

Predation risk and the organization of the Parus guild

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Many studies indicate that interspecific competition restricts the use of foraging sites in mixed-species winter flocks of tits. However, predation is a strong mortality factor for members of the tit guild and predation risk may restrict the selection of foraging sites and organisation of the mixed-species tit flock. We evaluated pygmy owl (*Glaucidium passerinum*) predation on North European tits and goldcrests. A literature analysis of six areas showed clearly that pygmy owls feed more heavily on those species that forage on exterior tree parts (coal tit *P. ater* and goldcrest *Regulus regulus*). These species are also subdominant in mixed-species flocks. The dominant species, crested tit (*P. cristatus*) and willow tit (*P. montanus*) were killed less frequently by pygmy owls. These two species forage on the inner parts of trees. The predation or competition hypothesis cannot alone explain the foraging site selection by the dominant species. There is more arthropod food on the outer parts of branches and predation pressure is also higher on the outer parts of the tree. The most dominant species, crested tit, forages in the middle part of branches. We suggest that in the *Parus* guild there is a trade-off between predation risk and interspecific competition for food. Also other facts, listed in the study, support the conjunction effect of predation risk and interspecific competition for food on the organization of the *Parus* guild.

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A traditional way of studying community structure has been to quantify patterns in resource partitioning among species. Such patterns have often been used to infer that interspecific competition is or has been an important force in community and guild organization (e.g. MacArthur 1972, Cody 1974, May 1974, Schoener 1974, 1983, Cody and Diamond 1975, Diamond 1978, Connell 1983, Wiens 1989a, b). However, in recent years a discernible shift has occurred towards the notion that predation often has the greater impact, reducing the importance of competition (e.g. Paine 1966, 1971, Connell 1975, Menge and Sutherland 1976, Caswell 1978, Zaret 1980, Jeffries and Lawton 1984, Kotler 1984, Sih et al. 1985, Werner 1986, Kotler and Holt 1989).

In particular for bird communities, interspecific competition has been raised as the main organizing factor (e.g. MacArthur 1972, Cody 1974, Wiens 1989a, b).

The importance of interspecific competition has been severely questioned (reviews in Wiens 1978, 1989a, b, Schoener 1982) and in some papers, predation has been demonstrated to influence the bird community and guild organization (Pulliam and Mills 1977, Ekman 1986, Lima et al. 1987, Székely et al. 1989, Watts 1990). In particular nest predation has been ignored in assemblage-level studies of birds (e.g. Martin 1988a, b, Paine et al. 1990, Sodhi et al. 1990). It seems that in the future we need a synthesis in which interspecific competition and predation in conjunction affect bird communities.

The northern coniferous forest tit guild represents an ideal system for the investigation of mechanisms that structure terrestrial communities. It is one of the most studied bird guilds (Gibb 1954, 1960, Haftorn 1956 etc.; for reviews see Alatalo 1982a, Alatalo et al. 1986). In the non-breeding season they form mixed-species flocks

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Table 1. Statistical test of the occurrence of each species in the caches of pygmy owl in relation to the abundance of each species in the field. K is proportion (%) tits and goldcrest cached by pygmy owl and A is the species abundance (%) in the field. P is the sign-test probability.

	K		A		n	P
	\bar{x}	\bar{x}	\bar{x}	SD		
Coal tit	20	9	3.99	8.7	6	0.016
Goldcrest	51	36	1.98	1.9	6	0.34
Crested tit	6	11	0.41	0.4	6	0.016
Willow tit	24	43	0.61	0.3	6	0.016

in which the heavier species are socially dominant over the lighter ones (Hogstad 1978, Morse 1978). Each species has specific preferences for different tree species and types of foraging sites within trees (Haftorn 1956, Alatalo 1982b). The tits and goldcrest exploit nonrenewable resources in their group territories during winter. These species have largely overlapping diets consisting of seeds, spiders and other arthropods (Palmgren 1932, Haftorn 1956, Jansson 1982). Arthropod food supply is a nonrenewable resource during winter (Askenmo et al. 1977, Jansson and Brömsen 1981) and the outer halves of spruce branches contain about three

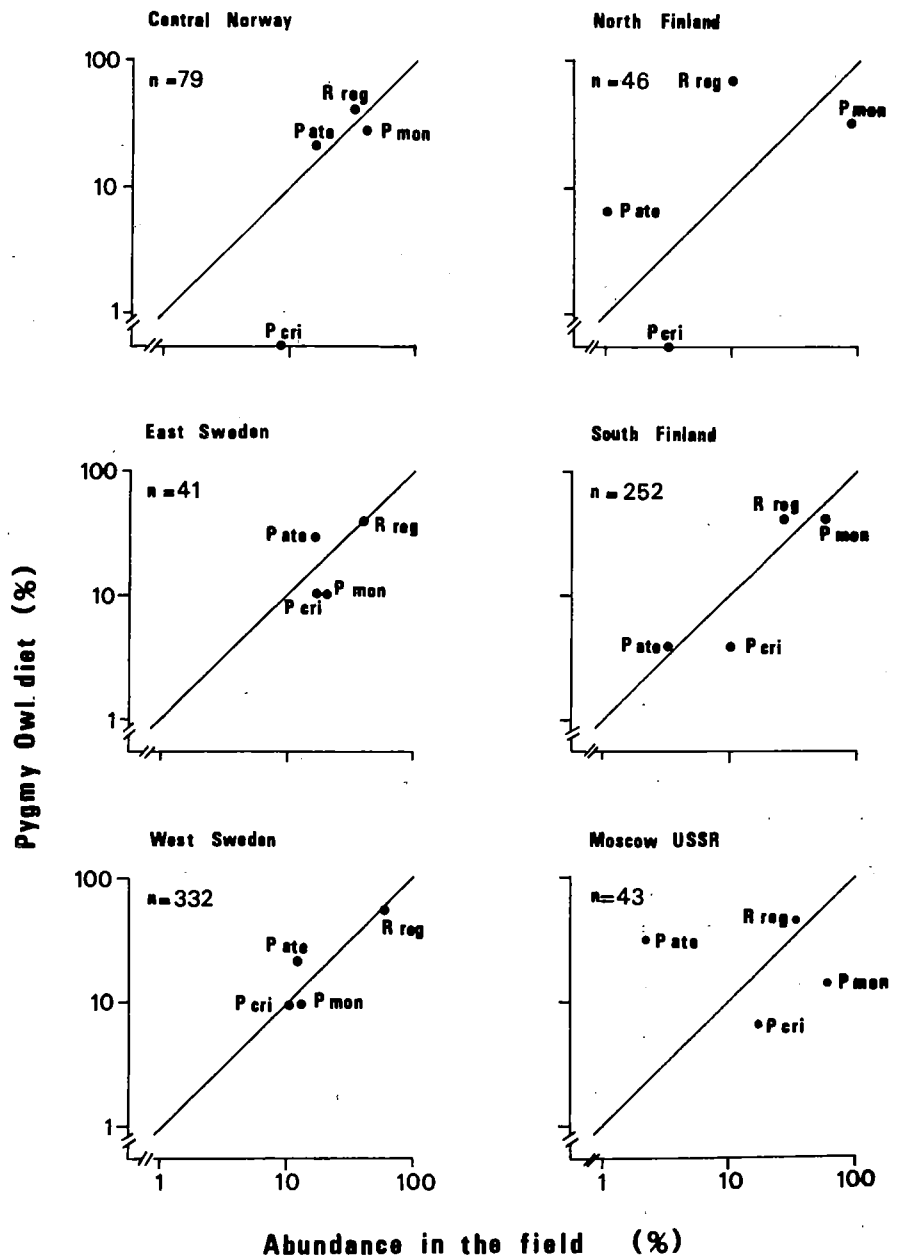


Fig. 1. Relative abundance (%) of coniferous forest tits and the goldcrest in the diet of pygmy owls and in the bird communities of six areas in Northern Europe. The continuous line indicates that proportions are similar both in the diet and the field. Species abbreviations: crested tit (P cri), willow tit (P mon), coal tit (P ate) and goldcrest (R reg). N indicates number of tit flock members found in caches of pygmy owl.

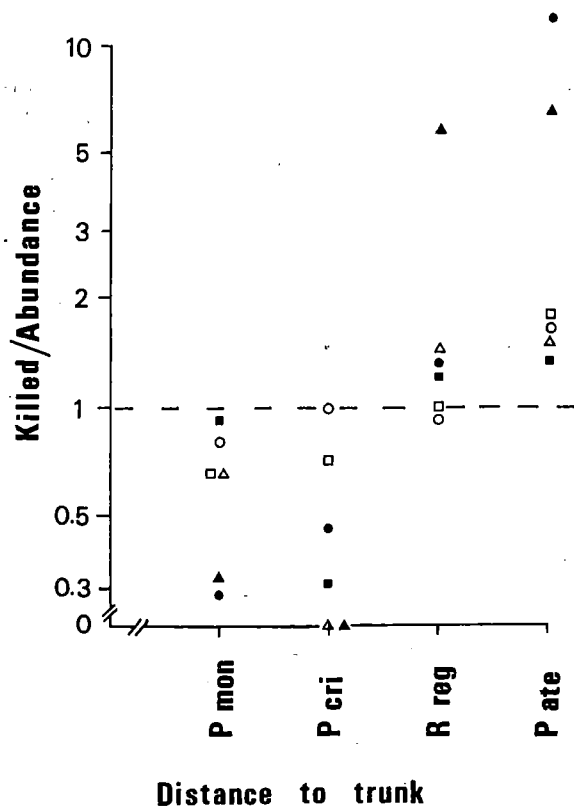


Fig. 2. Species ranked foraging distances to trunk plotted in relation to K/A-ratio, where K is proportion of species in the diet of pygmy owl and A is abundance of species in the field. The willow tit (P mon) forages closest to the tree trunk. The crested tit (P cri) forages centrally but somewhat more on the inner parts of trees than the goldcrest (R reg). The coal tit forages in the most exterior parts. Symbols above the horizontal line indicates that pygmy owls killed this species more frequently than could be expected from their relative abundances in the field and vice versa. The symbols indicates different areas; Δ : Central Norway, \blacktriangle : North Finland, \square : East Sweden, \blacksquare : South Finland, \circ : West Sweden and \bullet : Moscow area in Russia.

times more arthropods per bird than the inner halves of branches (Suhonen et al. 1992). Early investigations on this guild centred on the competition for food resources as an important factor limiting the foraging niches of each species (e.g. Alatalo 1981, 1982b, Alatalo et al. 1985, 1986, 1987, Alatalo and Moreno 1987). However, predation by pygmy owls, which is a diurnal predator, is a common source of winter mortality for members of the tit guild (Ekman et al. 1981, Jansson et al. 1981).

The predicted relationship between mortality risk by avian predators and tit guild structure is simple. It is assumed that the risk of predation is nonrandom across a given tree because the prey species segregate spatially according to their ability to utilize tree parts of varying risk (see Ekman 1986). In this paper we present data on pygmy owls preying on members of the North European

coniferous forest tit guild; willow tit, crested tit, coal tit and goldcrest. Our questions are: (1) Do pygmy owls kill more of those species that forage on exterior tree parts as suggested by Ekman (1986, 1987)? (2) Are subdominant species killed more by pygmy owls than the dominant species? We also discuss how competition for food and avoidance of predation can explain the use of foraging sites by tit species?

Material and methods

All data were extracted from the literature from six areas in Northern Europe; Norway, Russia and two areas both from Sweden and Finland (Appendix). Pygmy owl caches birds and small mammals in natural cavities and nestboxes during the late autumn and winter (Kellomäki 1966, 1977, Solheim 1984, Ekman 1986). Information on killed willow, crested and coal tits and goldcrests was extracted from papers studying food hoarding by the pygmy owl (Appendix). Relative abundances of wintering members of the tit guild were taken from winterbird censuses in each area, except in Central Norway and East Sweden. In these two areas we obtained estimates of relative species abundances from the number of individuals of each species reported in the flocks. In all areas, the relative abundances refer to average abundances in early or middle winter. The regional abundance data were compared with the birds cached by the pygmy owl as closely as possible from the same location. If one area had many small samples on cached birds, we calculated the relative abundances from pooled data.

We ranked the foraging sites of species according to distance from tree trunk using data in Alatalo et al. (1987) (rank number from inner to outer parts of tree is in brackets). The willow tit (1) forages closest to the tree trunk. The crested tit (2) forages centrally somewhat more on the inner parts of trees than the goldcrest (3). The coal tit (4) forages in the most exterior parts of trees. The social dominance hierarchy of the species is rather well established in the tit flocks. The heavier species are socially dominant over the lighter ones (Hogstad 1978, Morse 1978). The social dominance from top to bottom is as follows (rank numbers in brackets): crested tit (1), willow tit (2), coal tit (3) and goldcrest (4).

To ensure sufficient replication (see Hurlbert 1984) we used each of the six areas in Northern Europe as an independent observation for statistical testing. We used a sign-test to test whether pygmy owls killed each species more or less than could be expected from their relative abundances in the field. We divided species relative abundances in the caches of pygmy owl by their relative abundances in the field to get the killed/abundance ratio (K/A). We calculated Spearman rank correlation coefficients for all six areas independently, testing

Table 2. Summary of the effects of interspecific competition for food and predation-risk in tits.

1) Support for food competition effect, which cannot be explained by predation
A. Removal experiments: Remaining species increase foraging in the sites previously used by the removed species (Alatalo et al. 1985, 1987)
B. Geographical variation in foraging niches: There is a general pattern of niche expansion to the sites left vacant by the absent species (Alerstam et al. 1974, Hogstad 1978, Alatalo et al. 1986)
C. Variation in foraging niches among flocks of different species composition: A general pattern of shifts to forage as expected by interspecific competition hypothesis (Alatalo 1981)
D. Food limitation: Survival of individuals increases with extra food (Jansson et al. 1981)
2) Support for predation effects, which cannot be explained by competition
A. Predation-risk: Predation is a high mortality factor (Ekman et al. 1981, Jansson et al. 1981, Ekman 1984, 1986, this study)
B. Scanning behaviour: More scanning for predators in exterior parts of tree (Ekman 1987).
C. Foraging niches and predator presence: Species forage more on protected parts of trees when predation risk is high (J. Suhonen unpubl.)
D. Food supply and foraging sites: Dominant species do not forage in the parts of trees where the food supply is richest (Suhonen et al. 1992)

the foraging distance from tree trunk or species dominance rank and killed/abundance ratio. After that we used sign-tests for testing whether the six Spearman correlation coefficients were above zero. We used one-tailed tests, because the statistical alternative hypothesis (H_1) was that pygmy owl caught more species which were foraging in the outer parts of the trees and which were socially subdominant.

Results

There were consistent differences between the proportion of species killed by the pygmy owl and their abundance in the field. In all the six areas in Northern Europe, coal tits were found more often in the caches of pygmy owls than could be expected from their abundances in the field. (sign test $P = 0.016$) (Table 1, Figs 1, 2). Also, the goldcrest was in four areas found relatively more often in the caches compared to its abundance in the field. Both areas where pygmy owls killed slightly fewer goldcrests than expected are in Sweden. Coal tit and goldcrest use outer parts of trees and are subdominant in the guild. Both willow tits and crested tits were found in all six areas less frequently in the caches of pygmy owl than could be expected by their abundance in the field (sign test $P = 0.016$) (Table 1, Figs 1, 2).

We found that species which forage on outer parts of trees were more often included in the pygmy owl caches than expected (Fig. 2). In all six areas, Spearman rank correlations were positive for the distance from trunk and the risk of predation (mean of Spearman rank correlation = 0.86, SD = 0.11, range 0.74–1.00; sign test $P = 0.016$, $n = 6$). Likewise, subdominant species were killed significantly more often by the pygmy owl than dominant tits (sign test $P = 0.031$, $n = 5$; mean $r_s = 0.66$, SD = 0.34, range 0.00–0.95).

Discussion

Pygmy owl predation

Our results support the hypothesis of Ekman (1986), that pygmy owl predation is directed to species which forage in the outer parts of trees. The goldcrest and the coal tit are subdominant and the smallest species in the tit guild, and they were more often found in the caches of pygmy owl than expected from their field abundances. Ekman (1986) also found that pygmy owls killed crested tit more often than expected from their field abundances, but our data do not support this result. One explanation is that Ekman (1986) based his analysis on all wintering small passerine bird species, not only members of the tit guild. In the present analysis the killed/abundance ratio is slightly below unity in both of the Swedish areas. If the numbers of crested tits in the flock are greater in Sweden than in other areas (Ekman 1989), then intraspecific competition increases with increasing flock size and some subdominant crested tit individuals may forage more in places where they are vulnerable to predators.

Evidence for interspecific competition

There is much evidence for interspecific competition for food in the North European tit guild. Besides this, there

is evidence for predation on members of the tit guild, mainly by the pygmy owl. We have collected evidence both for interspecific competition for food and predation risk to the tit guild (Table 2).

It has been suggested that foraging site segregation by tits is caused by interspecific competition and several studies have shown that local absence of some species is associated with niche expansion of the remaining species (Alerstam et al. 1974, Hogstad 1978, Alatalo 1981, 1982a, Alatalo et al. 1986, Alatalo and Carlson 1987; for experimental evidence see Alatalo et al. 1985, 1987, Alatalo and Moreno 1987)(Table 2). It seems that crested tits and willow tits take up foraging sites where predation risk is smallest, while the two smaller species exploit the exterior tree parts. However, the choice of foraging sites cannot be understood solely in terms of avoiding predation. If food were not limiting at all, one would expect all species to seek the safer inner tree parts. Furthermore, supplementary feeding enhances winter survival of willow and crested tits showing directly that food resources are limiting (Jansson et al. 1981).

The coal tits and goldcrests 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) (Table 2). These shifts are likely to decrease predation risk. 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 the remaining species. Predation risk should have increased for the species which shifted to forage more in the outer tree parts. The shift suggests that the benefit of a higher food supply outweighed the increased predation risk.

Evidence for predation risk

Predation is a strong mortality factor for members of the tit guild. The pygmy owl kill a large proportion of wintering willow tits, especially juvenile individuals (Ekman et al. 1981, Jansson et al. 1981). The relative predation risk is higher on the outer parts of trees than on the inner parts (Ekman 1986, 1987, this study), and relative mortality rates by predators are lower for the dominant species than for the subordinate species as shown in this study.

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 extra food was provided, willow tits immediately retreated from pine to protected trees, spruces and inner branch sections (Ekman 1987).

When flock size increases, individuals scan less often for approaching predators. The time saved can be used

to increase feeding rates (Caraco 1979, Caraco et al. 1980, Elgar 1989), and when a predator is present scanning proportion increases (Caraco et al. 1980). Also in tit flocks, scanning decreases with increasing flock size (Ekman 1987, Hogstad 1988). The willow tits used more time for scanning in the outer parts of tree than in the inner parts (Ekman 1987). It is likely that avoidance of predation by joining in mixed species flocks has a positive effect on survival of all the species. Living in heterospecific groups could lead to a feeding advantage, intraspecific competition should be lower than in one-species groups and for that reason species can utilize its foraging sites more efficiently (Morse 1977).

The risk of predation by pygmy owls varies greatly with the availability of voles, which exhibit four-year population cycles (Hansson and Henttonen 1985). In Central Finland, willow and crested tits changed to forage on the inner tree parts in spruce after the vole populations had crashed and owls started to hunt on tits and goldcrest (Suhonen unpubl.). 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 (Table 2). However, we underline that this does not exclude the possibility that interspecific competition can be important in situations where smaller species respond to the presence of larger species (e.g. Alatalo et al. 1985) and vice versa (Alatalo et al. 1987).

According to the interspecific competition for food hypothesis we would predict that dominant species forage in the places which have the largest food supply. The most abundant food supply per bird was found on the outer and upper parts of spruce (Suhonen et al. 1992). The crested tit is a dominant species in tit guilds (Hogstad 1978), and if food competition was more important than predator avoidance, we would expect crested tits to forage in the best parts of tree. However, many field studies have shown that crested tits forage in the middle parts of branches when all species live in the same flocks (sympatry) (Table 2).

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 1988). During high risk of predation the coherence of tit individuals was higher, since more individuals were in the flocks than during times of low risk of predation (Ekman 1987). Furthermore, in willow tit flocks in Central Norway, the presence of adult individuals increased the survival of yearlings (Hogstad 1989).

To conclude, we can understand foraging separation of species only if both avoidance of predators and competition for food operate in conjunction in mixed species tit flocks. There could be a trade-off between food availability, predation risk and social dominance affect-

ing the ways in which the foraging sites within the guild are structured.

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Appendix. The data basis of this study. Data on the diet were extracted from papers on food hoarded by pygmy owls while relative abundances of wintering birds are from papers on bird censuses in six different areas.

In the diet of pygmy owl (source)	Available in the field (source)
West Sweden	
1	1
East Sweden	
2	3
Central Norway	
4, 5, 6	7
Moscow USSR	
8	9
South Finland (SW and south of 64° N)	
10, 11, 12, 13, 14, 15, 16	17, 18, 19, 20, 21, 22
North Finland (NW and north of 64° N)	
23, 24, 25, 26	17, 18, 19, 20, 21, 22

1 Ekman 1986, 2 Ahlbom 1973, 3 Alatalo et al. 1985, 4 Hagen 1952, 5 Arnekleiv 1978, 6 Solheim 1984, 7 Hogstad 1990, 8 Likachev 1971, 9 Bogolyvov and Preobrazhenskaya 1989, 10 Moilanen 1963, 11 Kellomäki 1966, 12 Hokkanen et al. 1977, 13 Mäkelä 1980, 14 Valkama 1982, 15 Halonen et al. 1992, 16 Lageström (unpubl.), 17–22 Sammalisto 1977, 1978, 1979, 1980, 1981, 1982, 23 Kaakinen and Mikkola 1972, 24 Huhta 1980, 25 Haataja and Kaarto 1986, 26 Järvi 1986.

