CHARACTERISTICS OF CACHE SITES MOST LIKELY TO BE ROBBED BY WILLOW TITS (*PARUS MONTANUS*)[1]

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Individuals of several food-hoarding bird species form flocks, with individuals sharing the same feeding area (e.g., tits [*Parus*] during winter). Food-caching tits hoard one item per site, with sites scattered over the winter territory (e.g., Haftorn 1956a). Individuals cache and recover food items while moving together as members of mixed species flocks. Individuals tend to store seeds in locations that are less used by other species (e.g., Alatalo and Carlson 1987, Petit et al. 1989, Suhonen and Alatalo 1991). Seeds stored by tits are frequently at least partly visible (Haftorn 1954, 1956a, 1956b, 1956c), which raises the possibility that other flock members may recover some of them. Vander Wall and Smith (1987) listed five sources of cache loss, one of which is cache robbers stealing food before an individual relocates its stored food. Cache robbers stole a considerable proportion of the seeds stored by Marsh Tits (*Parus palustris*) in the field (Sherry et al. 1982, Stevens and Krebs 1986).

Aviary experiments on Black-capped Chickadees (*P. atricapillus*) (Baker et al. 1988) and Willow Tits (*P. montanus*) (Suhonen and Inki 1992) showed that individuals recovered their own caches more easily than did other individuals of the same species, as predicted by the model of Andersson and Krebs (1978). However, conspecific individuals still found a considerable proportion of caches in both experimental studies. In this study, we investigated the kinds of caches made by Willow Tits that were robbed by conspecific individuals. We expected that visibly cached seeds would be robbed more often than hidden ones.

METHODS

Individual captive Willow Tits were allowed to recover caches made by other Willow Tit individuals. Eleven tits were caught in coniferous forests near Konnevesi Research Station (62°37′N, 26°20′E) in central Finland, with permission of the Ministry of the Environment. The birds were kept indoors in individual cages measuring 40 × 30 × 25 cm on a 12:12 light:dark cycle. Birds were fed mealworms, grated carrots, hard-boiled eggs, sunflower seeds and spruce seeds ad libitum and given water supplemented with vitamins. After the final experiments, all birds were released.

We tested the birds singly in a 2.3 × 2.1 × 2.0 m indoor aviary containing four 1.6 m long branches of spruce placed horizontally and two vertical 2.0 m high pieces of spruce trunk. Two branches were 0.5 m, and two 1.5 m above the floor. The pieces of spruce trunk were nailed vertically to the walls of the aviary. Before the experiments started, we let each bird habituate to the aviary during two 30-min periods.

Each Willow Tit was allowed to store only spruce seeds, which they often hoard in the field (e.g., Haftorn 1956a). We carefully recorded cache substrate and seed visibility. The substrate on which each seed was cached was recorded as either (1) trunk, (2) branch (diameter >10 mm), or (3) twig (diameter <10 mm). The proportion of the seed that was visible was estimated to the nearest 10%. If the seed was placed on a substrate without any cover it was completely visible (100%). Birds were allowed to store seeds for 15 min or if no seeds had been stored up to that point, until one seed had been cached. The bird was then removed from the aviary. After each storing session, another Willow Tit that had not been fed for 1 hr was introduced into the aviary and allowed to search for 30 min. The birds were placed in the aviary in darkness, and observations started when the light was switched on. We used each bird only once as cacher and retriever, respectively.

We recorded the number of seeds recovered and the time required to find each cached seed during the 30-min recovery period. If the tit did not recover any cached seeds, we used 30 min as the "recovery" time for the rank tests. The tit's use of foraging sites was also recorded during the retrieval period. These observations were made at 10-sec intervals prompted by a signal from a metronome, and up to 75 observations were made on the same individual. We used the same categorization of foraging locations as of storing sites. Each stored seed was used as an independent observation in statistical tests.

RESULTS

During a food storing session Willow Tits stored two seeds, on average, on branches, twigs or tree trunks. Willow Tits hide seeds in crevices of bark or among lichen. Only 2 of 23 cached seeds were completely visible. On average slightly more than half of each cached seed was visible ($\bar{x}$ = 55%, n = 23). In most (18 of 23) cases Willow Tits removed the wing of the seed before storing it. Cached seeds with wings were more visible than those with wings removed (Mann-Whitney *U*-test, $U = 4$, $P = 0.001$, 2-tailed).
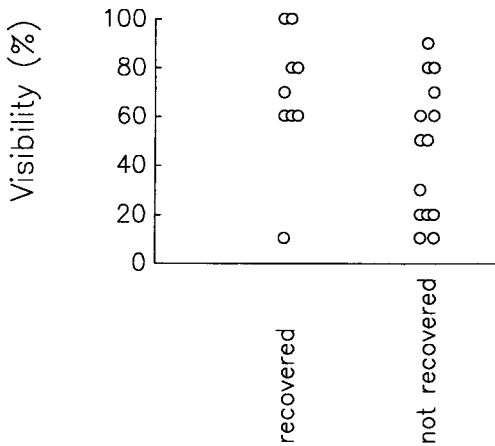
During the retrieval period nine of eleven Willow

FIGURE 1. Visibility (%) of seeds, which non-cacher Willow Tit individuals recovered and of seeds they did not recover.
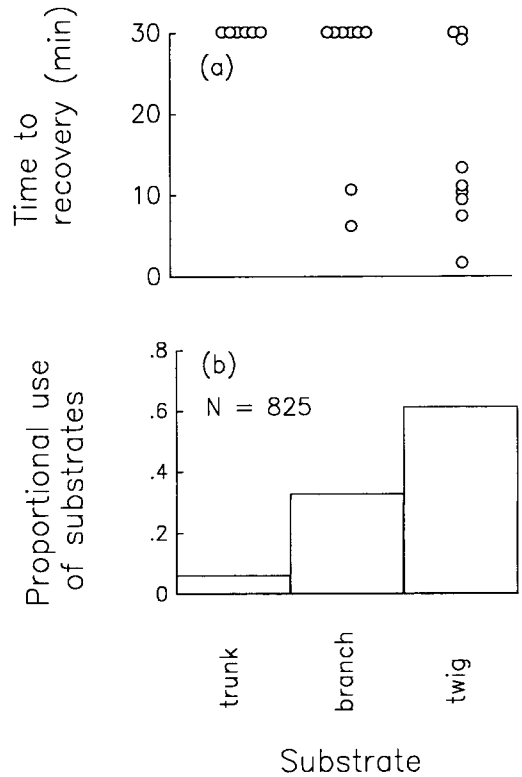

FIGURE 2. (a) Time to recover (minutes) caches made by other Willow Tits in relation to the kind of site where the seeds had been stored. The tits did not find cached seeds which have 30-min recovery time. (b) The relative use of different substrate in spruce in the aviary.

Tits found caches and in each case the individual found only one stored seed. More visible seeds were found more often than well-hidden ones. The average visibility for seeds found was 70% (SD = 30, n = 9) and 45% for seeds that remained undiscovered (SD = 30, n = 14; U = 35.5, P = 0.04, one-tailed; Fig. 1). Also the substrate on which a seed was stored had an effect on the probability of recovery by other Willow Tits (Kruskal-Wallis ANOVA, H = 8.3, df = 2, P = 0.015; Fig. 2a). They recovered more seeds from twigs because twigs were most frequently visited by the captive tits (Fig. 2b). Time to recover the found cached seeds on twigs did not correlate with percent visibility of the seeds (r_s = 0.39, n = 9, P > 0.10).

DISCUSSION

Willow Tits found cached seeds without having seen their conspecific store the seed. Our results indicate that risk of intraspecific cache stealing was rather high, in particular for caches which were located on the twigs. In the field, Willow Tits hoard mainly on thick branches and, with lower frequency, on tree trunks, twigs and among needles (Haftorn 1956a, 1956c; Suhonen and Alatalo 1991). However, they more often used spruce trunks than would be predicted from their foraging site preferences (Suhonen and Alatalo 1991).

Visible seeds were found quickly. However, the most visible seeds on twigs were not found any sooner than well-hidden seeds due to the fact that all seeds were highly visible ($\bar{x}$ = 75%). Haftorn's (1956c) field study showed that Willow Tits hid seeds under coverage and that more than 50% of stored spruce seeds were covered completely. It is advantageous to hide stored seeds carefully to reduce the probability that cache robbers find the caches. Another way to reduce conspecific cache stealing is to cache seeds in locations less often foraged by other animals. Thus, tits often avoid caching within the foraging niches of other species (Haftorn 1956a, Alatalo and Carlson 1987, Petit et al. 1989, Suhonen and Alatalo 1991). The results of these studies support

the idea that segregation of hoarding sites reduces the risk that conspecific individuals and/or individuals of other species find the stores.

Our data show that the risk of cache stealing was high, especially for caches which were located on twigs, but we want to emphasize that individuals which stored food may have traded the time it takes to hide a seed well against using this time for foraging or caching additional seeds.

LITERATURE CITED

ALATALO, R. V., AND A. CARLSON. 1987. Hoarding-site selection of the Willow Tit (*Parus montanus*) in the presence of the Siberian Tit (*Parus cinctus*). Ornis Fennica 64:1–9.

ANDERSSON, M., AND J. KREBS. 1978. On the evo-

lution of hoarding behaviour. Anim. Behav. 26: 707–711.

BAKER, M. C., E. STONE, A. E. M. BAKER, R. J. SHELDEN, P. SKILLCORN, AND M. D. MANTYCH. 1988. Evidence against observational learning in storage and recovery of seeds by Black-capped Chickadees. Auk 105:492–497.

HAFTORN, S. 1954. Contribution to the food biology of tits especially about storing surplus food. Part I. The Crested Tit (Parus c. cristatus L.). Kgl. Norske Vidensk. Selsk. Skr. 4:1–123.

HAFTORN, S. 1956a. Contribution to the food biology of tits especially about storing of surplus food. Part IV. A comparative analysis of (Parus atricapillus) L., (P. cristatus L.) and (P. ater L.). Kgl. Norske Vidensk. Selsk. Skr. 4:1–54.

HAFTORN, S. 1956b. Contribution to the food biology of tits especially about storing of surplus food. Part II. The Coal Tit (Parus a. ater L.). Kgl. Norske Vidensk. Selsk. Skr. 2:1–52.

HAFTORN, S. 1956c. Contribution to the food biology of tits especially about storing of surplus food. Part III. The Willow Tit (Parus atricapillus L.). Kgl. Norske Vidensk. Selsk. Skr. 3:1–19.

PETIT, D. R., L. J. PETIT, AND K. E. PETIT. 1989. Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. Condor 91:766–776.

SHERRY, D., M. AVERY, AND A. STEVENS. 1982. The spacing of stored food by Marsh Tits. Z. Tierpsychol. 58:153–162.

STEVENS, T. A., AND J. R. KREBS. 1986. Retrieval of stored seeds by Marsh Tits (Parus palustris) in the field. Ibis 128:513–525.

SUHONEN, J., AND R. V. ALATALO. 1991. Hoarding sites in mixed flocks of Willow and Crested Tits. Ornis Scand. 22:88–93.

SUHONEN, J., AND K. INKI. 1992. Recovery of Willow Tit food caches by other Willow Tits and Great Tits. Anim. Behav. 44:180–181.

VANDER WALL, S. B., AND K. G. SMITH. 1987. Cache-protection behavior of food-hoarding animals, p. 611–644. In A. C. Kamil, J. Krebs, and H. R. Pulliam [eds.], Foraging behavior. Plenum Publishing, New York.

THERMOREGULATION IN FREE-RANGING WHIP-POOR-WILLS[1]

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Torpor is a strategy that allows animals to reduce their body temperature as a means of saving energy during periods of low ambient temperature or low food availability. Brigham (1992) has shown that free-living Common Poorwills (*Phalaenoptilus nuttallii*) are capable of daily torpor. In contrast, free-living Common Nighthawks (*Chordeiles minor*) do not use torpor (Firman et al. 1993).

Interspecific variation in thermoregulatory patterns among caprimulgids could be the result of different foraging styles (Whip-poor-wills, *Caprimulgus vociferus*, sally from a perch whereas Common Nighthawks are aerial insectivores), body size, or reproductive biology (e.g., number of clutches per breeding season).

The biology of free-ranging caprimulgids is poorly understood and no studies have addressed the ther-

moregulatory behavior of Whip-poor-wills in the field. Brigham and Barclay (1992) predicted that Whip-poor-wills are incapable of torpor, and that this difference may explain different responses to levels of moonlight between Whip-poor-wills and Common Poorwills. Whip-poor-wills synchronize their breeding cycle to the lunar cycle (Mills 1986), whereas Common Poorwills do not.

In the Okanagan Valley, British Columbia, Brigham and Barclay (1992) found that two of five Common Poorwill pairs made second breeding attempts, whereas Mills (1986) found that only one out of eight pairs of Whip-poor-wills laid a second clutch. The ability to enter torpor may allow Common Poorwills to use their available energy reserves more efficiently and lay two clutches during the breeding season (Brigham and Barclay 1992). To successfully lay two clutches, Common Poorwills may have to begin laying their first clutch as early in the spring as possible, precluding them from synchronizing their nesting with the lunar cycle (Brigham and Barclay 1992).

Alternatively, if Whip-poor-wills lay only a single clutch, they may maximize their reproductive success by synchronizing their nesting cycle with the lunar cycle. This would ensure that eggs hatch during a waxing moon so that parents can increase their nightly foraging