

Does predation maintain tit community diversity?

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Kullberg, C. and Ekman, J. 2000. Does predation maintain tit community diversity? – *Oikos* 89: 41–45.

European tits of the genus *Parus* constitute a complex group of coexisting boreal birds. Here we present a survey of the distribution of three coniferous-living *Parus* species and one of their main predators, the pygmy owl (*Glaucidium passerinum*), on nine isolated islands in Scandinavia. On all islands the coal tit (*Parus ater*) is the sole tit species when the pygmy owl is absent. The two larger species, the willow tit (*P. montanus*) and the crested tit (*P. cristatus*), only coexist with the coal tit when pygmy owls are present. We suggest that the coexistence of willow tits, crested tits and coal tits is the result of a combination of competition for food and predator-safe foraging sites. The smaller coal tit is superior in exploitation competition for food, while the two larger species have an advantage in interference competition for predator-safe foraging sites. The association between the distribution of the pygmy owl and the two larger tit species on isolated islands in Scandinavia is consistent with the idea that the pygmy owl is a keystone predator.

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Coexisting congeners usually differ in morphology and resource use. One explanation for the non-random combination of trait values among sympatric congeners is that competition is a structuring force behind the composition of species assemblies (Lack 1971). Food depletion will result in mutual competition among species exploiting a common resource, and segregation in food use is a mechanism that allows coexistence. However, the outcome of interspecific competitive relationships involving food may shift depending on the exposure to predators when energy gain is traded against predator protection (Kotler and Holt 1989). Selective predation could then promote coexistence and maintain high diversity of prey species (Paine 1966, 1971). The presence of a predator, which selectively attacks species superior in exploiting food, will release food resources and allow coexistence by species more efficient at avoiding predators.

It is rare for more than two congeneric species to coexist in sympatry (Lack 1971). The Old World parids (genus *Parus*) are exceptional in the large number of

congeneric species that coexist without habitat separation (Haftorn 1956). Niche separation between species within the *Parus* genus has been subject to extensive studies to understand the basis for coexistence (e.g. Snow 1954, Haftorn 1956, Lack 1971, Hogstad 1978, Norberg 1979, Perrins 1979, Herrera 1981, Alatalo et al. 1986, Ekman 1986, Suhonen 1991, Suhonen et al. 1994, Wiggins and Møller 1997). Within habitat, coexisting species are separated in foraging niches by using different height portions of trees and different distances to the trunk while foraging (Haftorn 1956). Niche expansion in response to the absence of competitors provides compelling evidence that current competition constrains niche use (Alatalo et al. 1985, 1986, 1987).

Here we will focus on the distribution of three species inhabiting coniferous forest of Scandinavia. The two larger species, the willow tit (*P. montanus*; mass ~ 11 g) and the crested tit (*P. cristatus*; mass ~ 11.5 g) forage closer to the trunk than the relatively smaller coal tit (*P. ater*; mass ~ 8.5 g) (Haftorn 1956). On several islands around Scandinavia this community of tit spe-

Accepted 30 July 1999

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ISSN 0030-1299

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cies is depauperated with the coal tit as the only tit species. Niche expansion of the coal tit in the absence of the larger congeners suggests that its feeding sites are constrained by interspecific interactions in sympatry with the larger willow tit and crested tit (Alatalo et al. 1985). Flexibility in niche use of the tits (Alatalo et al. 1985, 1986, 1987, Alerstam et al. 1974) indicates current competition, but it does not reveal what underlying resources they compete for. Responses to food and cover have shown that niche use is the outcome of an energy gain/predation trade-off (Ekman 1987, Lens and Dhondt 1992, Suhonen 1993a, b, Kullberg 1998). Hence, the presence of a predator could affect the outcome of interspecific competition mediated through niche separation. Here we present results suggesting that competition governs not only niche expansions by coal tits on islands but the depauperated island communities of tits may themselves be the result of interspecific competitive exclusion in response to relaxed competition for predation protection.

The mechanism of competition

The coal tit exploits food resources more efficiently not only within its own niche space but also within the niche of larger congeneric competitors (willow tit – Alatalo and Moreno 1987, crested tit – Kothbauer-Hellmann and Winkler 1997). There is hence no segregation along a food resource axis that could account for the coexistence of the coal tit and its larger congeners. Competition for food alone would thus not be sufficient to explain coexistence within this parid community. The coal tit is not only a very efficient forager but it also has larger clutch sizes than the other species and in addition it is the only coniferous tit species that regularly have double broods during a breeding season (Cramp 1985). Probably, unless there is competition for other resources than food the coal tit would be able to outcompete its larger congeners. A multidimensional niche where interspecific competition is mediated through foraging efficiency in combination with interference competition for protection from predators can however reconcile coexistence among the parids with the fact that the coal tit is a more efficient forager. Simultaneous competition for food and predator safe foraging sites is consistent with the conclusion that niche use in the coniferous forest parids is the outcome of an energy gain/predation trade-off (Ekman 1987, Lens and Dhondt 1992, Suhonen 1993a, b). Predation will promote coexistence by providing a compensating benefit for the larger species (willow tit, crested tit) gained from monopolising foraging sites more protected from predation than those used by coal tits.

The pygmy owl (*Glaucidium passerinum*) is the main predator on species of the tit guild (Ekman et al. 1981,

Ekman 1986, Suhonen 1993a). Another raptor preying on boreal tits is the sparrowhawk. However, we do not think this partly migrating species has as big an influence on the species composition of tits as the pygmy owl since most individuals move south in winter and moreover the sparrowhawk has not the same hunting strategy as the pygmy owl. The risk of being killed by a pygmy owl is a function of tree height and distance from the trunk (Ekman 1986, 1987, Suhonen 1993a, b, Kullberg 1995). Species foraging peripherally in the trees such as the coal tit are over-represented among pygmy owl kills relative their numbers while species foraging closer to the trunk, such as willow tits and crested tits, are underrepresented among the prey (Ekman 1986, Suhonen 1993a, Suhonen et al. 1993). The access to cover reflects interference among the tits. The interspecific rank orders are mainly a function of size (Hogstad 1978, Alatalo and Moreno 1987) although the outcome of interactions may not be consistent when individuals of different sex and age meet (Haftorn 1993). The larger tits use their dominance to monopolise the inner sections of branches and refer coal tits to outer sections where they are more exposed to predators. Coal tits in accordance expand their niche into branch sections used by its larger congeneric competitors when they are removed (Alatalo et al. 1985, Alatalo and Moreno 1987).

Predictions and field data

Expected associations

Coal tits enjoy a foraging advantage regardless of the distance from the trunk although they confine their activities to the more peripheral parts, while the higher predator protection provides a compensating benefit for the inferior foraging efficiency of the larger species. However, this gradient exists only in the presence of a predator. In the absence of pygmy owls we would then predict that coal tits would be able to outcompete their larger congeners and be the sole tit species due to the higher potential for population growth and the efficient foraging of the species. Based on competition theory we therefore expect the willow tit and the crested tit to be absent in the absence of pygmy owls. However, outside the coal tit range willow tits and crested tits should occur regardless of the occurrence of pygmy owls.

Island data

These predictions were tested by comparing the composition of tit communities to the distribution of the pygmy owl on islands around Scandinavia. Since we base our hypothesis on the observed relative predation risk within coniferous trees, we have limited our study

Table 1. Area, distance to mainland, occurrence of breeding pairs of the different species and source of the information for the different islands. B = breeding, – = not breeding.

island	area (km ²)	distance to mainland (km)	pygmy owl	coal tit	willow tit	crested tit	source
Åland	970	50	B	B	B	B	G. Andersson
Ösel	3000	15	B	B	B	B	Renno 1993
Dagö	989	10	B	B	B	B	K. Rattiste
Karlö	200	7	B	B	B	B	Väisänen et al. 1998, J. Suhonen
Gotland	3140	85	–	B	–	–	Alerstam et al. 1974
Öland	1345	4	–	B	¹	–	P. Älind
Bornholm	587	35	–	B	–	–	P. Lygns
Hanö	2.2	4	–	B	–	–	P. Österblad
Visingsö	30	6	–	B	–	–	D. Steen

¹ = breeding intermittently and sparsely in the north of the island.

area to that kind of habitat and do not include islands in for example Denmark, where not only habitat differs but also they are inhabited by different sub-species of the tits. Information on the distribution of tits and pygmy owls was gathered from the literature and local ornithologists (Table 1). The distribution of the tit species (willow tit, crested tit, coal tit) on Scandinavian islands is well known (e.g. Alerstam et al. 1974, Alatalo et al. 1986). In contrast the pygmy owl is a species which is difficult to census and population estimates are hard to come by. It is an inconspicuous owl and song can be heard primarily around dawn or immediately before dusk in early spring and autumn. Unlike in many other owls the female sits hard without giving away the nest by responding to disturbance. Inspection of the nest cavity with a torch and mirror is usually the only method of confirming a nest. Inclusion of islands in our data set was therefore limited by the quality of information about pygmy owls. Based on our own field experience of pygmy owls we considered islands to have permanent populations of pygmy owls if calling was heard. Information that pygmy owls were absent was accepted only for islands with active and organised ornithological activities and comprehensive census data on the entire bird community. These requirements severely limited our data set to nine islands. The set of islands consists of the largest and most isolated islands of the Baltic Sea and one large island of an inland lake (Visingsö in Lake Vättern in Sweden, Fig. 1). Åland being an archipelago is an exception. To be conservative and not inflate sample sizes we choose to treat Åland as one island. The islands included in this comparison all contain coniferous forest without any apparent differences to the habitats that these species inhabit on the mainland.

Community composition

There is a significant association between the occurrence of pygmy owls and the composition of the tit

guild. Pygmy owls have been recorded on four out of the nine islands. These four islands are the only ones where all three tit species coexist. On the other five islands the pygmy owl is absent and the coal tit is the sole coniferous forest parid ($p < 0.01$, $n = 9$, Fisher's exact test). Difference in colonising capacities could be an alternative explanation for the distribution found. It has been suggested that coal tits are better at colonising isolated islands than the larger species (Wiggins and Møller 1997). However, in this study neither distance to mainland nor island area could explain the occurrence of the larger tit species or the pygmy owls (area: $n = 9$,

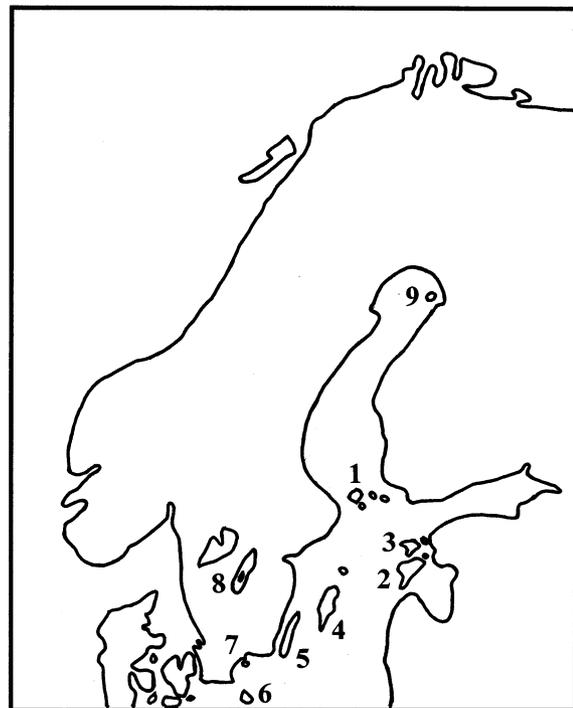


Fig. 1. Islands included in this study. 1. Åland, 2. Ösel (Saaremaa), 3. Dagö (Hiiumaa), 4. Gotland, 5. Öland, 6. Bornholm, 7. Hanö, 8. Visingsö, 9. Karlö (Hailuoto).

d.f. = 1, $\chi^2 = 0.75$, $p = 0.4$; distance to mainland: $n = 9$, d.f. = 1, $\chi^2 = 0.08$, $p = 0.8$; both logistic regression with log transformed data). Furthermore, willow tits have occasionally been observed on several islands where pygmy owls are absent without being able to establish breeding populations (Alerstam et al. 1974, Daniel Steen pers. comm.). In the northern part of the island of Öland, willow tits occur intermittently, and sometimes a few pairs even breed, but they never seem to establish a stable population.

Discussion

The study of interspecific competition is complicated by the fact that it involves questions on an evolutionary time scale (Connell 1980, Sih et al. 1985). Even if coexistence of congeneric species living in sympatry would be the product of competition the divergence allowing coexistence could be a response to selection operating in the past. Patterns in morphology and resource use may then be of little consequence for competition today. Further, coexistence may be possible only when congeners meet which are already sufficiently ecologically separated not to compete. Observations supposed to be indicative of competition such as character displacement suffer from regional differences in habitat and abiotic factors, and species differences can be a response to other factors than an interaction between species (Grant 1975, Strong et al. 1979, Sih et al. 1985).

The niche differences among closely related tit species could reflect morphological adaptations to different habitats in the past rather than a response to interspecific interactions acting today. However, plasticity in niche use in response to the composition of the *Parus* species community strongly suggests that current competition affects niche use and species segregation (Alatalo et al. 1985, 1986, 1987). For the Old World there is not only this evidence for competition structuring the tit community. The association between the distribution of the pygmy owl and the larger coniferous forest tit species is consistent with the idea that the pygmy owl is a keystone predator. Our survey shows a higher diversity on islands with a predator. This association has to be interpreted against the background that survival in these species reflects an energy gain/predation trade-off (Ekman 1987, Lens and Dhondt 1992, Suhonen 1993a, b). We suggest that niche expansion of the coal tit on islands is not a response to a competitive release in the absence of larger congeners, but primarily based on an increased population growth rate. Being selectively more heavily preyed upon than its larger congeners, coal tit numbers should respond more strongly to the absence of the pygmy owl. Given this advantage the coal tit will exclude the larger congeners that no longer

have any advantage of using protected sites in the absence of a predator. Accordingly, the number of coal tits on the island of Gotland equals the joint abundance of coal tits, crested tits and willow tits on the mainland (Alerstam et al. 1974). The fact that willow tits intermittently have occurred on some islands where pygmy owls are absent without establishing stable populations suggests that the distribution of species found cannot be explained by limited dispersal propensity in this species. Furthermore, since willow tits and crested tits have the same habitat requirements as the coal tits on the mainland, lack of habitat could not explain the absence of the two larger species on some islands. The islands inhabited by all three tit species are the ones located furthest north and east which might imply that these are the islands with the most severe winter climate. One might then argue that harsh winter climate could be an alternative factor (instead of the pygmy owl) influencing the tit community. Harsh winters might be more disadvantageous for the smaller coal tit than for the larger species and hence reduce the coal tit population to levels where the tit species can coexist. However, we do not find this alternative hypothesis of species distribution on the islands convincing since no such pattern in relation to climate can be observed on the mainland.

The competing coniferous forest specialists among the Old World tits differ in size. This difference can be understood from the energy gain/predation dichotomy that explains niche use. The high foraging efficiency of coal tits is linked to small body size. The larger willow tit and crested tit appear to be less efficient foragers because of their larger body mass. There are several reasons why small body mass improves foraging efficiency. Energetically, locomotion is less costly with a small body mass. The moment of inertia is lower which makes the bird more agile. Less energy is needed to support the requirements of a smaller body, which should make starvation risk less sensitive to food density. Finally, a smaller bird can find support on finer branches while foraging. However, while a small body mass improves foraging efficiency, larger birds have an advantage in interference competition. Although the larger willow tits and crested tits do not consistently dominate in interactions with the smaller coal tit due to variation in age and sex (Haftorn 1993) there appears to be a general association between size and dominance (Hogstad 1978, Morse 1978, Alatalo and Moreno 1987). By virtue of their dominance the larger tits monopolise feeding sites close to the trunk where predator protection is better (Ekman 1986, 1987). The small body mass gives the coal tit an advantage in foraging efficiency, while the large bodies of willow tits and crested tits allow them to assert predator-safe foraging sites. The coexistence of willow tits and crested tits on the one hand and the coal tit on the other would reflect specialisation when there is simultaneous competition for food and predator-safe foraging sites.

Acknowledgements – We thank Birgitta Tullberg and Jukka Suhonen for valuable comments on the manuscript. We also want to thank Göran Andersson, Peter Lyngs, Kalev Rattiste, Daniel Steen, Jukka Suhonen, Per Ålind and Patrik Österblad for information about occurrence of the tit species and the pygmy owls on the different islands.

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