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Low Rate of Loss of Willow Tit Caches May Increase Adaptiveness of Long-term Hoarding

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Pilfering of hoarded food will reduce the adaptive value of hoarding, which is a problem especially for scatter hoarders that cannot protect their stores against scroungers. In nature, pilfering of scatter-hoarded food is poorly known, but in experiments on both birds and mammals, 50 to 80% of artificially cached food disappeared (Vander Wall 1990:89–90). In experiments with hoarding Marsh Tits (*Parus palustris*), 28 to 62% of artificially cached seeds disappeared during the first 24 h, with the rate depending on the spacing of caches (calculated from Sherry et al. 1982:fig. 1). With such high disappearance rates, caches disappeared fast and, after three days, the retrieval success for hoarders had declined to zero (Stevens and Krebs 1986). Marsh Tits made most recovery attempts within two days after storing and, in experiments involving hoarding in Willow Tits (*P. montanus*), most hoarded seeds also were retrieved within a few days (Brodin 1992). High pilfering rates should reduce the adaptive value of long-term hoarding, which is reported for resident boreal parids like Willow Tits (Haftorn 1956a, Pravosudov 1985, Nakamura and Wako 1988).

Sherry (1982, 1984) has demonstrated that Marsh Tits and Black-capped Chickadees (*P. atricapillus*) remember which caches are already emptied and avoid revisiting them. These species are close relatives of the Willow Tit, and it is probable that all three have similar memory mechanisms. Since hoarders do not revisit previously emptied cache locations, at least not as long as caches are remembered, the disappearance of seeds from rebaited caches should be a good measure of the loss of seeds stored under natural conditions.

In most studies of hoarding parids in the field, feeding devices have been used to provide seeds (Cowie et al. 1981, Moreno et al. 1981, Sherry et al. 1982, Stevens and Krebs 1986, Nakamura and Wako 1988, Petit et al. 1989, Suhonen and Alatalo 1991, Brodin 1992), leading to a local concentration of stored food. Parids store most seeds within 50 m of the feeder (Cowie et al. 1981, Sherry et al. 1982, Stevens and Krebs 1986, Petit et al. 1989). Even when seeds are spaced out to minimize pilfering (Sherry et al. 1982, Stevens and Krebs 1986), they are concentrated compared to the rest of the territory, where sunflower seeds and peanuts are absent.

Disappearance during the night can be ascribed to pilfering by rodents, whereas daytime disappearance probably is due to the resident Willow Tit flock or other birds. Since co-existing hoarding tit species utilize different parts of the tree, and even prefer different tree species (Haftorn 1956b, Suhonen and Alatalo 1991), it is probable that the most serious competitors for caches are conspecifics in the same territory. In a longer time perspective, cache losses also may depend on rain, snow, wind, etc.

In this study I investigated whether the loss of Willow Tits' stores is compatible with long-term hoarding, and if a concentration of hoarded seeds (as around a feeder) will attract seed pilferers and increase the disappearance rate.

Methods.—Winter territories of Willow Tits in my study area, a forest reserve 20 km south of Stockholm, averaged about 27 ha. Conifers dominate the landscape with interspersed deciduous trees (see Brodin 1992).

In hoarding experiments during the winters 1989–1990 and 1990–1991, I provided Willow Tits with sunflower seeds labelled with radioactive Technetium 99-m, which I then traced with a portable scintillation counter (Brodin 1992), a technique developed by Cowie et al. (1981). I marked the position of located seeds with inconspicuous map pins and followed their disappearance. Most sunflower seeds were retrieved within a few days of hoarding (Brodin 1992).

Following naturally hoarding Willow Tit flocks during the autumn 1991, I marked caching locations and followed the disappearance of caches in a similar way. The seeds most frequently stored were from junipers (*Juniperus communis*), and the seeds were present in the caches much longer than in the hoarding experiments, for weeks or months (Brodin 1993). In both treatments almost all located seeds had been stored in trees, mostly pine (*Pinus silvestris*) and spruce (*Picea abies*).

A minimum time span of two weeks after the hoarded seed had been retrieved, I positioned a new seed of the same kind as the original one (i.e. sunflower or juniper) in the emptied caching location. Hereby, I could follow the pilfering from locations actually chosen by Willow Tits. I made sure that all seeds were more visible than the original seed, which normally had been difficult to spot under lichens or stuck deep into bark crevices. The idea was both to facilitate inspection and to avoid underestimating rates of cache loss.

In 1991 I rebaited 100 emptied caching locations of which 80 originated from the feeding experiments (sunflower) and 20 from foraging under natural conditions (juniper). The sunflower caches were rebaited 3 January and the juniper seeds 18 October. I checked the rebaited caches in both treatments for 126 days.

I considered the last registration of a seed as disappearance date, although it also could have been taken during the time until the next visit. The sunflower seeds were visited at approximately 12-day intervals, with some variation depending on the weather. The juniper seeds were checked at more irregular intervals, as several locations were too far apart to be visited in a day. The long intervals give coarse resolution of short-term events, but the risk of attracting pilferers by frequent visits is minimized. The rebaited caches were fairly evenly dispersed over eight flock winter territories and the original seeds were hoarded by at least 21 different Willow Tits.

I made artificial caches around five feeders to test whether a concentration of hoarded seeds would attract seed eaters (e.g. the hoarding Willow Tits) and increase pilfering. As I introduced a feeder I used playback recordings of Willow Tit song to attract the resident group, which started hoarding immediately. The feeders, which were identical in construction and contained 0.5 kg unshelled sunflower seeds, were removed after three days.

Directly after removal, I "cached" five sunflower seeds in four straight lines, at 10-m intervals from the feeder in the four cardinal points. In total, 20 seeds were artificially cached at distances from 10 to 50 m around each feeder. As controls I used seeds in the same locations, but with no feeder in the center. In two replications I started with the control design, and in three with the feeder. If I started with the experimental design, I allowed 10 days to pass before rebaiting the caches for a control design.

Cowie et al. (1981) judged nighttime pilfering (by rodents) to be low, whereas Sherry et al. (1982) and Stevens and Krebs (1986) reported a considerable nighttime disappearance. Thus, I checked the artificial caches at dusk and dawn for five days, and then once a day for five more days.

Results.—Sunflower seeds rebaited in caches from hoarding experiments, and juniper seeds rebaited in natural caches disappeared with almost identical rates (Fig. 1). Together, the treatments can be fitted to a negative exponential curve:

$$Y = e^{(0.09-0.013X)}$$

($P < 0.001$, $r^2 = 99.25$, regression analysis, two-tailed) suggesting a constant probability of detection for cached items. The daily proportional disappearance is then about 1.3%. The proportion remaining at the end of the experiment, day 126, should be 0.21 or 21 seeds according to the regression curve, which is close to the 20 actually remaining (16 sunflower and 4 juniper). The regression predicts half-life of 60 days, when 50 seeds should remain. I did not check the seeds exactly at 60 days, but 52 seeds, 43 sunflower (day 57), and 9 juniper (day 49) remained at approximately that time.

Treating sunflower seeds separately, the half-life for the rebaited seeds was 59.5 days compared to 2.6 days for the sunflower seeds originally hoarded by the birds in the very same caches. Similarly, for juniper seeds separately, the half-life for rebaited seeds was 53 days, compared to 9.7 days for the original seeds. Both differences are significant ($P < 0.001$, $n = 80$, and $P = 0.002$, $n = 20$, respectively; Wilcoxon signed ranks, matched pairs, two-tailed).

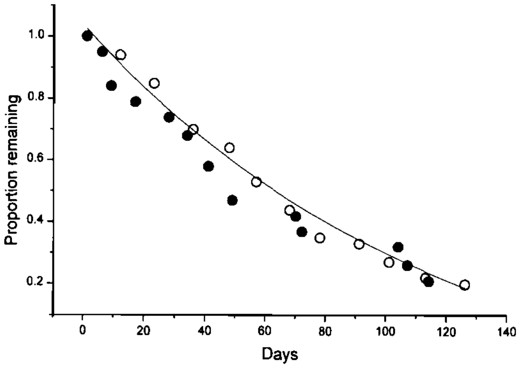

Fig. 1. Disappearance of seeds from rebaited Willow Tit caches during 126 days. Open circles represent caches located in hoarding experiments; filled circles are caches located during natural foraging. Curve is an exponential regression $Y = e^{(0.09-0.013X)}$ ($P < 0.001$, $r^2 = 99.25$).

Most sunflower seeds turned brown during the winter, probably dyed from water running down the bark on the trees. The seeds remaining at the end of both treatments finally became very cryptic. Five seeds might have disappeared when I tried to uncover them from snow. In April and May, three sunflower seeds rotted and gradually disappeared.

I use the longevity of a cached seed, from 1 to 10 days, as a measure of survival when caches at different distances are compared. Longevity for artificial caches was low close to feeders and decreased with distance ($P < 0.001$, $n = 25$, $r_s = 0.69$, Spearman rank correlation), with no such effect on control seeds (Fig. 2). Several functions can be fitted to pilfering as a function of distance from the central food source, and it is better described by a linear ($r^2 = 0.42$, $P < 0.001$, $Y = 7.32 + 106X$) than an exponential regression ($r^2 = 0.22$, $P = 0.018$). Mean longevity for all 20 seeds irrespective of distance was 6.56 days ± SE of 0.53. If the artificially cached seeds are compared with their controls the disappearance was higher at distances of 10, 20 and 30 m ($P = 0.03$ in all three tests) but not on 40 ($P = 0.09$) and 50 ($P = 0.21$; Wilcoxon matched pairs, signed ranks, one-tailed, $n = 5$).

The proportion of seeds disappearing daily was high during the first four days after the removal of the feeder; thereafter it was lower during days 5 through 8. During days 9 and 10 no seeds disappeared (Fig. 3). This decrease with time is significant ($P = 0.007$, $n = 10$, $r_s = -0.90$, Spearman rank correlation). In total, 11 of 100 control seeds disappeared during the

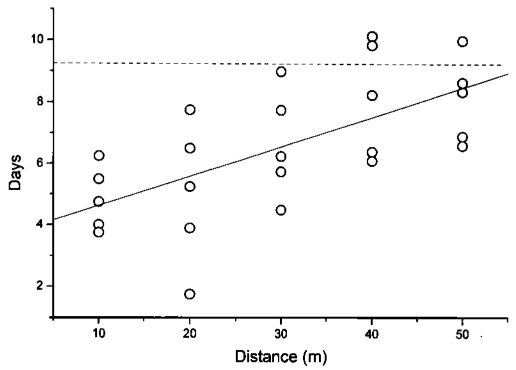

Fig. 2. Longevity of artificially cached seeds after removal of feeder as function of distance from feeder. Circles represent mean longevity (in days) of the four seeds at each distance in one experiment. Solid line is a linear regression $Y = 7.32 + 1.06X$. Dotted line represents mean disappearance for controls (i.e. for same locations without any feeder in center).

10 days. Controls had a mean longevity of 9.25 days ± 0.24, with a daily proportional disappearance of 1.3% ($P < 0.001$, $r^2 = 88.6$ or $r^2 = 88.1$, exponential or linear regression, respectively). This 1.3%, represented as a dashed line in Figure 2, I consider to be the background disappearance rate in the area in the absence of feeding devices.

During the whole experiment, only one seed (controls included) disappeared during the night. This indicates that pilfering by rodents was insignificant. I observed Great Tits (*P. major*) taking seeds from two feeders in the period preceding the removal. During the 10 days after removal, I once observed a Great Tit foraging in one of the experimental areas, whereas Willow Tits frequently foraged in the caching areas the days after removal.

Discussion.—Seeds in rebaited Willow Tit caches disappeared at a low rate of about 1.3% daily. This estimate was remarkably constant for two treatments in two different winters. Also, the disappearance for the controls in the feeder experiments was 1.3% per day. The similar disappearance rates between controls and rebaited caches indicate that my chosen artificial caching locations resemble the locations normally preferred by hoarding willow tits.

In all treatments the rebaited seeds were more conspicuous than the original seeds, which normally were difficult to find. Hence, the true "background" disappearance rate should be lower than my estimate. Also, some of the rebaited seeds may have been spotted by the original hoarder, even if the caching area is not revisited in order to retrieve caches. Thus, the daily long-term pilfering actually experienced by a hoarding Willow Tit should be considerably lower than my estimated disappearance rate of 1.3%, perhaps in the magnitude of 0.5%. With this low pilfering rate, a substantial proportion of stores from the autumn could still remain in late winter.

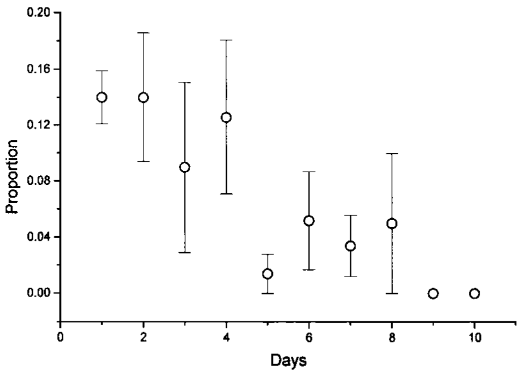

Fig. 3. Proportion of artificially cached seeds that disappeared as function of days after removal of feeder. Proportions would have been higher if only seeds closest to feeder had been included (see Fig. 2). Vertical bars indicate standard errors.

A high rate of cache loss in field experiments has made the idea of long-term hoarding in parids hard to reconcile with the economics that are required for evolutionary stability. Black-capped Chickadees remember the location of caches for at least four weeks (Hitchcock and Sherry 1990). During natural foraging Willow Tits separate caches vertically between individuals in the same territory (Brodin 1993), which should reduce cache losses. With a long-lasting memory and small cache losses, long-term hoarding in parids makes more sense. Only when hoarded seeds were accumulated in a restricted area (e.g. close to feeders) did the pilfering rate in my study approach the high levels reported for Marsh Tits.

Rebaited caches were monitored from mid-October to early May and since a constant proportion of seeds disappeared each day, the risk that a cache will be pilfered was constant during this period. This indicates that cache pilferers make the same searching effort irrespective of season. This seems difficult to reconcile with the fact that more time is allocated to search for food during late winter (Ekman 1987), when the food supply normally is low. The seeds could, however, become increasingly difficult to find, as they get more cryptic. Also, the winters of 1990–1991 and 1991–1992 were extremely mild, with only short periods below the freezing point. At least for foraging tits, this could mean a relaxed foraging stress, with less need to search for hoarded seeds.

In experiments with high pilfering rates, large seeds like sunflower or peanuts were provided (Cowie et al. 1981, Stevens and Krebs 1986). The seeds Willow Tits store under natural conditions are normally much smaller (Haftorn 1956a), and large seeds probably are more attractive for cache pilferers. Seeds hoarded around a feeder are retrieved faster than the same amount of seeds scattered over the territory (Brodin 1992). This could be adaptive considering the high pilfering rate close to the feeder.

Hoarded items may disappear for several reasons. First there is active recovery of short-term hoarded items with memory as a recovery mechanism, as in related species (Löhrl 1950, Cowie et al. 1981, Sherry et al. 1981, Sherry 1982, 1984, Shettleworth and Krebs 1982, 1986, Hitchcock and Sherry 1990). If caches are concentrated in a restricted area, the retrieval is probably combined with pilfering of caches of other flock members, since seeds artificially hoarded around a feeder disappear fast. This high pilfering rate, however, seems to be a short-term phenomenon intimately associated with the recovery of concentrated caches in the days after storing. A similar level of cache pilfering may also occur for naturally foraging Willow Tits, as I have observed Great Tits, Blue Tits (*P. caeruleus*) and dominant conspecifics steal food when it is stored. There is also a low, steady loss of seeds hoarded under natural conditions, which may be due both to pilfering and rain, wind, etc. This loss rate, however, is small enough to make long-term hoarding profitable.

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