadees were found in slightly smaller trees than were White-breasted Nuthatches.

Cache location. Nuthatches were highly selective in their use of cache sites. In contrast, chickadees and titmice used a variety of sites although they also differed statistically from each other (Table 5 summarizes species differences).

DISCUSSION

INTERPOPULATIONAL VARIATION

Nuthatches, titmice, and chickadees stored food in locations generally similar to those described in the literature as foraging sites (e.g., Grubb 1975, 1982; Watt 1975; Pierce and Grubb 1979; Whiting 1979; pers. observ.), although some important differences do occur (Petit, unpubl.). Each species demonstrated a distinct pattern of seed storage and there was considerable variation from population to population. Interpopulational differences may be attributable to at least four sources of variation. First, individuals may alter cache-site selection because of the local pool of potential cache robbers. On our study sites, however, there were few differences in bird species composition (e.g., 75% of all nonraptorial species seen were common to all four study plots). White-breasted Nuthatches, Tufted Titmice, and chickadees used all feeders and their numbers were similar at all sites. Thus, although interspecific interaction does not appear to have substantially altered bird caching ecology among populations, more detailed study of this possibility is necessary before this question can be addressed satisfactorily. Within the group of focal species, however, interaction among heterospecifics may have influenced cache-site selection. Most notably, nuthatches stored food closer to the feeder than did the parids. Our observations suggest that this relationship was dominance-related, as nuthatches were aggressive toward chickadees and titmice near (<10 m) the feeding stations (also see Waite and Grubb 1988).

Secondly, genetic or learned differences in selection of cache sites may exist among populations. Individual Marsh Tits (*Parus palustris*) showed distinct preferences for certain cache sites, at least on a short-term basis (Cowie et al. 1981). Because we probably dealt with only two to 16 individuals of a species at each location, simple variation among individuals (or populations) in cache-site selection could explain the overall lack of agreement among populations. A comparison of intra- vs. interpopulational variation in caching ecology or experimental relocation of individuals among populations may provide some resolution to the question of population-specific cache-site selection.

Thirdly, site-specific elements, such as weather, presence of con- and heterospecifics, and overall abundance of other food sources, could act randomly to produce variation among populations. Certainly, some of those factors affect how birds forage (e.g., Grubb 1975, 1977; Peters and Grubb 1983), so we would expect those processes to act on caching behavior, as well. A fruitful approach to this problem might be to quantify

TABLE 5. Pairwise species comparisons of caching ecology of White-breasted Nuthatches, Tufted Titmice, and chickadee species.

Variable	Comparison: Chickadee/titmouse	Comparison: Chickadee/nuthatch	Comparison: Titmouse/nuthatch
Distance	ns[a]	***	***
Substrate	***	***	***
Height	ns	**	ns
Microsubstrate	***	***	***
Microsubstrate diameter	ns	***	***
Cover	ns	***	***
Shell	ns	ns	ns
Horizontal position	ns	***	***
Tree diameter	ns	***	***
Cache location	***	***	***

[a] *G*-test except for distance and height (ANOVA); ** = $P \leq 0.01$, *** = $P \leq 0.001$, ns = not significant.

caching behavior of marked individuals under various weather and social situations.

Finally, habitat differences among study areas could influence caching ecology. Although all study sites were situated within deciduous woodlands, there were several substantial differences among them in vegetation structure and floristic composition, and that heterogeneity could account for the interpopulational variation in cache-site selection documented here. If habitat had a significant impact on caching ecology, then we would expect that the more similar two plots were in vegetation composition and structure, the more closely the two avian populations inhabiting those sites would be in their use of cache sites. To test this idea, we calculated overlap values (Schoener 1968) for all pairwise combinations of (1) habitat structure on the four study sites, and (2) habitat use by the four populations of each species. The habitat variables used were those shown in Figure 1; that is, both percentage of stems and percentage of basal area (1) in different size classes of trees, and (2) in different categories of tree species. The corresponding cache-site variables used were simply the percent use of different tree size classes or tree species categories by a given population. Finally, we computed Spearman's correlation coefficient (r_s) for each set of habitat overlap indices (six pairwise combinations) with the corresponding overlap indices of habitat use. Correlation coefficients were computed separately for each species. Results (Table 6) showed that there was little relationship between similarity of the four sites in their distribution of stems across size classes and

TABLE 6. Spearman's correlation coefficients comparing similarity in vegetation structure and composition on the four study areas with similarity in selection of tree species and size classes by the bird species. Correlation coefficients were computed for each species by comparing the six pairwise combinations of overlap indices for habitat availability with the six pairwise combinations of overlap indices for habitat use. See text for further details.

Habitat variable	White-breasted Nuthatch	Tufted Titmouse	Chickadees
(1) Tree size classes			
(a) stems	−0.21	−0.64	−0.33
(b) basal area	0.71	0.77	0.60
(2) Tree species			
(a) stems	−0.01	−0.36	0.07
(b) basal area	0.71	0.66	1.00

tree species and the similarity in the three species' use of those habitat features. Conversely, when habitat was expressed in terms of basal area, there were consistent trends for populations to cache on more similar-sized trees and on more similar tree species when the local habitats were in closer conformity with one another. This analysis suggests that local habitat structure may have influenced selection of cache sites. Use of different-sized trees or tree species by birds may alter other characteristics of cache sites because of the varied opportunities encountered on different types of substrates.

CACHE PROTECTION

Environmental factors. To increase the probability of recovering stored food, birds may avoid certain types of storage sites vulnerable to snow and ice cover. For example, Haftorn (1974) suggested that Boreal Chickadees (*Parus hudsonicus*) in Alaska alleviated this potential problem by storing food low in trees, but above the ground and on the bottom sides of branches. Although this trend was not observed by Haftorn (1954, 1956) for two European parids, it is theoretically one means by which birds can retain access to stored food regardless of environmental conditions (Vander Wall and Smith 1987). In this study, nuthatches and chickadees stored a greater proportion of seeds on bottoms of branches than would be expected by chance. However, seeds were cached on tops of branches in proportions at least as large as that expected (i.e., few seeds were stored on sides of branches). Likewise, tree trunks often are covered with ice and snow after storms, but only the side facing the prevailing wind direction becomes covered (pers. observ.). Thus, we would predict that birds would avoid those sides of trunks that were most likely to be covered by snow. However, all species used trunk aspect randomly. Thus, in our study, selection of a branch side or trunk aspect does not appear to be a response to potential snow and ice cover.

Heterospecifics. Chickadees, titmice, and nuthatches travel in mixed-species flocks during winter and the potential benefits gained by that behavior are well-known (e.g., Morse 1980). Flocking may be disadvantageous to individuals, however, when a large group is involved in storing food taken from a single source. By hoarding seeds in close proximity to many individuals, a bird may jeopardize the secrecy of its cache sites. To protect their caches from cache robbers, then, birds can employ several protective measures (see Vander Wall and Smith 1987): (1) aggressively defend the hoarded food, (2) space seeds at distances that reduce the probability of a cache robber finding a cache site based upon a previously located site, (3) alter the cache site so as to increase the crypticity of the cache, and (4) store food in locations which limit their accessability to other species. All species studied here are scatter-hoarders (Morris 1962, Stapanian and Smith 1978); that is, they store food in numerous, dispersed locations. Although some scatter-hoarding species aggressively defend their stores, this behavior is not practiced by smaller species, such as the ones in this study.

There is some evidence that Marsh Tits space cached seeds at nearest neighbor distances that significantly reduce the chances that cache robbers will locate a given seed based upon the location of another seed(s). Cowie et al. (1981) and Sherry et al. (1981) found that individual Marsh Tits spaced sunflower seeds at a nearest neighbor distance of approximately 7 m. Although our study was not designed to address the question of optimal spacing of cache sites, observations of several color-marked individuals suggest that titmice space caches 5–15 m apart.

Cache concealment by passerines is usually achieved by either actively covering the food reserve with such materials as bark, lichens, or soil, or by placing seeds in naturally concealed locations, e.g., under bark or in furrows on tree trunks (Haftorn 1954, Cowie et al. 1981, James and Verbeek 1983, pers. observ.). In this study, only White-breasted Nuthatches covered their stored seeds on a regular basis. All species frequently chose cache locations that were naturally cryptic, at least to the human eye: furrows, cracks, under bark on trees, and in curled dead leaves. Even here, though, nuthatches (98%) utilized the above naturally concealed sites more than did either titmice (65%) or chickadees (77%). By combining concealed sites with covering of stored seeds, nuthatches clearly concealed a higher proportion of their caches than did the parids.

All species selected cache sites that were somewhat inaccessible to other birds, although the type of site varied among species. Chickadees and titmice placed seeds on smaller branches and twigs, frequently on the outer portion of tree canopies. Both species, but especially chickadees, reduced the size of the seed before caching it. This may be a response to the relatively small cracks and strips of loose bark that are available on small twigs and branches as compared to larger branches and trunks used by nuthatches and, to some extent, titmice. The practice of storing only portions of seeds also may reduce the probability that wind might dislodge the seeds from shallow cracks or from under small pieces of loose bark. Nuthatches used their long bills to wedge whole seeds into deep furrows or far under loose bark.

How do White-breasted Nuthatches, Tufted Titmice, and Black-capped and Carolina chickadees protect their stored food from heterospecifics? It appears that chickadees and titmice primarily rely upon inaccessability of cache sites, while nuthatches utilize both difficult-to-reach locations and crypticity to prevent seeds from being stolen by other species. Differences between parids and the nuthatch in cache-site selection may be determined by both morphological constraints placed on each species and by the number of potential cache robbers likely to encounter each species' cache sites during normal foraging bouts. For example, morphology of the bill and legs restricts a species in the types of substrates that it can exploit (e.g., Richardson 1942, Schoener 1965, Partridge 1976). The positioning of the legs of titmice and chickadees allows for mobile maneuvering (most notably, hanging) on small substrates, such as twigs, whereas the nuthatches' more posteriorly positioned legs restrict this species to larger branches and trunks (Richardson 1942, Osterhaus 1962, Partridge 1976). Bill length and shape, too, probably influence caching behavior as they do birds' foraging ecology (e.g., Schoener 1965). The relatively short bills of parids cannot cache, and then retrieve, seeds placed deep into furrows or under large strips of bark, but can efficiently manipulate a seed into a small crack in a twig or in a small bud.

The local pool of potential cache robbers also may dictate where birds store food and the degree of concealment that is necessary. In our study, White-breasted Nuthatches apparently relied upon cryptic (both natural and altered) cache sites to a greater extent than did either titmice or chickadees as a defense against kleptoparasites. This result may be due to more species on our study sites foraging in ways comparable to nuthatches than to chickadees and titmice. We recorded nine species that are similar to White-breasted Nuthatches in their foraging ecology: Pileated (*Dryocopus pileatus*), Red-bellied (*Melanerpes carolinus*), Red-headed (*M. erythrocephalus*), Hairy (*Picoides villosus*), and Downy woodpeckers (*P. pubescens*), Northern Flicker (*Colaptes auratus*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Brown Creeper (*Certhia americana*), and Red-breasted Nuthatch (*Sitta canadensis*). Alternatively, only two species were seen that forage in locations frequented by chickadees and titmice: Golden-crowned Kinglets (*Regulus satrapa*) and Purple Finches (*Carpodacus purpureus*). Kilham (1974) postulated that White-breasted Nuthatches covered their stored food because of local competitors.

Our results suggest that caching behavior may be shaped by local environmental conditions. The importance of protecting stored food, both from other birds and from the environment, may have caused each species in this study to occupy a distinct caching niche. In addition, morphological constraints placed on species may limit the number of sites suitable for effective storage and recovery of food.

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