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Academic Dissertation

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To my son Juhana

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PREDATION RISK AND COMPETITION IN MIXED SPECIES TIT FLOCKS

Jukka Suhonen

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In coniferous forests of Northern Europe, tits (*Parus* spp.) and the goldcrest (*Regulus regulus*) exploit nonrenewable resources in their group territories during winter. Results of many studies have indicated that interspecific competition restricts the use of foraging sites in mixed species winter flocks of tits. There was a high correlation between food abundance and bird density over different parts of spruce suggesting that the availability of food influences the distribution of foraging sites of tits and goldcrest. However, foraging site distributions cannot be explained solely by food abundance. In outer tree parts there were fewer birds than would be expected from arthropod biomass.

A possible explanation is that the risk of predation by pygmy owls (*Glaucidium passerinum*) is high in the outer tree parts reducing the net benefit of foraging in the food-richest tree parts. The risk of predation by the pygmy owl is higher for subdominant species foraging in the exterior tree parts, i.e. the coal tit (*P. ater*) and the goldcrest. The dominant species, the crested tit (*P. cristatus*) and the willow tit (*P. montanus*), which forage on inner tree parts, were killed less frequently by the pygmy owl. The risk of predation by pygmy owls varies greatly with the availability of voles as the preferred prey. Both willow and crested tits changed to forage in inner parts of coniferous trees after the vole populations had crashed and when pygmy owls started to hunt tits. Additionally both in pine and birch willow tits moved towards the tree tops, the safest sites of those trees, under high predation risk. However, there were individual differences in the response to the change in the predation risk level. Both female crested tits and adult willow tits moved from outer parts of spruce towards the tree trunk with increased risk of predation. However, male crested tits, which are highest in social rank in the flock, exhibited no response to the pygmy owl, but they were rather safe from predation in any case. It seems that both interspecific competition and site-dependent risk of predation govern the

ways in which these four bird species select their foraging sites in spruce.

Additional food has been shown to increase winter survival of tits. Tits regularly hoard enormous amounts of seeds mainly during the autumn presumably to be used during the winter. Willow and crested tits tended to avoid to hoard in the locations in which the other species forages, suggesting that the risk of interspecific kleptoparasitism influences the selection of hoarding sites. An aviary experiment demonstrated that the cacher willow tit has a higher recovery rate for its own caches than for caches made by other individuals. Moreover, the individuals of another species included in the experiment, great tits, had lowest recovery rate of caches. It seems that food storing is adaptive to the cachers because they have the best recovery rate for their own stored seeds. However, the results indicate that there remained a high risk to lose the caches to conspecific individuals and low probability to lose the caches to individuals of other species.

Key words: *Parus*; *Regulus regulus*; *Glaucidium passerinum*; arthropod food supply; predation; competition; social organization; food hoarding.

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The thesis is based on the following papers, which will be referred to in the text by the Roman numerals I-VI:

I. Suhonen, J., Alatalo, R. V., Carlson, A. & Höglund, J. 1991: Food resource distribution and the organization of the *Parus* guild in a spruce forest. - In manuscript (submitted).

II. Suhonen, J. 1991: Predation risk influences the use of foraging sites by tits. - In manuscript (submitted).

III. Suhonen, J. 1991: Risk of predation and foraging sites of individual tits in mixed-species flocks. - In manuscript (submitted).

IV. Suhonen, J., Halonen, M. & Mappes, T. 1991: Predation-risk and the organization of the Parus guild. In manuscript (submitted).

V. Suhonen, J. & Alatalo, R.V. 1991: Hoarding sites in mixed flocks of willow and crested tits. - Ornis Scand. 22:88-93.

VI. Suhonen, J. & Inki, K. 1991: Recovery of food caches by other individuals in mixed species tit (*Parus*) flocks. - In manuscript (submitted).

Contents

1. Introduction

Interspecific competition has often been invoked as the main organizing factor in particular, for bird communities (e.g. MacArthur 1972, Cody 1974, Alatalo 1981, 1982a,b, Schoener 1974, 1982, Alatalo et al. 1985, 1986, 1987, Alatalo & Moreno 1987, Wiens 1989a,b), but its importance has also been severely questioned (reviews in Wiens 1977, 1989a,b, Schoener 1982) and in some papers predation has been demonstrated to influence the bird community and guild organisation (Pulliam & Mills 1977, Ekman 1986, Lima et al. 1987, Székely et al. 1989, Lima & Valone 1991, Watts 1991). The best evidence for the importance of predators comes from the work in aquatic communities (e.g. Paine 1966, Zaret 1980, Sih et al. 1985). The issue is much less clear for terrestrial communities or guilds, although the importance of predation has been well recognized at the level of single populations. For instance several studies indicate that cover-dependent birds perceive a high risk of predation while feeding away from cover and thus prefer to feed as close to it as possible (e.g. Grubb & Greenwald 1982, Schneider 1984, Ekman 1987, see also Lima & Dill 1990), where they need not spend as much time for antipredatory vigilance (Caraco et al. 1980a, Ekman 1987, Lima 1987).

Experimental additions of food have demonstrated that tits are food limited during winter (Jansson et al. 1981). However, much less has been done to directly study the distribution of food resources with respect to the organization of the guild exploiting them. Studies of resource partitioning have a long history in bird ecology (see Wiens 1989a,b), but detailed studies including the resource availability of birds have been done only in Darwin's finhes (Grant 1986), in nectarivorous birds (for a review see Wiens 1989b), in forest passerines (Holmes and Schultz 1988) and in birds of prey (e.g. Korpimäki & Norrdahl 1991).

The northern coniferous forest tit guild is one of the most studied bird guilds (Gibb 1954, 1960, Haftorn 1956; for reviews see Alatalo 1982b, Alatalo et al. 1986). In the non-breeding season the members of the guild form mixed flocks, each species having preferences for different tree species and type of foraging sites within trees (Haftorn 1956, Ulfstrand 1977, Alatalo 1982a). These species have largely overlapping diets

consisting of seeds, spiders and other arthropods (Palmgren 1932, Haftorn 1956, Jansson 1982). Arthropod food is a nonrenewable resource during the winter (Askenmo et al. 1977, Jansson & Brömssen 1981). Crested tits, willow tits, coal tits and Siberian tits (P. cinctus) regularly hoard food (Haftorn 1953, 1956, Pravosudov 1985, 1987, Alatalo & Carlson 1987). In tit flocks the heavier species are socially dominant over the lighter ones (Hogstad 1978, Morse 1978). The pygmy owl (*Glaucidium passerinum*) is the main diurnal predator of small passerines during winter in Northern Europe (Ekman 1986). It caches birds and small mammals to holes and nestboxes during late autumn and winter (Kellomäki 1966, 1977, Solheim 1984).

To understand foraging site selection of tits and goldcrest, we need data from many factors such as food resource distribution, interspecific competition, predation and their interaction. In this study I investigate the following questions: (1) Do different tit species and goldcrest segregate spatially with respect to their food resources (I). (2) How does predation risk affect foraging site selection (II, III, IV). (3) Does interspecific kleptoparasitism affect the choice of hoarding sites (V) and (4) do other members of the tit flock find seeds stored by the willow tit (VI).

2. Study areas

The study was conducted in two different areas, one around the Grimsö Wildlife Research Station in Central Sweden (59°40' N, 15°25' E) and another around the Konnevesi Research Station (62°37' N, 26°20'E) in Central Finland. The area in Sweden is situated in the southernmost part of the boreal zone and is mainly covered by coniferous forest dominated by spruce (*Picea abies*) and pine (*Pinus silvestris*). The study area in Finland is covered mainly by coniferous forest of spruce and pine including some deciduous birches (*Betula* spp). Both study areas have long winters with snow-cover usually lasting over five months.

3. Material and methods

3.1. Arthropod sampling

Study I

Arthropod prey in spruce was sampled in Central Sweden from 4 and 6 trees in 1985 and 1986, respectively. The samples were collected in late November when temperatures already were below zero and the arthropods were inactive. Hence, the samples represent the total amount of these nonrenewable resources, which tits and goldcrests exploit throughout the rest of the winter. In spruce-dominated forest, ten spruces (>18 m high) were randomly selected as sampling units. We randomly selected one branch in each of the four height quarters of the tree. We counted the number of branches 0.5 m above and below the sampled branch to be able to estimate the total numbers and biomasses of arthropods in each quarter and the whole tree. In the laboratory each sampled tree part was weighed. Arthropods larger than 1 mm in size were collected and preserved in 70% ethanol. Each item was measured to the nearest 0.5 mm (body length) and weighed with a microbalance after drying for 24 hours in an oven (60^{o}C).

3.2. Foraging and hoarding sites

Studies I, II, III, V

The use of foraging sites by tits was observed during midwinter (January - early March). The type of substrate (or tree part) in this study was divided into four categories (trunk; branch, > 1 cm in diameter; twig, < 1 cm in diameter; and needled twig, usually < 1 cm in diameter) as has

been done in many other studies (Alerstam et al. 1974, Alatalo 1982a,b, Alatalo et al. 1985, 1987). It is sometimes difficult to see the type of substrate in the inner parts of spruce and we also estimated the distance of the bird from the trunk and the length of the branch used by the bird. Distance from trunk was transformed to relative distance (distance/branch length) and divided into two or four categories for further analysis. In the same way the height in trees was transformed into four relative heights. Observations on a focal bird were made at 15 s intervals prompted by a signal from a metronome and up to 10 (usually <4) observations were made on the same individual on each occasion. To randomize observation, the first records were made 15 seconds after the bird was sighted. All the observations were dictated to a tape-recorder and transcribed later.

The hoarding sites used by tits were recorded from late autumn to early winter (October - early December). The tits were followed after they collected seeds from the feeder and for each act of caching, typically 10-30 m from the feeder, we recorded the following information: tree species, substrate type, distance from trunk, length of branch and height of tree.

3.3. Winter diet of the pygmy owl

Studies II, III, IV

The diet of the pygmy owl, which cache prey items in nestboxes, was studied around the Konnevesi Research Station during winters 1988-1990. The nestboxes had an entrance hole (45 mm) too small to be used by any other owls (Solheim 1984) (II, III).

Data from the pygmy owl predation on members of tit flocks were also extracted from the literature from six areas in Northern Europe. Information on killed willow, crested and coal tits and goldcrests was extracted from papers on the food hoarding by the pygmy owl. Relative abundances of members of the tit guild were received from winter bird censuses in the same areas (IV).

3.4. Age and sex of captured birds

Study III

I captured willow and crested tits with mist nets from 15 September to 15 December using song play-back and artificial feeding sites to mark the individuals with colour rings. Tail and wing length were measured with a ruler to the nearest 0.5 mm. I separated first year birds from older individuals by the abrasion and shape of tail, which is a reliable indicator particularly in early winter (Laaksonen & Lehikoinen 1976). For sexing I used the wing length (see Haftorn 1982, Hogstad 1987, Koivula & Orell 1988). The error in sexing the birds by this criterion is about 5 % (see Alatalo & Helle 1990).

3.5. Aviary experiment

Study VI

The experiment was conducted in an aviary measuring 2.3 x 2.1 x 2.0 m with roof and walls covered with plastic sheet. There were four branches of spruce and two pieces of spruce trunk in the aviary. The observations were made through small windows (15 x 5 cm) in walls. In the experiment we used eleven willow tits and eleven great tits. The birds were kept indoors in individual cages on a 12:12 hour light:dark cycle. They were fed mainly with seeds, mealworms and water. Each bird was permitted to forage singly in the aviary to habituate the birds to the aviary. Later each willow tit individual was allowed to cache spruce seeds in the aviary and search 30 minutes for its own caches 24h later. In addition to this, both another willow tit individual and a great tit was permitted to search caches made by each willow tit.

3.6. Statistical analyses

To ensure appropriate replication (see Hurlbert 1984) each geographical area (IV), flock (II, V) or individual bird (III, VI) was used as independent observations for statistical testing. Overlap in foraging and hoarding niche utilization was estimated by the overlap index: $O = \Sigma \min (p_{xi}, p_{yi})$ where p_{xi} and p_{yi} are the proportions of hoarding or feeding in site i by species x and y respectively, and min indicates minimum (Renkonen 1938, see also Hurlbert 1978:Eq. 1).

4. Results

4.1. Food resource distribution and the organization of the *Parus* guild

The number of arthropods on branches increased with relative tree height both in the inner and the outer parts of branches (I). Outer parts of the branches held significantly more items than the inner parts on all heights. Arthropods were somewhat smaller in size in the upper tree parts. However, there were no differences in the size of arthropods between the inner and the outer halves of branches. The biomasses were highest in the uppermost quarters and outermost halves of branches creating a very uneven distribution of food resources for tits within spruce trees.

If resource availability is crucial for the organization of resource utilization one would expect a good correspondence between the arthropod biomass in each section and the total number of birds exploiting that section. The total number of birds was in fact highly correlated with food abundance ($r_s = 0.90$, $P < 0.01$, $n = 8$). However there is a general tendency of fewer birds in relation to arthropod biomass in the outer halves of branches compared to inner halves. A way to look at

the resource availability for each species is to estimate the average arthropod biomass in the foraging niche of each species. The average food abundance was highest for the coal tit, followed by the goldcrest, crested and the willow tit.

4.2. Risk of predation and foraging sites of tits

Predation risk by pygmy owls varies greatly with the availability of voles that have three to five year population cycles (Hansson & Henttonen 1985). In Central Finland both willow and crested tits changed to forage in the inner parts of coniferous trees after vole populations had crashed and owls started to hunt on tits. Additionally, both in pine and birch willow tit moved towards the tree tops, the saftest part of those trees, under high predation risk(II). There were more willow tits and goldcrests in the flocks in the high predation risk winter, and the flocks were larger than in the low risk year (II). However, there were individual differences in response to the change in predation risk (III). In general under high predation risk individuals foraged more on the inner parts of spruce, except male crested tits that exhibited no response to increased risk of predation. Juvenile willow tits did not change their relative distance from tree trunk, but they foraged more on the lower parts of spruce in the presence of predators.

Ekman (1986, 1987) suggested that the risk of predation by pygmy owls is higher for tits foraging in exterior and lower tree parts. This idea is supported by a comparison of six different areas in Northern Europe and Russia (IV). Coal tits and goldcrests, mostly feeding in the exterior tree parts, were overrepresented in the food caches of pygmy owls. In contrast willow and crested tits that forage in inner tree parts were always underrepresented compared with their local abundances (VI).

4.3. Food hoarding in mixed species tit flocks

In mixed species tit flocks both crested tits and willow tits avoid the locations in which the other species forages, suggesting that the risk of interspecific kleptoparasitism influences the selection of hoarding sites

(V). Overlaps in hoarding sites were smaller than overlaps in the foraging niches in spruce. The reduction in the overlap of hoarding sites was due to crested tits hoarding relatively many seeds in the outer parts of spruce branches and willow tits hoarding many seeds on the trunk and the thickest branches (V). However, a considerable overlap remained in the feeding and hoarding sites of the two species.

In addition, willow tits have large overlap in foraging with great tits. Aviary experiments demonstrated that willow tits found a greater proportion of their own caches and on a faster rate than other flock members. On the other hand, willow tits were much better in finding cached seeds of another willow tit than were the great tits. The willow tits hide seeds carefully, which decreases the possibility that other individuals find the caches (IV).

5. Discussion

5.1. Food resource distribution and organization of *Parus* guild

Is the tit guild saturated relation to food availability? One indication of this is the amount of food available for an individual bird, and how does this vary between species. The species differ only slightly in this last respect, maximum difference being in the order of 40-70 % (coal tit vs willow tit) (I). If food resources were unimportant, the differences between species could easily be much higher, since food supply itself varies over the tree parts much more. The outer halves of branches highest up have about 20 times more food than inner branches lowest down. Finally, the importance of food resources is most directly visible in the high correlation between food abundance and the number of birds foraging in each section of the spruce.

The species seem to divide the resources quite equally between them. However, an alternative way to look at saturation of resource use is to see how evenly distributed is the food abundance per individual bird

over each tree part. In this case, we see that variation over tree parts is much higher, outer tree parts having approximately three times more arthropods per bird than the inner tree parts. If we assume that limited availability of the arthropod food is the main selective factor influencing the foraging site selection of each individual bird in the flocks, then a higher number of tits should be feeding in the outer tree parts. Arthropods were most abundant in the foraging sites of the most subdominant species, a fact that also speaks against the idea that food availability alone could explain the ways in which a mixed species flock of tits and goldcrest is spatially organized.

One possibility is that the value of food items differs between tree parts or between the different species foraging niches. It is also possible that the exterior tree parts require more energy-demanding food searching methods (Norberg 1977, Alatalo 1982c, Alatalo & Moreno 1987). Therefore the heavier species, willow and crested tit could be less efficient in using the outer tree parts. The food in outer tree parts might also be less accessible to birds, in particular during the days when the trees are covered by snow.

5.2. Interspecific competition

There is a non-random pattern that in the absence of some species the remaining species do partly fill the vacant foraging niche (Alatalo et al. 1986, for experimental evidence see Alatalo et al. 1985, 1987, see also IV). It is the species morphologically most similar to the one absent that is likely to shift its foraging niche. This result supports the idea that interspecific competition restricts the use of foraging sites. The coal tits and goldcrest increased foraging on the inner parts of tree, when willow tits and crested tits were not in the area (allopatry; Alerstam et al. 1974) or when they were experimentally removed (Alatalo et al. 1985). These shifts are likely to decrease the risk of predation. However, the experimental removal of the two smaller species resulted in crested and willow tits increasing the use of exterior tree parts (Alatalo et al. 1987). In this case interspecific competition decreased between remaining species. Risk of predation should have increased for the species which shifted to forage more in the outer tree parts. It is likely that the net benefit was

higher than the cost of increased risk of predation, higher food supply compensating the costs (IV).

When the predation risk was high, both willow and crested tits changed to forage in the inner tree parts in spruce and so did also the willow tits in pine. However there were more subdominant goldcrest individuals in the flocks during high predation risk winter and interspecific competition may explain this kind of niche shift. The goldcrest forages more on exterior parts of tree than the dominant crested and willow tits (Alatalo et al. 1985, 1987). In the field experiment Alatalo et al. (1987) found that crested tits foraged farther outwards on branches of spruce in flocks, in which both coal tits and goldcrest were removed than in the control flocks. Likewise willow tits foraged more on outer tree parts of pine in experimental flocks than in control flocks (Alatalo et al. 1987). The willow tits foraged on lower parts of spruce when risk of predation was high probably because dominant crested tits changed to forage closer the trunk. As a consequence of their low social status the willow tits may be not able to forage freely in all parts of spruce. A support for this idea comes from the experiments where the dominant adults, foraging higher up in trees, were removed from willow tit flocks, and subdominant first year birds changed to forage more on the higher parts of tree (Ekman & Askenmo 1984, Hogstad 1988b).

5.3. Predation by pygmy owl

The most likely explanation for the discrepancies is a higher risk of predation in less covered, outer tree parts. This hypothesis is supported by Ekman (1986) and paper VI. In both studies coal tits and goldcrests had a higher risk of predation by pygmy owls than crested or willow tits. There could be a trade-off between food availability, predation risk and dominance affecting the ways in which the foraging sites within the guild are structured.

The number of willow and crested tits killed by pygmy owls in winter also decreases significantly when extra food is provided (Jansson et al. 1981) suggesting that such time adjustments have direct bearing on predation risk. When food was provided, willow tits immediately

retreated to the most protected sites (in the inner sections of spruce, Ekman 1987).

When the risk of predation was high, both willow and crested tits changed to forage on the inner tree parts in spruce (II, III). Additionally, both in pine and birch willow tits moved towards the tree tops under high predation risk. Since all the foraging shifts were towards the sites that are safest from predation risk, it seems that predation risk influences the use of foraging sites by tits in coniferous forest. There are many other factors supporting the predation risk hypothesis. The willow tits spend more time scanning for predators on outer parts of spruce than in inner parts (Ekman 1987). When predation risk increases, birds do increase their time for predator scanning and the proportion of time for foraging decreases (e.g. Caraco et al. 1980b) It is therefore beneficial to forage in inner parts of tree, where birds are more protected from attacking predators and have more time for feeding (Caraco et al. 1980a, Ekman 1987).

The subordinate members of the flock seem to gain only limited access to preferred microhabitats. Despite the subordination cost, flocking is still a better alternative for subordinates than to remain solitary since they can reduce vigilance time as flock members (Ekman 1987; Hogstad 1988a). During high risk of predation the coherence of tit individuals was higher, since more individuals were in the flocks than during the time of low risk of predation (Ekman 1987, II). One should expect, as was found by Ekman et al. (1981) that the winter survival rate of willow tits in the flocks of average size made up solely of juveniles to be equal to that of members in mixed-aged flocks. However, the recorded decrease in the winter survival rate of juvenile willow tits when adults were removed suggests that the juveniles achieve an improvement in their fitness by keeping company with adults (Hogstad 1989).

Also other individuals than the subordinates may benefit from flocking. For dominant males it may be beneficial that their mates survive over the period when risk of predation is high, as they otherwise risk losing the next breeding season. The dominant pair can be seen as a cooperative alliance based on mutual benefits. For males the benefits are not immediately recognizable, but it will pay for males to provide protection for females in winter if they can expect with sufficiently high probability that the help is returned by the female in reproductive success (Ekman 1990).

5.4. Food hoarding

Additional food increased winter survival of tits (Jansson et al. 1981). The habit of tits to hoard food to be used later in the winter (Haftorn 1956, Pravosudov 1987, V) may have important effects on winter survival and on the choice of foraging niche. When extra food was provided, willow tits immediately retreated from pine to the protected trees, spruces, and inner branch sections (Ekman 1987). It may be economical to hoard in the same sites in trees where the individuals will be searching for the non-hoarded food. It may also be that some sites are more suitable for hoarding (see Petit et al. 1989) influencing thus the choice of foraging sites. Tits can remember their caches at least over periods of few days (e.g. Sherry et al. 1981, for more references see paper VI) and may be they can do so for the much longer periods necessary to find the caches later in winter. Alternatively or additionally, the caches are found by using certain types of sites for hoarding and by looking later for similar types of sites. Tits, especially crested and coal tits, usually hide only partly their caches suggesting that other individuals, including individuals of other species may find the caches (VI). Crested and willow tits differed more in their hoarding than they did in their foraging sites (V). Also the studies by Haftorn (1956) in Norway show the trend that coal tits avoid hoarding in the sites where other species are foraging. Interspecific kleptoparasitism may thus restrict the use of hoarding sites and consequently as a correlated response it might also influence the choice of foraging sites. The aviary experiment demonstrated that conspecific individuals, but also individuals of other species may recover caches made by willow tits (VI). Food caching may, however, be adaptive to the cachers because they have the best recovery rate for their own stored seeds. Both non-cacher willow tits and great tits found cached seeds, even if they had not seen caching of the seeds in question. The results indicated that risk of intraspecific cache stealing was high and of interspecific stealing low.

Conclusions

The availability of arthropods, no doubt influences the organization of the tit guild in terms of their distribution to different parts of a spruce. In earlier studies this has been verified by the shift of each species to exploit the sites of other species in their absence, may it be experimental (Alatalo et al 1985, 1987) or natural (Alatalo et al. 1986). Likewise, the experimental increase of food has led to increased survival of coniferous forest tits (Jansson et al. 1981), suggesting that the winter food is limited. In this study, food limitation is suggested by relatively equal sharing of the arthropod food by four species and the high correlation between bird numbers and arthropod biomasses over the different sections of the spruce.

However, our results also suggest that there is much else than food competition influencing the ways in which individuals of each species choose their foraging sites in spruce. There would have been a clear foraging advantage of preferring the outer tree parts with the highest arthropod abundance. However, the species that are socially most dominant stayed in the inner tree parts so frequently, that they ended up having the poorest sites in terms of arthropod abundance. This suggests that other factors are also important in the organization of the guild in terms of species abundances and foraging sites. The risk of predation may well be another main factor influencing the organization of this coniferous forest guild.

My field data (II, III) show that risk of predation can cause foraging niche shifts in tits, but I will underline that this does not exclude the possibility that interspecific competition can be important in situations where smaller species respond to the presence of large species (e.g. Alatalo et al. 1985) and vice versa (Alatalo et al. 1987). I suggest that in the *Parus* guild there is a trade-off between predation risk and interspecific competition for food.

In general, I wish to underline that many factors are influencing species composition, foraging niches and abundances within each ecological guild. In the past much attention has been paid to the role of food competition, and in particular on testing the mere presence or absence of competition. In the future it will be important to test the possible influence of other factors, such as predation, and it will also be important to try estimate the relative importance of each factor. To that end it will be necessary to begin to look at the selective forces that influence the foraging site selection and survival of each individual.

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Selostus

Saalistusriskin ja lajienvälisen kilpailun vaikutus tiaisparven rakenteeseen.

Tiaisten (*Parus* spp.) ja hippiäisen (*Regulus regulus*) ruokailupaikan valintaan vaikuttavia tekijöitä tutkittiin sekä Konnevedellä Keski-Suomessa että Grimsön alueella Keski-Ruotsissa. Tiasparven rakenteeseen vaikuttavat ravinnonjakautuminen puussa, lajinsisäinen ja lajienvälinen kilpailu ravinnosta sekä petouhka. Lisäksi tiaiset varastoivat ravintoa, mikä todennäköisesti vähentää lintujen talvikuolleisuutta.

Tiaisten ja hippiäisen talviravinto, kuusessa elävät selkärangattomat eläimet, on jakautunut epätasaisesti. Selkärangaton ravinto on jakautunut epätasaisesti kuusessa. Puun ulko- ja yläosissa oli enemmän ravintoa kuin puun sisä- ja alaosissa. Lintujen ruokailupaikat jakautuivat kuusen eri osiin samoin kuin ravinto: siellä, missä oli runsaasti ravintoa oli myös enemmän ruokailevia lintuyksilöitä. Poikkeuksen muodostivat oksien kärkiosat, joissa ruokaili vähemmän yksilöitä kuin ravinnon runsauden perusteella olisi voinut odottaa.

Tiasparven jäsenten välillä on sosiaalinen arvojärjestys. Korkeimmassa asemassa oleva töyhtötiainen ja toiseksi korkeimmassa asemassa oleva hömötiainen eivät kuitenkaan ruokailleet ravinnontarjonnan suhteen parhaassa paikassa, vaan enemmän pedoilta suojatuissa puun sisäosissa.

Varpuspöllön talviravintoa ovat sekä pikkunisäkkäät että pienet varpuslinnut. Kun maastossa on runsaasti myyriä, varpuspöllöt syövät niitä, mutta myyräkantojen romahdettua ne pyydystävät lintuja, pääasiassa tiaisia ja hippiäisiä. Riski joutua varpuspöllön saaliiksi on suurin puun ulko-osissa. Sellaisena talvena, jolloin myyriä oli vähän ja pöllöjen saalistus kohdistui pääasiassa lintuihin, töyhtö- että hömötiaiset ruokailivat enemmän kuusen sisäosissa. Kun myyriä oli runsaasti ja pöllöjen saalistus kohdistui vähemmän lintuihin, mainitut tiaislajit ruokailivat enemmän kuusen uloimmissa osissa. Hömötiaiset ruokailivat enemmän männyn ja koivun latvaosissa varpuspöllön saalistaessa lintuja verrattuna vuoteen jolloin pöllö pyydysti myyriä ravinnokseen. Eri tiaisyksilöt suhtautuivat kuitenkin erilailla saalistusriskiin. Koirastöyhtötiaiset eivät vaihtaneet ruokailupaikkaansa kuusessa. Naarastöyhtötiaiset ruokailivat kuusen oksien kärkiosissa, kun todennäköisyys joutua varpuspöllön saaliiksi oli pieni. Seuraavana talvena, jolloin pöllö pyydysti lintuja, tiaiset siirtyivät ruokailemaan lähelle kuusenrunkoa. Vanhat hömötiaiset siirsivät ruokailupaikkaansa samoin kuin töyhtötiaisnaaraat. Ilmeisesti tämän seurauksena nuoret hömötiaiset, jotka ovat kaikkein alistetuimmassa sosiaalisessa asemassa, joutuivat ruokailemaan enemmän puiden alaosissa. Alistetuille yksilöille on kuitenkin edullista liikkua tiaisparvessa, koska riski joutua pedon saaliiksi pienenee. Lisäksi 'useampi silmä' havaitsee pedon nopeammin.

Lisäravinto pienentää lintujen talvikuolleisuutta. Tiaiset varastoivat ravintoa syksyllä ja luultavasti käyttävät talvella osan varastoistaan. Hömö- ja töyhtötiainen pyrkivät välttämään toistensa ruokailualueita varastoidessaan siemeniä kuuseen. Näin riski että toisen lajin edustaja käyttäisi siemenen pienenee, mutta varastoja on kuitenkin toisenkin lajin ruokailualueella. Hömötiainen varastoi siemenet huolellisesti kaarnanrakosiin ja jäkälän sekaan. Varastoiva hömötiainen löysi suuremman osan varastoista ja nopeimmin. Varastoja tuntemattomat hömötiaisyksilöt löysivät tehokkaammin varastoja kuin talitiainen. Riski menettää varasto lajikumppanille on huomattavasti suurempi kuin menettää se eri lajin yksilölle.

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ORIGINAL PAPERS

I

FOOD RESOURCE DISTRIBUTION AND THE ORGANIZATION OF THE *PARUS* GUILD IN A SPRUCE FOREST

Manuscript (submitted)

by

Jukka Suhonen, Rauno V. Alatalo, Allan Carlson & Jacob Höglund

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II

PREDATION RISK INFLUENCES THE USE OF FORAGING SITES BY TITS

Manuscript (submitted)

by

Jukka Suhonen

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III

RISK OF PREDATION AND FORAGING SITES OF INDIVIDUALS IN MIXED-SPECIES TIT FLOCKS

Manuscript (submitted)

by

Jukka Suhonen

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IV

PREDATION-RISK AND THE ORGANIZATION OF THE *PARUS* GUILD

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by

Jukka Suhonen, Matti Halonen & Tapio Mappes

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V

HOARDING SITES IN MIXED FLOCKS OF WILLOW AND CRESTED TITS

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Jukka Suhonen & Rauno V. Alatalo

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VI

RECOVERY OF FOOD CACHES BY OTHER INDIVIDUALS IN MIXED SPECIES TIT (*PARUS*) FLOCKS

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by

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