Hoarding-site selection of the Willow Tit *Parus montanus* in the presence of the Siberian Tit *Parus cinctus*

Rauno V. Alatalo & Allan Carlson

Alatalo, R. V. & Carlson, A. 1987: Hoarding-site selection of the Willow Tit *Parus montanus* in the presence of the Siberian Tit *Parus cinctus*. — Ornis Fennica 64:1–9.

We studied the food-storing behaviour of the Willow Tit and the Siberian Tit feeding on an exceptionally good crop of spruce seeds in Northern Sweden during winter 1984. The two species form mixed flocks in the province of Lappland, while in Norrbotten, nearer the Baltic coast, only the Willow Tit is present. The aim was to examine whether the presence of the Siberian Tit has any effect on the food-storing behaviour of the Willow Tit. Our study areas were very similar in terms of tree species composition and canopy height.

When alone, Willow Tits hoarded spruce seeds on the three major tree species (spruce, pine and birch) in almost the same proportions in which these occurred. In Lappland Willow Tits hoarded less in pine and more in birch, while Siberian Tits showed a preference for pine and spruce. In Norrbotten Willow Tits mainly hoarded in the upper half of the trees but in Lappland they most often hoarded in the lower half. Siberian Tits in Lappland clearly preferred to store seeds in the upper half of the trees. Willow Tits transported seeds, on average, almost twice as far in Lappland as in Norrbotten, whereas Siberian Tits in Lappland flew distances as short as those flown by Willow Tits in Norrbotten. Agonistically, Siberian Tits were dominant over Willow Tits. These results suggest that, where the two species are sympatric, interspecific competition with Siberian Tits influences the choice of hoarding sites of individual Willow Tits.

Rauno V. Alatalo, Department of Biology, University of Jyväskylä, Yliopistonkatu 9, SF-40100, Jyväskylä, Finland and Allan Carlson, Department of Wildlife Ecology, The Swedish University of Agricultural Sciences, S-75007, Uppsala, Sweden.

Introduction

Several species of tits of the genus *Parus* coexist in the coniferous forests of Northern Europe. Each of these species usually frequents separate foraging sites (Haftorn 1956, Ulfstrand 1977, Alatalo 1982a). That this ecological segregation is at least partly caused by interspecific competition is suggested by several cases in which local absences of some of the species are accompanied by an expansion of the foraging niche of the remaining species (Alerstam et al. 1974, Hogstad 1978, Alatalo 1981, 1982b, Alatalo et al. 1986, for experimental evidence see Alatalo et al. 1985, 1987).

Four tit species inhabiting coniferous forest in Northern Europe regularly hoard food, mainly seeds of Pine (*Pinus silvestris*) and Spruce (*Picea abies*); viz. the Crested Tit (*Parus cristatus*), Willow Tit (*P. montanus*), Coal Tit (*P. ater*) and Siberian Tit (*P. cinctus*) (Haftorn 1953, 1956). These species are also frequently found foraging in mixed species flocks during the winter period. Andersson & Krebs (1978) presented a model stating the conditions necessary for hoarding to be adaptive in group-living species. They argue that, unless kin selection is important, hoarding will become established throughout a population of group-living species only when a hoarding individual is more likely to recover the items it has stored than any other group member.

Two possible mechanisms leading to the conditions stipulated by Andersson and Krebs have been suggested, namely memory of the exact storing sites and/or individually different patterns of storing sites coupled with individually different patterns of food searching (Andersson & Krebs 1978). Marsh Tits (*P. palustris*) have in fact been shown to memorize their storing sites exactly and to return to them to recover stored food (Cowie et al. 1981, Sherry 1982, Sherry et al. 1982, Shettleworth 1983). Marsh Tits almost always recovered stored seeds within a couple of days, but we may expect tits in northern coniferous forests to store food for longer periods, because they are known to store enormous amounts of seeds when these are abundant (Haftorn 1956). Haftorn's (1956) study showed that, at the species level, the distribution of the hoarding sites of coniferous forest tits fairly closely resembles the distribution of their winter foraging locations. When seed crops are abundant, tits are not likely to compete for this nearly non-limited resource, but seeds in

cones are available only during short periods, and interspecific competition for hoarded seeds is quite possible.

How is storage of food organized when members of two species occur in mixed flocks? In such a situation an individual should select hoarding sites that differ not only from those used by other individuals of the same species, but also from those used by individuals of the other species. Coexisting species do differ in their hoarding sites (Haftorn 1956, Moreno et al. 1981), but differences can be expected even in the absence of any interspecific competition. To test the possibility of interspecific competition, we studied the hoarding behaviour of Willow Tits in two areas in Northern Sweden. In the northernmost parts of the province of Norrbotten, Willow Tits occur in monospecific flocks, whereas in the province of Lappland they form mixed species flocks with Siberian Tits. If interspecific competition exists, Willow Tits should avoid hoarding sites used by Siberian Tits in the area of sympatry in Lappland.

Material and methods

In Northern Fennoscandia the spruce sets abundant seed crops only about twice during each decade, and the seeds usually become available to the tits in late winter, that is, March–April. In 1984 the seed crop of spruce was very plentiful and the cones opened relatively early. This study was carried out between 8 and 26 March and at that time the food eaten and hoarded by the Willow and Siberian Tits consisted almost exclusively of spruce seeds. To avoid seasonal bias, the observations in Norrbotten were made in the middle (10—15 March) of the two study periods used in Lappland (8—9 March and 16—26 March; 30 % of local observations in the earlier period). The average ambient temperature for the days of observation was –4.4°C (SD = 2.2, n = 6) in Norrbotten and –4.8°C (SD = 3.0, n = 13) in Lappland, so the weather conditions were similar.

The study locations are shown in Fig. 1. The study sites in the two provinces are separated by a distance of about 100 km; the altitude of the study sites was 130 to 375 m in Norrbotten, and 280 to 530 m in Lappland. In both study areas, we searched for tit flocks, concentrating upon areas with spruce, where most of the tits were spending their time. When we encountered a flock (= birds moving together at the time of observation) we made a description of the habitat in which the birds were hoarding. We estimated the relative frequency of different tree species (proportion of stems among the tall trees within 50 m) and the height of the canopy (<10 m or >10 m).

For each hoarding observation we recorded:

1) The height of the forest canopy.

2) The height from which the seed was taken and the height of the tree in question. Sometimes tits took seeds that had fallen on the snow (Norrbotten 14.5 % and Lappland 5 % of observations).

3) The distance from the seed source to the hoarding site.

4) The tree species used for hoarding.

5) The height of the hoarding site and the height of the tree used for hoarding. Relative hoarding heights (lowest quarter, second q., third q., top q.) were derived from these values and the absolute values are not presented here, as they did not add anything to the major patterns derived from the analysis of relative heights.

6) The type of branch on which food was hoarded (trunk, branch over 4 cm in diameter, 1—4 cm branch, twig less than 1 cm in diameter, needled twig).

7) The type of hoarding site (bark crevice, lichen, bud capsule, twig junction).

8) The horizontal position of the hoarding site (below, at the side, on the branch).

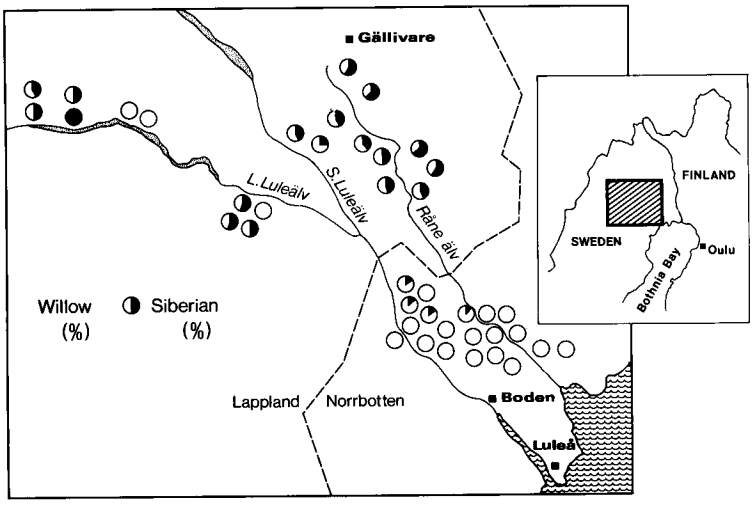


Fig. 1. Location of the study sites (circles) in the two provinces of Northern Sweden. At each site the proportion of recorded birds that were Siberian Tits is shown in black and Willow Tits in white.

All our hoarding records include information on points 1—5, but the type of branch could not always be seen (Willow Tit: 16.3 % in Norrbotten, 25.0 % in Lappland; Siberian Tit: 30.7 %). The type of hoarding site and its horizontal position were frequently missed, and we can therefore only present an approximate estimate of these variables biased to easily observable locations.

For each flock we observed up to 30 cases of hoarding for each tit species. Observations within a flock are obviously interdependent, and in the statistical tests we counted each flock as a single observation (average value). When testing the difference between hoarding sites of the Willow Tit in the presence and absence of Siberian Tits, we used one-tailed tests, since the statistical alternative hypothesis (H_1) is that Willow Tits avoid hoarding sites of Siberian Tits in their presence. We also recorded the composition of each flock and all hostile interactions between species.

To measure overlap of hoarding sites, we used the simple index of proportional overlap (= $\Sigma\min(p_{xi}, p_{yi})$), where p is the proportion, x and y are species, and i is the type of hoarding site. The direction and degree of shifts in hoarding sites of the Willow Tit were estimated by comparing the actual overlap between Siberian and Willow Tits in Lappland with that expected if Willow Tits had foraged as they did in Norrbotten (see Alatalo 1981, Alatalo 1982b).

Results

Flock composition

The winter flocks in Norrbotten mainly consisted of Willow Tits. Very few Siberian Tits, Crested Tits, Goldcrests (*Regulus regulus*), Great Tits (*Parus major*) or Treecreepers (*Certhia familiaris*) were seen in the study sites (Table 1). It should be noted that further south and along the coast all the other species are more abundant, except the Siberian Tit (e.g. at Boden, pers. obs.). It is therefore a rather narrow zone where Willow Tits so clearly outnumber all the other species in the tit flocks. Usually, 2—4 Willow Tits composed the flocks, with a maximum of 8 individuals. It may be that at the time of observation the flock had divided and we observed only a part of it, but this applies to both study areas.

The average total flock size in Lappland did not differ from that in Norrbotten (Table 1). Willow Tits were still encountered in almost all the flocks, but their numbers were only half of that in Norrbotten. Siberian Tits were almost as abundant in total numbers as Willow Tits in Lappland, though they were absent from approximately 40 % of the flocks encountered.

Table 1. Flock size (Mean no. of individuals) and composition in the two study areas (Constancy = percent of all flocks joined by the species).

	Norrbotten		Lappland	
	Size Ind.	Const. %	Size Ind.	Const. %
Willow Tit *Parus montanus*	3.70	96.2	1.97	94.3
Siberian Tit *P. cinctus*	0.13	9.4	1.66	61.4
Crested Tit *P. cristatus*	0.11	7.5	—	—
Great Tit *P. major*	0.08	5.7	0.27	17.1
Goldcrest *Regulus regulus*	0.04	1.9	—	—
Treecreeper *Certhia familiaris*	0.08	7.5	—	—
Average flock size	4.14		3.90	
Willow Tit %	89.4		50.5	
Siberian Tit %	3.1		42.6	
Other species %	7.5		6.9	
No. of flocks	53		70	

Table 2. Relative frequencies of tree species in habitats in the two study areas.

	Habitat of all flocks		Habitat in Lappland	
	Norrbotten	Lappland	Willow Tit flocks	Willow Tit + Siberian Tit flocks
Spruce *Picea abies*	0.442	0.416	0.421	0.428
Pine *Pinus silvestris*	0.293	0.278	0.277	0.286
Birch *Betula pubescens*	0.247	0.298	0.348	0.278
Aspen *Populus tremula*	0.007	0.007	—	0.008
Alder *Alnus incana*	0.011	—	—	—
Canopy height over 10 m (%)	92.5	90.0	77	97.5
No. of sampling sites	53	70	26	40

Habitat

There were no dramatic differences between the two provinces in the average composition of the tree species in the habitats where we recorded tits hoarding spruce seeds (Table 2). Birch was slightly more abundant in Lappland. In Norrbotten the average canopy height for the forests where Willow Tits hoarded was 15.6 m (SE = 0.51, n = 51) and in Lappland 16.7 m (SE = 0.52, n = 62, t-test, t = 1.43, P > 0.10). Within Lappland there was a slight difference in the habitats where we found flocks with only Willow Tits and where we encountered flocks with both Willow Tits and Siberian Tits. Sites where both species were found together had more pine and less birch than sites where the flocks consisted only of Willow Tits.

Hoarding tree

Willow Tits hoarded spruce seeds in the three major tree species (spruce, pine and birch) in almost the same proportion as these tree species occurred in Norrbotten (Fig. 2). In Lappland, however, they hoarded less in pine and more in birch, these differences being much greater than the slight

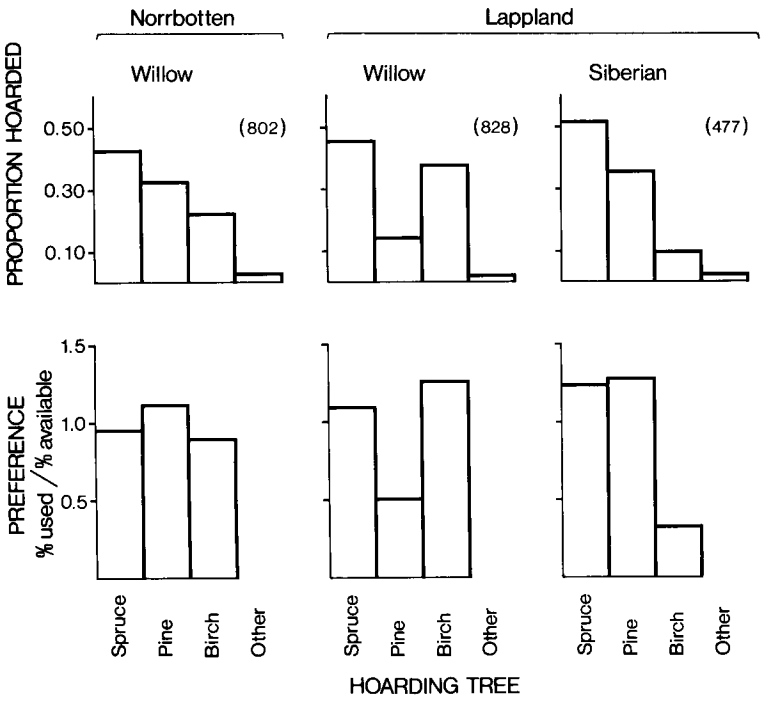


Fig. 2. Hoarding tree utilization and preference by the Willow Tit and the Siberian Tit in relation to tree availability in the two provinces. Numbers of observations in parentheses. In the flocks with at least five observations for the Willow Tit, its frequency of hoarding in pine was lower in Lapland (average 0.152, SD = 0.232, n = 54 flocks) than in Norrbotten (average 0.300, SD = 0.256, n = 45, Mann-Whitney U-test, z = 2.98, P < 0.01).

differences in the frequency of these tree species. Comparison of the flocks with at least five hoarding observations for the Willow Tit showed that the frequency of hoarding in pine was lower in Lappland than in Norrbotten (0.15 and 0.30, respectively, P < 0.01), although there was no significant difference in the frequency of pines in the hoarding areas of these flocks (Mann-Whitney U-test, z = 1.28, P > 0.20). Siberian Tits in Lappland preferred pine and spruce to birch, which was seldom used. The overlap index for the hoarding tree was 0.699 in Lappland, which is 0.181 less than would be expected (0.850) if Willow Tits had had the same pattern of hoarding tree exploitation as in Norrbotten.

Hoarding height

In Norrbotten the Willow Tits mainly hoarded in the upper half of the trees, but in Lappland the lower half was preferred (Fig. 3). The Siberian Tits stored most of their seeds in the upper half of the trees (Fig. 3). The difference in the hoarding height preferred by the Willow Tits in Lappland reduces the overlap in hoarding sites remarkably, by 0.340 units in spruce and 0.494 units in pine, the reduction in birch being intermediate (0.410).

For each flock with a minimum of 5 hoarding observations recorded in the given tree species, we calculated the relative hoarding height for the Willow and Siberian Tits (Fig. 3). In all three tree species, the hoarding heights were highly significantly (P < 0.001) lower for Willow Tits in Lappland than in Norrbotten.

Type of hoarding branch

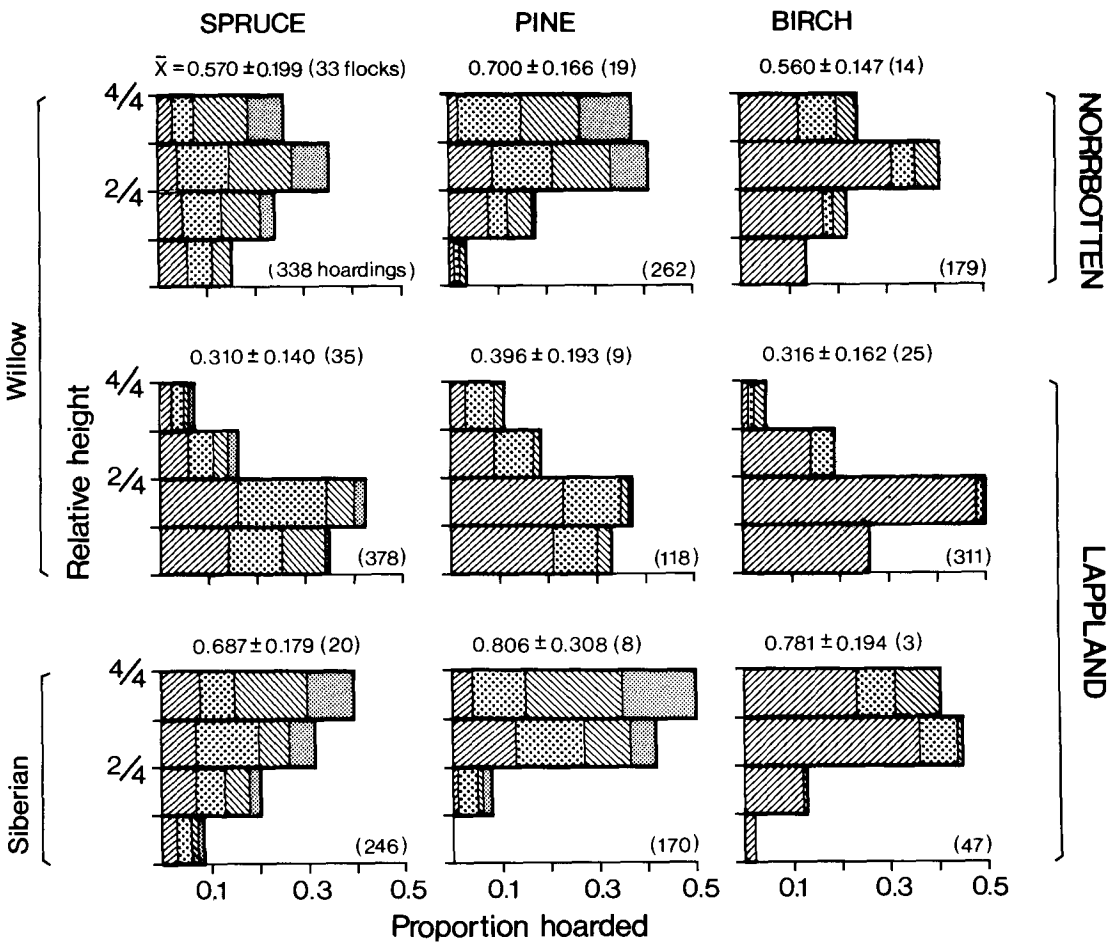
The type of branch was correlated with the relative hoarding height, the trunk and thick branches being used more at the lower heights (Fig. 3). However, relative height was more important than branch type for the separation of the two tit species in Lappland. The overlaps with respect to branch type are 0.796 in spruce, 0.578 in pine and 0.682 in birch, and for relative height they are 0.518, 0.378 and 0.387, respectively. In all three tree species and at each relative height, Willow Tits used inner tree parts more in the presence of Siberian Tits, so the difference in hoarding sites is not merely due to the difference in their height from the ground.

Type of hoarding site

The exact location of a hoarding site could usually not be seen. The data are therefore biased towards easily spotted sites, such as crevices on trunks. Bark crevices and lichen were the most frequently observed hoarding sites (Table 3). In both provinces Willow Tits preferred lichens on spruce, whereas bark crevices were the most common hoarding site in pine. In birch both species hoarded mainly in bark crevices. Both species stored seeds as often on the underside of twigs and branches as above them.

Hoarding distance

Willow Tits flew almost twice as far from a seed source to a hoarding site in Lappland as in



Height overlap in Lappland	SPRUCE	PINE	BIRCH
OBSERVED	0.518	0.378	0.387
EXPECTED	0.858	0.872	0.797
CHANGE	-0.340	-0.494	-0.410

Fig. 3. The hoarding site distribution (relative height and branch type) in spruce, pine and birch for the Willow and Siberian Tit in the two study areas. The average relative hoarding height (± SD) and the observed and expected (= data from Norrbotten for the Willow Tit) overlap in hoarding heights for Lappland are shown. Tree parts at each height from left to right; trunk (hatched rising), branch (stippled), twig (hatched declining) and needles (densely stippled). The relative hoarding height of the Willow Tit differed between flocks in the two provinces in spruce (Mann-Whitney U-test: $z = 5.21$, $P < 0.001$), pine ($z = 3.30$, $P < 0.001$) and birch ($z = 3.75$, $P < 0.001$).

Norrbotten (10.8 m, SD = 3.5, n = 54 flocks; 6.0 m, SD = 2.0, n = 46, respectively; $z = 6.70$, $P < 0.001$). Siberian Tits, on the other hand, had short hoarding distances (5.7 m, SD = 2.3, n = 29); they flew about the same distance as Willow Tits did in Norrbotten (Fig. 4). As the height of the spruces varied between the observation places, the seeds were available at different heights and the hoarding distances were shorter for the lower heights of collection (Fig. 4). This is probably simply due to differences in the availability of suitable hoarding sites near the cones. Still, this fact cannot explain the difference in the hoarding distances of the Willow Tits in the two provinces, since the heights of seed

Table 3. Type of hoarding sites.

	Norrbotten				Lappland			
	Crevices	Lichen	Other	n	Crevices	Lichen	Other	n
Spruce								
Willow Tit	0.24	0.67	0.09	103	0.30	0.64	0.06	56
Siberian Tit	—	—	—	—	0.14	0.75	0.11	36
Pine								
Willow Tit	0.59	0.37	0.04	56	0.73	0.21	0.06	33
Siberian Tit	—	—	—		0.22	0.61	0.17	23

collection were not lower in Lappland. It was only for seeds collected from snow or cones at a very low height (< 5 m) that there were no differences in the distance flown by Willow Tits in Norrbotten and Lappland.

Interference and hoarding behaviour

Comparison of Willow Tits in Lappland in flocks with and without Siberian Tits shows that they hoarded at slightly lower relative heights in spruce and in birch when the flock contained both species (Fig. 5). In the statistical tests we have combined data from flocks with less than five Willow Tit observations in spruce or birch, so that all combined flocks included at least this minimum number of observations. Since Willow Tits used pine much less in Lappland, even with such a combination of flocks, the data were too scarce to make any realistic test for this tree species. The difference in the foraging heights of Willow Tits is significant in both spruce and birch (Fig. 5), but the shifts are relatively slight, the overlap reductions being only 0.144 in spruce and 0.097 in birch. Even in flocks that at the moment of observation did not include any Siberian Tits, Willow Tits hoarded their seeds lower than in Norrbotten.

We recorded all the interspecific interactions in mixed species flocks and observed that Siberian Tits supplanted or chased Willow Tits in 37 cases, while the opposite happened only 3 times (binomial test, $P < 0.001$). Typically, supplanting attacks took place in spruce tops when tits were collecting seeds. At the hoarding site, a Siberian Tit supplanted a Willow Tit only once, apparently trying to take over the seed. Altogether, interference at the sites where the seeds are hidden is relatively infrequent, and we observed intraspecific interference only three times for Willow Tits; such interference was more frequent at the spruce tops where seeds were collected.

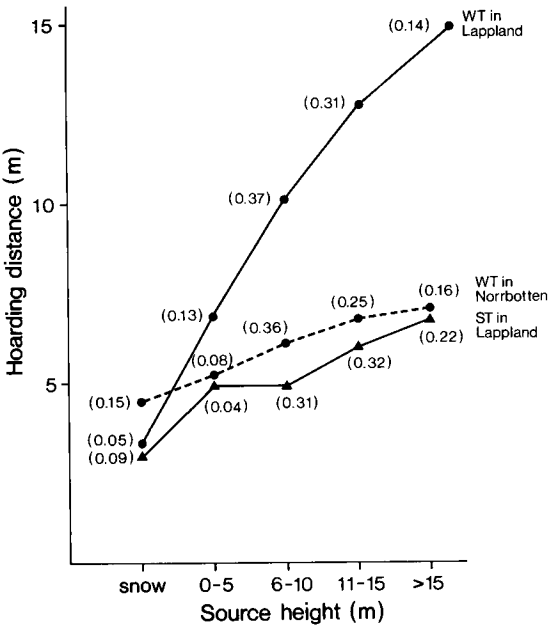


Fig. 4. The average distance between seed source and hoarding site in relation to the height of the seed source. Figures in brackets show the proportional use of various source heights, which are largely determined by the height of spruces in each place of observation. For numbers of observations see Fig. 2 and for tests see text (WT = Willow Tit, ST = Siberian Tit).

Discussion

The problem in interpreting geographical niche shifts is that any two areas under comparison are likely to differ in several environmental characters besides the presence or absence of putative competitors, and these environmental differences may be responsible for changes in foraging niches (Grant 1975, Connell 1980, Alatalo 1982b, Wiens 1983, Strong et al. 1984, Alatalo et al. 1986). The absence of Siberian Tits from Norrbotten is probably related to environmental differences, in climate or habitat, or both (see Järvinen & Väisänen 1979). In the present case, however, the likelihood that environmental differences caused the differences observed in the distribution of hoarding sites chosen by Willow Tits is reduced by the following three circumstances:

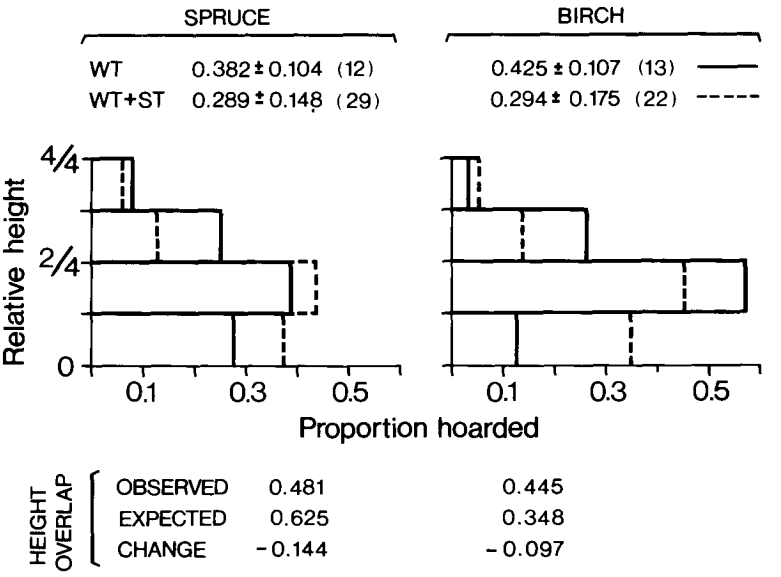


Fig. 5. The distribution of Willow Tit (WT) hoarding sites in Lappland in spruce and birch for monospecific flocks and flocks containing Siberian Tits (ST). The average relative hoarding heights (± SD, numbers of flocks in parentheses), under the name of the tree, were significantly different in both spruce (Mann-Whitney U-test; z=1.91, P < 0.05, one-tailed) and birch (z=2.24, P<0.025). The observed and expected (data from monospecific flocks of WT) overlaps of hoarding heights in two-species flocks are also shown.

1) Willow Tits avoid hoarding high in trees in the presence of Siberian Tits; this pattern is repeated in all of the three major tree species (spruce, pine, birch). Furthermore Willow Tits changed the preference of tree species used for hoarding in a way that reduced the overlap with Siberian Tits, and there is also a difference in hoarding heights between flocks that are joined by Siberian Tits and flocks where Willow Tits are alone. It seems unlikely that any environmental differences would produce such a consistent pattern of changes in the exact directions expected from interspecific competition.

2) The differences in hoarding heights were more pronounced than the differences in environment. The same tree species, with similar canopy heights and in almost similar proportions, were found in the two areas. In general, foraging niches of tits are rather insensitive to slight environmental variation between geographical areas; if there is no change in the presence of close competitors, differences in foraging niches are slight (Alatalo et al. 1986). Pronounced short-term changes in foraging site utilization may occur in response to changes in food availability (Alatalo 1980), and the shortness of our study period may be a problem. However, in this case we are studying the hoarding sites of food items collected from similar places in the two areas. The height from the ground of the seed source does influence the hoarding behaviour, but there were no marked differences in the distribution of source heights between the two provinces, and in the presence of Siberian Tits the behaviour of Willow Tits changed even in habitats where seeds were available at the same height (Fig. 4).

3) Willow Tits have been studied in several areas of Fennoscandia, and these studies show a remarkably consistent pattern of foraging niche shifts with changes in guild structure. Further south, in the presence of other species (Coal Tit, Crested Tit, Goldcrest), Willow Tits forage nearer the trunk and lower down in trees, avoiding the foraging sites of the three other species, which generally use higher and more exterior tree parts (Alatalo 1982b, Alatalo et al. 1986). The absence of a consistent latitudinal trend, with lower and inner foraging in the northern latitudes, rules out the possibility of some environmental explanation (e.g. effects of cold weather) connected with the latitude. Nor is there any consistent trend with respect to altitude, since with increasing altitude in Norway Willow Tits moved upwards and outwards in trees in the absence of Crested Tits (Hogstad 1978), while in this study Willow Tits foraged farther down at higher altitudes.

The most likely explanation is that the presence of Siberian Tits causes a change in the hoarding site selection of Willow Tits, but what is the exact reason for this change? If the use of stored seeds is mainly based on memory the change might not appear necessary. However, if Willow Tits are forced by interspecific competition to use lower tree parts for foraging for non-hoarded food, it should be economical to use the same parts for hoarding, to avoid an extra flight cost during the critical periods of food shortage when the stored food is consumed. Furthermore, it is conceivable that the tits can find food hoarded by other individuals, as the seeds are not always well hidden (see Haftorn 1953, 1956), and then it is obviously advantageous to avoid locations where individuals of another species are searching for food.

Given the difference in the height distribution, why is it the Willow Tits that hoard lower in trees and the Siberian Tits that use the upper parts? Ekman and Askenmo (1984) found that dominant Willow Tit

individuals foraged higher in trees than young subdominant individuals. The advantage of foraging higher in trees may lie in a smaller risk of predation or better food availability. When the dominants were removed, the subdominants moved upwards in the trees. Such interference competition may operate interspecifically between Siberian and Willow Tits. Siberian Tits were clearly dominant over Willow Tits, perhaps because of their slightly larger size. According to 10 museum specimens (British Museum) from Northern Fennoscandia, Siberian Tits have a wing length of 67.5 mm (SE = 0.45, n = 10) and tarsus length of 16.5 mm (SE = 0.12, n = 10). Willow Tits measured in the field in Northern Finland (Oulu, Tornio) had a wing length of 64.1 mm (SE = 0.52, n = 14) and tarsus length of 15.9 mm (SE = 0.07, n = 14).

In general, the species in the tit guild differ chiefly in the type of branch used for seeking food, and differences in foraging height are mainly a direct consequence of the fact that thin twigs and needled twigs occur more frequently higher in trees (Alatalo 1982a). The smallest species forage on the outermost tree parts and the heaviest on the innermost parts, which may partly be due to a relationship between the size of the birds and their foraging efficiency on different types of branches. Siberian and Willow Tits are similar in morphology, and therefore specific adaptations improving their foraging efficiency in their respective foraging sites are perhaps not very important and the species may segregate at different foraging heights due to social dominance relationships rather than to the type of foraging branches.

The differences in hoarding sites between flocks with and without Siberian Tits in Lappland were slight, and even in flocks without Siberian Tits the Willow Tits hoarded the food relatively low on the trees as compared with the hoarding sites in Norrbotten. It is probable that Siberian Tits occur in all of the flocks in the province of Lappland, and that they were only temporarily separated from Willow Tits during the observation periods, which usually lasted less than an hour per flock. The food items are hoarded for later use, and it may be too risky to hide the seeds high in trees, because Siberian Tits may join the flocks on other occasions and then exploit the upper tree parts.

In Lappland Willow Tits had to fly twice as far between the seed source and the hoarding sites, since they hoarded in the lower half of trees even when seeds were available in cones in tree tops. A substantial energetic cost is incurred in the longer transportation (see Tatner & Bryant 1986 for high costs of flying) in the area of sympatry, as seeds were stored intensively, up to several times per minute (see also Haftorn 1956).

In conclusion, it is likely that interspecific competition by Siberian Tits restricts the use of hoarding sites by Willow Tits in the area of sympatry. The segregation in hoarding sites is probably related to the separation in foraging sites. It is economical to hoard in the same sites in which the bird forages for other food items. This will also reduce the risk of other individuals finding the stored food items. There are many open questions with respect to the mechanisms of competition, but it is possible that social dominance (interference competition) is the reason why Siberian Tits use the highest sections in trees.

Acknowledgements. We thank J. Ekman, T. Fagerström, S. G. Nilsson, M. Orell and S. Ulfstrand for valuable comments on the manuscript. The study was supported by grants from the Swedish Natural Science Research Council and the Academy of Finland.

Selostus: **Ravinnon varastointipaikat hömötiaisella lapintiaisten läsnäollessa**

Me tutkimme hömö- ja lapintiaisen ravinnonvarastointipaikkoja Pohjois-Ruotsissa talvella 1984, jolloin kuusen siemensato oli poikkeuksellisen runsas. Lapplandin läänissä molemmat lajit esiintyvät sekaparvissa, kun taas Norrbottenin läänissä lähempänä Perämeren rannikkoa tiaisparvet koostuvat pääosin pelkästään hömötiaisista (kuva 1, taulukko 1). Tarkoituksena oli tutkia mikäli lajien välinen kilpailu vaikuttaa ravinnonvarastointipaikkojen valintaan, jolloin voidaan odottaa hömötiaisten muuttavan käyttäytymistään lapintiaisen läsnäollessa. Kuusen siemenet varastoidaan yleensä yksitellen puun kuoren koloihin tai jäkälän suojaan (taulukko 3). Muiden tutkimusten mukaan on todennäköistä, että linnut varastoivat niihin puunosiin, joista ne myös muutoin etsivät ravintoa. Samoin tiaiset voivat muistaa suuriakin määriä varastointipaikkoja.

Norrbottenissa hömötiaiset varastoivat kuusen siemeniä kolmeen pääpuulajiin (kuusi, mänty, koivu) lähes samassa suhteessa kuin näitä puulajeja oli tarjolla kyseisillä biotoopeilla (taulukko 2, kuva 2). Lapplandissa hömötiaiset vähensivät mäntyihin varastoimista ja lisäsivät koivun käyttöä, kun taas lapintiaiset suosivat mäntyä ja kuusta. Vielä selvempi muutos tapahtui siementen sijoittamisessa puun eri osiin (kuva 3). Lapintiaiset varastoivat yleisesti puiden yläosiin, ja niinpä hömötiaiset suosivat selvästi puiden alaosia Lapplandissa kun ne Norrbottenissa varastoivat runsaasti myös puiden yläosiin. Lapplandissa hömötiaiset joutuivat kuljettamaan siemeniä keskimäärin kaksi kertaa pitemmän matkan kuin hömötiaiset Norrbottenissa tai lapintiaiset Lapplandissa (kuva 4). Lapintiaiset olivat sosiaalisesti dominoivia hömötiaisiin nähden.

Tulokset tukevat näkemystä, että lajien välinen kilpailu vaikuttaa tiaisten ravinnonvarastointipaikkojen valintaan. On epätodennäköistä, että muutokset hömötiaisella selittyisivät pelkästään ympäristötekijöiden alueellisilla eroilla. Puusto ja puiden korkeus olivat sangen samanlaisia Norrbottenissa ja Lapplandissa (taulukko 2). Luonnollisesti ympäristö ei kuitenkaan ole täysin samanlainen, mutta olisi yllättävää että ympäristötekijät pystyisivät aiheuttamaan kaikki hömötiaisella havaitut muutokset, jotka olivat aina siihen suuntaan kuin on odotettavissa jos lajien välinen kilpailu on muutosten syynä. Hömötiaiset muuttivat sekä puulajivalintaa että suhteellista varastointikorkeutta kaikissa kolmessa puulajissa. Lisäksi vertailtaessa Lapplandin eri parvia hömötiaiset varastoivat puihin hieman alemmaksi niissä parvissa, joissa lapintiaiset olivat läsnä verrattuna parviin, joissa hömötiaiset

olivat havaintohetkellä yksinään (kuva 5). Lisäksi muutokset varastopaikkojen korkeuksissa olivat erittäin selviä, kun yleensä tiaiset eivät juuri muuta ruokailupaikkojen valintaa saman puulajin sisällä eri maantieteellisillä alueilla mikäli lajienvälinen kilpailupaine on muuttumaton. Hömötiaisia on tutkittu myös monilla muilla alueilla Pohjoismaissa ja lajin ruokailupaikat vaihtelevat nimenomaan sen mukaan mitä kilpailevia tiaislajeja kullakin alueella esiintyy.

Voisi kysyä, miten lajien välinen kilpailu voi vaikuttaa varastointipaikkojen valintaan, jos tiaiset muistavat varastoitujen siementensä tarkat paikat. On kuitenkin mahdollista, että myös toiset yksilöt voivat löytää varastoja. Lisäksi liikkumistarpeen vähentämiseksi ravinnon kannalta kriittisinä aikoina on edullista varastoida niihin puun osiin, joissa kukin yksilö muutoinkin etsii ravintoansa, ja kilpailun vaikutus voisi silloin myös näkyä varastointipaikkojen valinnassa.

References

Alatalo, R. V. 1980: Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. — Oecologia (Berl.) 45:190–196.

Alatalo, R. V. 1981: Interspecific competition in tits Parus spp. and the goldcrest Regulus regulus: foraging shifts in multispecies flocks. — Oikos 37:335–344.

Alatalo, R. V. 1982a: Multidimensional niche organization of foliage-gleaning birds in northern Finland. — Ornis Scand. 13:56–71.

Alatalo, R. V. 1982b: Evidence for interspecific competition among European tits Parus spp.: a review. — Ann. Zool. Fennici 19:309–317.

Alatalo, R. V., Gustafsson, L., Linden, M. & Lundberg, A. 1985: Interspecific competition and niche shifts in tits and the goldcrest: an experiment. — J. Anim. Ecol. 54: 977–984.

Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1986: Interspecific competition and niche shifts in tits Parus: evaluation of non-experimental data. — Amer. Nat. 127: 819–834.

Alatalo, R. V., Eriksson, D., Gustafsson, L. & Larsson, K. 1987: Exploitation competition influences the use of foraging sites by tits: experimental evidence. — Ecology, in press.

Alerstam, T., Nilsson, S. G. & Ulfstrand, S. 1974: Niche organization during winter in woodland birds in southern Sweden and the island of Gotland. — Oikos 25:321–330.

Andersson, M. & Krebs, J. R. 1978: On the evolution of hoarding behaviour. — Anim. Behav. 26:707–711.

Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of the competition past. — Oikos 35:131–138.

Cowie, R. J., Krebs, J. R. & Sherry, D. F. 1981: Food storing by marsh tits. — Anim. Behav. 29:1252–1259.

Ekman, J. & Askenmo, C. 1984: Social rank and habitat use in willow tit groups. — Anim. Behav. 32:508–514.

Grant, P. R. 1975: The classical case of character displacement. — Evol. Biol. 8:237–337.

Haftorn, S. 1953: Observasjoner over hamstring av naering også hos lappmeis Parus c. cinctus Bodd. — Kgl. Norske Vidensk. Selsk. Forh. 26:76–82.

Haftorn, S. 1956: Contribution to the food biology of tits, especially about storing 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.

Hogstad, O. 1978: Differentiation of foraging niche among tits, Parus spp., in Norway during winter. — Ibis 120:139–146.

Järvinen, O. & Väisänen, R. A. 1979: Climate changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. — Oikos 33:261–271.

Moreno, J., Lundberg, A. & Carlson, A. 1981: Hoarding of individual nuthatches Sitta europaea and marsh tits Parus palustris. — Holarct. Ecol. 4:263–269.

Sherry, D. F. 1982: Food storage, memory, and marsh tits. — Anim. Behav. 30:631–632.

Sherry, D. F., Avery, M. & Stevens, A. 1982: The spacing of stored food by marsh tits. — Z. Tierpsycho. 58:153–162.

Shettleworth, S. J. 1983: Memory in food-hoarding birds. — Sci. Am. 248:86–94.

Strong, D. R., Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. 1984: Ecological communities: conceptual issues and the evidence. — Princeton Univ. Press, Princeton, NJ.

Tatner, P. & Bryant, D. M. 1986: Flight cost of a small passerine measured using doubly labeled water: implications for energetic studies. — Auk 103:169–180.

Ulfstrand, S. 1977: Foraging niche dynamics and overlap in a guild of passerine birds in a South Swedish coniferous woodland. — Oecologia (Berl.) 27:23–45.

Wiens, J. A. 1983: Avian community ecology: an iconoclastic view. — In: Brush, A. H. & Clark, G. A. (eds.), Perspectives in ornithology, pp. 355–403. Cambridge Univ. Press, Cambridge.

Received December 1986, accepted February 1987