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Selection of foraging sites in mixed Willow and Crested Tit flocks: rank-dependent survival strategies

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The selection of foraging sites by Willow *Parus montanus* and Crested Tit *P. cristatus* flock members was studied in relation to the abundance of their arthropod prey in the plantations of young Scots pine *Pinus sylvestris* and in relation to hunting behaviour of Sparrowhawks *Accipiter nisus*. Arthropods were most abundant in the upper parts of the canopy and on the surface of ground vegetation. Sparrowhawks were seen attacking parids only in the upper parts of the canopy. The lowest parts of the pines were safer and this was confirmed by the anti-predatory vigilance of the birds. Crested Tits, top-ranking individuals in the mixed flocks, tended to be frequent ground feeders under snow-free conditions, which was not the case under snowy conditions suggesting the importance of snow cover. Although the lowest parts of trees was the poorest site in terms of arthropod abundance, dominant individuals of the Crested Tit remained there under snowy conditions. Foraging height of alpha individuals of the Willow Tit did not differ from one climate condition to the other. Subordinate Willow and Crested Tits, by contrast, significantly increased their foraging heights. Although subordinate Willow Tits foraged in the highest canopy parts, however, their survival rates did not differ from those of higher-ranked Willow Tits. The results suggest that foraging in the most vulnerable tree parts may not be always linked to the decreased survival. The observed shift of subordinate Willow Tits supposedly made their anti-predatory vigilance more effective, suggesting a possible trade-off between concealment and visibility.

1. Introduction

Resources such as food and cover against attacking predators are crucial to the winter survival of parids (Jansson et al. 1981, Ekman 1986, Jabłoński & Lee 2000). Dominant individuals in tit flocks usually defend the contested resources against subordinate flock-mates (Ekman & Askenmo 1984, Pöysä 1988), thus monopolizing preferred, presumably safe, microhabitats (Koivula et al. 1994, Krams 1996). Rank-related access to resources may show up in the form of better winter survival rates among dominants (Ekman & Askenmo 1984, Koivula & Orell 1988, Desrochers et al. 1988, Koivula et al. 1996). There have been many studies on foraging niche separation in tits where tree use patterns were interpreted in terms of predation risk and social dominance (Alatalo et al. 1986, Ekman 1986, Desrochers 1989, Suhonen 1993a, b, Jabłoński & Lee 1999). Although trade-offs between the risk of predation and energy intake are particularly relevant to the ecology of predator-prey interactions (Lima & Dill 1990), the hunting behaviour of predators and the actual food resources in free-ranging individuals are considered together only in a few field studies (Suhonen et al. 1992).

In the trees of mature forest, dominant individuals of some parid species prefer the upper parts, while subordinates usually forage lower in the canopy (Ekman & Askenmo 1984). Some studies indicate that tits are more vulnerable in the lower parts of the mature forest tree canopy (Ekman & Askenmo 1984, Ekman 1986). Not surprisingly then, ground foraging is unusual for parids, since the individuals that feed on the ground have been excluded from safer foraging sites by higher ranking individuals (Ekman & Askenmo 1984, Suhonen 1993a, b). Recently it was observed that dominant individuals might shift to the lower canopy parts as soon as mixed-species flocks of Willow *Parus montanus* and Crested Tits *P. cristatus* enter the plantations of young pines (Krams 1996). The top-ranking mixed-species flock members was observed on the ground much more frequently there (our unpubl obs) indirectly indicating that the ground level may be a profitable or safe foraging site.

The aim of this study was to investigate how Willow and Crested Tits in mixed-species flocks select the foraging sites in pine plantations with respect to the food resources and the risk of being attacked by Sparrowhawks *Accipiter nisus*. We estimated arthropod density on the ground level and in the canopy of young pines, and observed foraging behaviour of the tits under both snow-free conditions and under snowy conditions. Since changes in snow conditions affect the availability of ground as a foraging substrate, not the availability of different canopy layers, in accordance with the theory of survival maximization (Lima 1986, McNamara & Houston 1990) the birds are expected to accept a greater risk of predation in higher canopy under snowy conditions. Still we predicted that dominant individuals have higher survival rates than their subordinate flock mates.

2. Material and methods

2.1. Study area and birds

We studied foraging site selection of Willow and Crested Tits near the town of Krāslava, Latvia during the four successive autumn/winter seasons of 1994–1997. The study area consists mainly of coniferous forests dominated by Scots pine *Pinus sylvestris*. Mixed species flocks in this study used territories of about 10 ha in extent containing pines of 8 m average height. During winter months the ambient temperatures are below 0°C and regularly fall below –15°C. Permanent snow cover usually appears in November and remains on average for five months.

Each year all members of 2–6 mixed-species flocks (18 flocks in total) containing Willow Tits (mean number of individuals = 4.1, SE = 0.67) and Crested Tits (mean number of individuals = 3.8, SE = 0.43) were captured at temporary feeders, individually colour-marked, sexed and aged (as adult or juvenile). The shape of the rectrices of Willow and Crested Tits (Laaksonen & Lehikoinen 1976) and the colour of the iris of Crested Tits (Lens & Dhondt 1992) were used to determine age. The sexual dimorphism in wing and tarsus length was used for sexing (Koivula & Orell 1988).

2.2. Dominance ranks

Ranking of members of the flocks was based on pairwise interactions at the feeders between September and October. To determine individual rank we followed the procedures of Koivula and Orell (1988). Within each dyad, the individual was considered to be dominant if it won significantly more interactions than the other (sign-test, 2-tailed). The results obtained were in accordance with previous reports (Hogstad 1987, Krams 1996, 1998a, b) that Crested Tits dominate Willow Tits, males dominate females and, within sex, adults generally dominate juveniles. We divided the flock members within each of the species into two dominance categories: dominants and subordinates. In each species the two highest-ranking individuals were scored as dominants and the others as subordinates. To avoid possible habitat and between-year variations, we compared the dominants and subordinates within each flock.

2.3. Foraging sites

The use of foraging sites was observed within a week before the appearance of permanent snow cover on ground usually between November and December, and we recorded the tit behaviour between 1100 and 1400 hours. Repeated observations were done not later than two days after the first snowfall. All foraging site recordings took place under calm and dry weather when all of the feeders were already removed. For each observation we estimated foraging height of the bird and height of the tree. Foraging heights were expressed as proportions of canopy height and divided into four categories. To control for predator exposure at canopies, which might be different in the volume, we estimated the distance of the bird from the tree trunk and the length of the branch used. Distance from trunk was transformed to a relative distance and divided into four categories. Observations on the foraging height and the distance from trunk of the individual were separated by at least 5-min intervals. To avoid a discovery bias (Ekman 1987), the foraging site use was recorded with a delay of 10 s, using an electronic metronome, between the identification of a bird and the recording of its position in the tree. Since the predator effect may be influenced by height of trees, we avoided the data collection closer than 50 m from the edge of the plantations of pines and mature pine forest. To reduce statistical dependence between the observations, only one record was made per individual per tree. Foraging sites of each individual were recorded during one day both under snow-free conditions and under snowy conditions, and up to 10 observations of the same individual were made. All of the members of a flock were observed on the same day on each occasion. The analysis of foraging heights was made quarter by quarter. We used percentages as response variable and foraging heights of dominants and subordinates within a flock were compared by Wilcoxon's matched-pairs signed-ranks tests.

2.4. Arthropod sampling

Data on arthropods were collected in the autumn of 1997 in the same area where we studied the niche dynamics. Arthropods were sampled from 11 young pines by procedures previously used in spruce by Suhonen et al. (1992). We also estimated food resources on the ground surface on 10 squares each 1 m^2 size (10 m^2 in total) randomly selected below the trees in the plantations of young pines. We collected samples in late November when temperatures were below zero.

We randomly selected pines not less than 7 m in height and used them as sampling units. One branch was randomly selected in each of the four height quarters of the tree. The number of branches 0.5 m above and below the sampled branch was counted to estimate the total numbers and biomasses of arthropods in each quarter and the whole tree. The lowest height quarter contained 8.6 branches followed by 14.0, 15.0 and 14.2 branches at the second, third and the fourth height quarter, respectively. The whole branch was cut and let down to ground, where it was cut into equally long pieces on a plastic sheet. Parts from each four portions of the branch were carefully enclosed in separate plastic bags. Consequently, from each pine, eight samples were taken.

Each of the randomly selected ground vegetation plots were marked and divided into four smaller squares. Then they were extracted and carefully laid down on the plastic sheets. The plots of ground vegetation layer were put into plastic bags and immediately transported to laboratory. After the arthropod sampling procedure all of the samples of ground vegetation were returned back to the forest.

In laboratory each part of a sampled pine canopy was kept in a white bowl and several times shaken, beaten against the walls of bowl. We included in the analysis only data on active arthropods extracted during the first 5 min of the procedure. All of the ground vegetation samples also were processed immediately after their collection in the field. To reach higher comparability of the sampling methods for canopy and ground, each of the smaller sample plots was turned upside-down, gently shaken and beaten by palm and fingers to extract active and the surface living arthropods only. To standardize sampling, the same person did this part of the study every time. After this, all the arthropods larger than 1 mm in size were collected. Since small arthropods and their eggs make up an insignificant proportion of the diet of the forest wintering tits (Palmgren 1932, Jansson & Brömssen 1981), we did not include data on the smallest food items (< 1 mm) in the further analysis. The arthropods collected within pine canopy (n = 312) and on ground vegetation (n = 856) were preserved in 80% ethanol. The body length of arthropods was measured to the nearest 0.5 mm and they were weighed with a microbalance after drying for 24 hours in oven (60°C). The arthropods were identified, and in the canopy the main part of the individuals were spiders *Araneae* (86.9%), followed by *Homoptera* (5.7), *Hymenoptera* (3.8), *Diptera* (2.0), *Heteroptera* (0.4), *Psocoptera* (0.3), *Lepidoptera* (0.3), *Coleoptera* (0.2) and other insect orders (0.4). The ground vegetation also mainly contained spiders (70.3%) which were followed by *Heteroptera* (6.2), *Diptera* (5.4), *Homoptera* (5.3), *Hymenoptera* (5.0), *Dermaptera* (2.2), *Coleoptera* (2.1), *Psocoptera* (1.7), *Lepidoptera* (1.6), and other insects (0.2).

2.5. Predation risk and vigilance

In Europe, the Sparrowhawk is one of the most important predators of tits (Newton 1986) and it was the principal airborne predator on small passerines also in our study area (Priednieks et al. 1989, Krams 1996, 1998a, b). Sparrowhawks were seen in the area on average every second day. Hunting for their prey, sparrowhawks flew just above the canopy level in the area of young pines. This hunting manner probably was caused by closed structure of lower branches in the pine plantations providing, thus, a cover to airborne predators. We observed some successful attacks on Coal Tits *Parus ater* (n = 2) and Goldcrests *Regulus regulus* (n = 4) which occasionally joined the mixed-species flocks. These species forage more in outer and upper parts of trees (Alatalo 1981). To determine whether tits adjusted their foraging positions to the risk of predation, we measured vigilance of food consuming individuals. To obtain a measure of vigilance, we recorded the number of times per minute that a bird looked up while handling and eating a larger food item. The behaviour of tits also was observed both before and after the appearance of snow cover during 1994–1997. Observations of the foraging site selection and the anti-predatory behaviour of the focal individual were separated by at least 5 min. This part of the study was carried out to avoid between-flock variation because of varying day-lengths and habitat. We compared vigilance of dominants and subordinates pairwise within each flock (n = 14).

In northern Europe the forest wintering tits face their greatest threat also from the Pygmy Owl *Glaucidium passerinum* (Mikkola 1983, Ekman 1986, Suhonen et al. 1993, Suhonen et al. 1994, Kullberg 1995). However, the distribution of this avian predator in Latvia is not even and can be primarily attributed to old spruce and mixed forests (Priednieks et al. 1989). We could not confirm presence of Pygmy Owls in the dry growths of young pines of our study site either by direct observations throughout the year or by inspecting nest-boxes for their caches in winter. Although some Tawny Owls *Strix aluco* were present in the study area, no evidence exists for winter predation of tits by this predator. The density of the marten *Martes martes* was so low that this predator was not recorded at the study site. We were not able to attribute predation of the red fox *Vulpes vulpes*, a common mammal at our study site, to the forest wintering parids either by the field observations or the local literature (Kronītis 1972).

3. Results

3.1. Arthropod distribution

In young pine the numbers of arthropods varied at different canopy heights (Friedman's non-parametric ANOVA with height as the factor and tree as the block: (χ^2 = 16.98, df = 3, P < 0.01, Table 1). Comparisons among the relative heights revealed the greatest number of arthropods in the uppermost part of pines (Scheffé's test, P < 0.05, Fig. 1), whereas the branches of the lowermost canopy had fewest arthropods (Scheffé's test, P < 0.05, Fig. 1). There was significant variation in arthropod abundance also horizontally since we found more arthropods in outer than in inner parts of the branche at all height quarters (Scheffé's test, P < 0.05, Table 1). Arthropods were significantly different in size within the canopy (a Friedman's non-parametric ANOVA: (χ^2 = 15.05, df = 3, P < 0.01, Table 1) and they were significantly smaller in the upper tree parts (Scheffé's test, P < 0.05). However, there were no differences in the size of arthropods between the inner and the outer parts of branches (Scheffé's test, P > 0.05, Table 1).

Our estimation shows that the arthropod biomasses varied significantly over the canopy parts (a Friedman's non-parametric ANOVA: (χ^2 = 9.61, df = 3, P < 0.05, Fig. 1), and highest values of the biomass were found in the upper (Scheffé's test, P < 0.05) and outermost (Scheffé's test, P < 0.05) parts of canopy.

We collected 57.5 ± 4.12 (mean and SE) arthropods per 1 m^2 plot (n = 10) of ground vegetation. Arthropods were significantly larger in size on the ground (2.9 ± 1.4 mm, mean and SE) than in the canopy (1.93 ± 0.37 mm, mean and SE, Table 1) (t-test, n_1 = 575, n_2 = 312, P < 0.05). Each vegetation plot on average contained 17.54 ± 1.26 (mean and SE) mg dry weight of arthropods.

3.2. Estimation of food resources

The numbers of arthropods per branch at different height quarters, the body mass data, and the numbers of branches allowed us to estimate the total number and the arthropod biomass in different canopy parts and on the forest floor. Arthropods were more abundant towards the tree top and their biomasses also increased towards the uppermost height quarters and the outermost parts of the canopy with 80.89 mg mean dry total weight per a young pine (Fig. 1). Pines in our study area grow with a density of 4378 ± 139 trees (mean, SE) per ha (15 sampling plots each of 625 m^2 in

Table 1. Mean number, mean length (mm) and dry weight of arthropods in four relative heights of pine canopy in saplings. Numerals indicate the height quarters from 1 as the lowest to 4 as the uppermost canopy part.

	Number of arthropods per branch					Length of arthropods						Weight of arthropods					
	Inner branch		Outer branch			Inner branch			Outer branch			Inner branch			Outer branch		
Relative height	Mean	SE	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
4	4.1	1.57	7.0	2.05	11	1.53	0.25	41	1.43	0.24	70	0.18	0.03	41	0.17	0.04	70
3	3.0	0.98	5.9	1.93	11	1.91	0.46	30	1.86	0.34	59	0.19	0.06	30	0.18	0.05	59
2	1.9	0.87	4.2	1.78	11	2.30	0.49	19	1.99	0.33	42	0.22	0.06	19	0.20	0.09	42
1	1.8	0.81	3.3	0.96	11	2.28	0.44	18	2.11	0.42	33	0.28	0.09	18	0.25	0.08	33

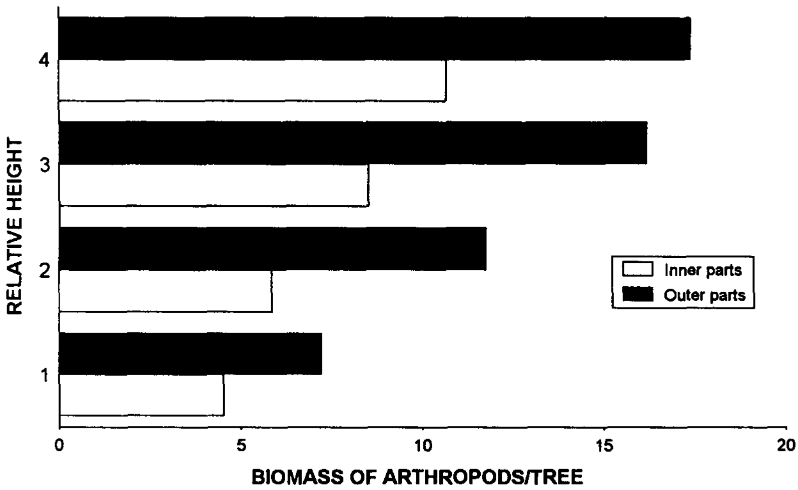

Fig. 1. Estimated biomass (dry weight mg/tree) of arthropods per one pine in the four relative height. Each quarter was divided into inner and outer parts of branches.

size) and arthropod dry weight reaches 0.354 kg in the trees per 1 ha. Our rough estimates show that in the plantations of young pines approximately a third of the total arthropod food is concentrated on the surface of ground vegetation.

3.3. Relative foraging height of the birds

Before the snow cover formed, Crested Tits foraged lower in the canopy than did Willow Tits when compared within each flock (2-tailed Wilcoxon's matched-pairs signed-ranks tests: $T = 23$, $n = 18$, $P < 0.01$, Table 2). In the Willow Tit, dominants foraged significantly lower than their subordinate flock-mates (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 38$, $n = 18$, $P < 0.05$, Table 2). Dominant individuals of the Crested Tit foraged in the lowest parts of young pines. The foraging height of dominant and subordinate Crested Tits did not differ significantly (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 48$, $n = 18$, $P > 0.05$, Table 2). Higher-ranking Crested Tits were the most frequent ground feeders: 11 birds out of 20 top-individuals were often seen on the ground. In contrast, only one dominant individual out of 67 dominants and subordinates of the Willow Tit frequently foraged on the ground.

Snow can create foraging problems for ground feeders. However, only subordinate Willow Tits and subordinate Crested Tits responded to snowfall: they were observed foraging higher in the canopy (Table 2). A significant difference was found between foraging heights of subordinate and dominant individuals of the Crested Tit (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 36$, $n = 18$, $P < 0.05$). The birds were not seen searching for food on snow, leading to a change of the foraging substrate in dominant Crested Tits (2-tailed sign-test, $P < 0.001$).

3.4. Relative distance to trunk

All members of mixed flocks foraged close to the tree trunk (Table 2). On average, there were no significant differences in levels of exposure either among Willow Tit individuals (Kruskal Wallis one-way ANOVA, $H = 18$, $n = 74$, $P > 0.05$) or among Crested Tit individuals ($H = 26$, $n = 68$, $P > 0.05$). No significant changes in exposure of the birds appeared after forming of snow cover (Table 2).

3.5. Vigilance

Vigilance of the birds increased from dominant Crested Tits to subordinate Willow Tits before the snow cover formed (Table 3). However, the only significant differences were found in comparisons between the species (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 19$, $n = 14$, $P < 0.01$). Comparisons within each species did not reveal differences in vigilance among dominants and subordinates. After forming of snow cover subordinate Willow and dominant Crested Tits significantly increased their vigilance rates whereas vigilance of dominant Willow Tits did not change. By contrast vigilance of subordinate Crested Tits significantly decreased during snowy conditions (Table 3).

3.6. Survival

A total of 57 (77%) of the 74 Willow Tits and 56 (82%) of the 68 Crested Tits studied in winters of 1994/95, 1995/96, 1996/97 and 1997/98 survived from the beginning of October to the middle of February (Table 4). The birds which disappeared in the course of winter but were found again outside the study area in spring were included in the analysis as survivors. The two species did not differ in their overall survival rates (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 60$, $n = 18$, $P > 0.05$). There was a relationship between rank and survival in the Crested Tit: the median rank of survivors was higher than that of the birds which disappeared from the study area (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 12$, $n = 18$, $P < 0.001$, Table 4). However, rank did not influence the winter survival of the Willow Tit: the median rank of survivors was not higher than the median rank of the disappeared individuals (2-tailed Wilcoxon's matched-pairs signed-ranks test: $T = 50$, $n = 18$, $P > 0.05$, Table 4).

4. Discussion

In the canopy of young pines, arthropod biomass was highest in the upper part of the tree, where we estimated about 60% of the total canopy biomass. Suhonen and co-workers obtained similar results (Suhonen et al. 1992) for spruce and this might indicate a general pattern of arthropod distribution in coniferous trees in the Northern Europe. This pattern for coniferous trees may be explained by preferences of arthropods for branches with needles (Gunnarsson 1990). We found abundant arthropod food also on the ground vegetation layer where arthropods were significantly larger than in the canopy. However, our field data should be taken into account cautiously

Table 2. The relative foraging heights and the relative distance to trunk of Willow and Crested Tits in pine saplings at the absence and presence of snow cover (means of the medians, n = number of individuals).

	Relative foraging height							Relative distance to trunk						
	Without snow cover		With snow cover					Without snow cover		With snow cover				
	Mean	SE	Mean	SE	n	T	P*	Mean	SE	Mean	SE	n	T	P*
Willow Tits														
Dominants	0.51	0.02	0.49	0.02	36	273	ns	0.23	0.02	0.27	0.02	36	218	ns
Subordinates	0.67	0.03	0.76	0.03	38	148	< 0.05	0.25	0.01	0.29	0.02	38	396	ns
Crested Tits														
Dominants	0.27	0.02	0.31	0.05	36	251	ns	0.27	0.02	0.31	0.04	36	241	ns
Subordinates	0.33	0.02	0.41	0.02	32	132	< 0.05	0.32	0.02	0.30	0.01	32	189	ns

* 2-tailed, Wilcoxon's matched-pairs signed-ranks test.

because of the different sampling methods.

In general, vertical separation of foraging sites of parids in the plantations of pines was rank-dependent, confirming previous studies (Ekman & Askenmo 1984, Hogstad 1988a, Suhonen 1993a, b, Krams 1996, Jabłoński & Lee 1999, 2000). Similar findings were obtained in the Black-capped Chickadee *Parus atricapillus* whose preference for lower foraging sites in young trees was related to predation risk (Desrochers et al. 1988). Under snow-free conditions dominant Crested Tits were foraging close to ground and they were the most frequent ground feeders. Since ground vegetation contained more food items than lower tree parts, ground feeding was probably profitable. Willow Tits were more vigilant than Crested Tits and this may indicate that the birds perceived the foraging in higher parts of the canopy as a risky affair (Ekman 1987). The feeding sites on ground can be completely hidden by appearance of snow cover and we expected therefore to observe a change of the feeding niches of the tits between the two climate conditions. However, only subordinate Willow Tits and Crested Tits increased their foraging height under snowy conditions. Surprisingly, dominant Crested Tit individuals did not change their feeding sites upwards, remaining in the lower canopy after disappearance of their food sources on the ground surface. Thus, the species that is socially dominant stayed in the inner and lower pine parts so frequently, that it ended up having the poorest sites in terms of arthropod abundance during normal, snowy conditions. Considering predation risk and starvation risk together, the minimum joint risk could be achieved on the ground level when there is no snow. Under snowy conditions the joint risk could be achieved higher in the canopy. However, dominant Crested Tits remained in the same canopy parts and this may suggest that there was no reason for dominants to trade in foraging options for predator protection because they appar-

Table 3. Changes in anti-predatory vigilance (look-up/s) of Willow and Crested Tits in pine saplings at the absence and presence of snow cover (means of the medians, n = number of individuals).

	Without snow cover		With snow cover					
	Mean	SE	Mean	SE	n	df	t	P*
Willow Tits								
Dominants	0.90	0.08	0.91	0.09	14	13	1.75	ns
Subordinates	0.92	0.11	1.13	0.10	14	13	3.58	<0.01
Crested Tits								
Dominants	0.53	0.06	0.61	0.05	14	13	2.27	<0.05
Subordinates	0.88	0.09	0.64	0.07	14	13	3.74	<0.01

* 2-tailed paired t-test

Table 4. Winter survival of Willow Tits and Crested Tits in different sex and age classes. The data obtained during 1994-1997 are pooled.

	Willow Tit				Crested Tit			
Age/Sex	Survived		Disappeared		Survived		Disappeared	
	n	%	n	%	n	%	n	%
Adult males	14	77.8	4	22.2	16	88.9	2	11.1
Juvenile males	18	78.3	5	21.7	12	70.6	5	29.4
Adult females	14	77.8	4	22.2	17	94.4	1	5.6
Juvenile females	11	73.3	4	26.7	11	73.3	4	26.7

ently still had enough food. The decreased vigilance of dominant Crested Tits in snowy conditions may indicate that the birds devoted more time to feeding during the periods of higher energy demand (Ekman 1987). Moreover, dominant Crested Tits usually carry smaller subcutaneous fat reserves than subordinates in our study area (Krams 1998a, b) and this may suggest that they maintained a neutral energy balance in the poorest canopy parts. Still, the survival of the birds was higher than in other studies of Willow and Crested Tits in Fennoscandia (Ekman et al. 1981, Jansson et al. 1981, Koivula & Orell 1988, Hogstad 1988b, Ekman 1990, Kivula et al. 1996) suggesting that food was not limiting factor for the winter survival in Latvia.

Under snowy conditions subordinate Crested Tits increased their foraging height, possibly due to intraspecific competition for the decreasing feeding substrate (Krams 1998b). As a consequence of their low social status, Willow Tits were unable to forage freely in all parts of the pine canopy (Ekman & Askenmo 1984, Suhonen 1993a, b) and lowest-ranking Willow Tits foraging in uppermost tree parts supposedly were most vulnerable to attacks by Sparrowhawks. This was supported by raised rates of vigilance of subordinate Willow Tits. Although the increased requirements of subordinate Willow Tits were supposedly covered by greater arthropod biomass in upper canopy parts (Krams 1998a, b), the observed significant shift of their foraging height to the upper canopy was unexpected. Moreover, we did not find any significant rank-dependent differences in the survival among Willow Tits. This is a contradictory result with the findings of the previous studies (Ekman & Askenmo 1984, Koivula & Orell 1988, Desrochers et al. 1988, Koivula et al. 1996) and our own field observations confirming the presence of Sparrowhawks.

Our results suggest that the selection of foraging sites in tits can be more complex than it was previously considered and there could be not only a trade-off between energy intake and the predation risk (McNamara & Houston 1990, Lima & Dill 1990, Houston et al. 1993). Since foraging in more exposed parts of the canopy was not linked with decreased survival rates, the anti-predatory behaviour of subordinates should be crucial. Although all cover is probably both protective and obstructive to some degree (Lima 1990, Lazarus & Symonds 1992), the early detection of the approaching predator may be suggested as one of the possible ways to avoid the risk of predation. To improve the effect of anti-predatory vigilance, the subordinate Willow Tits could increase their foraging height closer to the tops of young pines where less density of branches allows more visibility (Götmark et al. 1995). The increased vigilance observed in subordinate Willow Tits may add more safety (Krams 1998c). Thus, the possible trade-off between concealment and better view of the surroundings (Lima et al. 1987, Götmark et al. 1995) of subordinate members deserves more attention in future studies of anti-predatory behaviour of the forest wintering birds.

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Selostus: **Hömö- ja töyhtötiaisten ruokailupaikan valinta latvialaisissa tiaissekaparvissa**

Tiaisten ruokailupaikan valintaa tutkittiin latvialaisissa istutusmänniköissä syystalvina 1994-1997. Kirjoittajat selvittivät, kuinka ravintoresurssit ja petopaine vaikuttivat hömö- ja töyhtötiaisten ruokailupaikan valintaan. Havaintoja kerättiin sekä lumettomana että lumisena ajankohtana. Tiaisten ravintonaan käyttämät niveljalkaiset esiintyivät runsaimpina lehvästön yläosissa ja ulko-osissa kuin alaosissa tai lähellä puun runkoa. Niveljalkaisten koko oli suurempi kenttäkerroksen kasvillisuudessa kuin lehvästössä. Varpushaukan havaittiin saalistavan tiaisia ainoastaan lehvästön yläosissa. Lumettomana aikana hömötiaisten suhteen valta-asemassa olevat töyhtötiaiset ruokailivat hömötiaisia useammin lehvästön alaosissa. Dominantit hömötiaiset ruokailivat alempana kuin subdominantit hömötiaiset. Töyhtötiaisilla ei havaittu yksilön valta-asemaan liittyviä eroja ruokailukorkeudessa; tosin valta-asemassa olevat yksilöt ruokailivat usein maassa. Lumen tulo voi vaikuttaa yksilöiden ruokailupaikan valintaan. Tässä tutkimuksessa vain alistetussa asemassa olevat töyhtö- ja hömötiaiset reagoivat lumen tuloon alkamalla ruokailemaan korkeammalla lehvästössä. Lumen tulo ei vaikuttanut siihen, ruokailivatko linnut lähellä vai kaukana puun rungosta. Hömötiaiset käyttivät töyhtötiaisia enemmän aikaansa varuillaanoloon. Latvialaisten töyhtö- ja hömötiaisten talven yli selviytymisessä ei ollut eroja. Hömötiaisista säilyi hengissä 77% ja töyhtötiaisista 82%. Yksilöiden arvoaseman havaittiin vaikuttavan töyhtötiaisten (valta-asemassa olevat yksilöt säilyivät paremmin), mutta ei hömötiaisten hengissä säilymiseen. Saadut tulokset viittavaat siihen, ettei tiaisten hengissä säilyminen ole välttämättä riippuvaista siitä, missä osassa puuta ne ruokailevat.

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