HETEROSPECIFIC ATTRACTION IN BREEDING BIRD COMMUNITIES

Implications to habitat selection and species interactions in a landscape perspective

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Department of Biology

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Abstract

I studied the structure of European breeding forest bird communities on several spatial scales focusing on heterospecific attraction among birds (i.e., the attraction of individuals to the company of interspecifics). Namely, I examined how heterospecific attraction affects habitat selection in migrant birds and the potential role of predation risk in enhancing heterospecific attraction during breeding with particular emphasis regarding the interaction between resident and migrant birds.

Geographically, low densities and low relative proportions of resident titmice (*Parus* and *Aegithalos* spp.) were associated with harsh winter conditions. The densities of northern European titmice populations are suggested to be lower than expected on the basis of summer productivity potentially causing geographical variation with respect to the interactions between resident and migrant birds. As expected, the associations between titmice and migrants appear stronger and more positive in northern Europe than elsewhere.

Heterospecific attraction in habitat selection among migrant species was studied both experimentally and theoretically. An increased density of titmice resulted in a higher number and abundance of migrant species than the removal treatment, suggesting that resident birds are used as cues for locating profitable breeding sites. From a theoretical perspective and under most conditions, the use of heterospecific cues proved to be a better habitat selection strategy than selection of sites based on direct assessment of the relative quality of habitat patches. Only when interactions (both positive and negative) between migrants and residents were weak and sampling costs of both strategies were about equivalent, did individuals using direct sampling gain in fitness.

Heterospecific attraction during breeding in relation to predation risk was assessed by examining the spatial distribution of birds. Both experimentally increased perceived predation risk and naturally occurring predation risk created by the presence of sparrowhawk (*Accipiter nisus*) i.e., relative to the vicinity of nesting hawk, resulted in more clumped distribution of birds than areas of lower risk. Around sparrowhawks nest, however, clumping was apparent for only one forest type and only among study plots including both large (≥ 20 g, preferred prey) and small birds (< 20 g).

To conclude, heterospecific attraction of migrants to resident birds contributes to the structure of local avian communities in forest landscapes. Heterospecific attraction among birds is strengthened by increased predation risk causing variation in species interactions when considered in a landscape perspective.

Keywords: forest birds, competition, *Parus*, predation

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As I have struggled with my thesis, a small spruce has grown behind the window of my office. It has grown little by little and nowadays it is so big that it can peep into my room and follow my daily works. For a spruce campus area made of concrete is perhaps not the best possible place to grow but for me, I believe, this has been a fruitful time period. The biggest thanks on account of this thesis and providing a rich and solid soil for my positive (hopefully) professional growth belong admittedly to my supervisor, Mikko Mönkkönen. He has guided me since I started my M.S. work. His enthusiasm for science and his wild but positive attitude for everything have been invaluable in the course of this project. He is a jolly good fellow. I want also to express my warmest gratitude to my closest friends, Jouko Inkeröinen and Pasi Reunanen. Their help and company in the field and during free time is something that can not be measured. With Mikko, Jouko and Pasi I have had trips and adventures both in Finland and in eastern and southern countries, which I will always remember with warmth. I started my bird census business with Jouko, and the philosophical conversations I had with him about the deepest meaning of bird censusing and bird censusers have helped me in the early summer mornings when the why-questions are easily aroused. Juha Tuomi and Roger Härdling introduced me the fascinating world of theoretical ecology. Without their help this work would lack the theoretical aspect. The previous and present members of the Society of Serious Coffee Drinkers (Lluís Brotons, Esa Huhta, Marko Hyvärinen, Arja Kaitala, Kari Koivula, Minna Käkelä, Kimmo Lahti, Seppo Rytkönen, Claudia Siffczyk, Paavo Tunkkari plus all the hang-arounds) at the Zoological Museum have provided me with a lot of good coffee and hilarious words about non-scientific matters. Bohdan Slepkovych kindly revised the English and my mixed metaphors of the summary of the thesis.

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Oulu, April 2000 Jukka Forsman

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Forsman JT & Mönkkönen M (2000) Titmice in European breeding bird assemblages: the role of climatic conditions and association with migrant birds. Manuscript (submitted).

II Forsman JT, Mönkkönen M, Helle P & Inkeröinen J (1998) Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. Oecologia 115: 278-286.

III Mönkkönen M, Härdling R, Forsman JT & Tuomi J (1999) Evolution of heterospecific attraction: using other species as cues in habitat selection. Evolutionary Ecology 13: 91-104.

IV Forsman JT, Mönkkönen M, Inkeröinen J & Reunanen P (1998) Aggregate dispersion of birds after encountering a predator: experimental evidence. Journal of Avian Biology 29: 44-48.

V Forsman JT, Mönkkönen M & Hukkanen M (2000) Effects of predation on community assembly and spatial dispersion of breeding forest birds. Ecology, in press.

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1. Introduction

1.1. Scale issues in species assemblages

Beauty is in the eyes of the beholder and with similar consideration this wise phrase may be extended to include structure, since species assemblages can be viewed and interpreted at several different scales. Patterns and processes differ between scales, but spatial and temporal scales are not mutually exclusive and should not be viewed in isolation. As such, the hierarchical nature of ecological dimensions enables that the patterns at some spatial level may be used to provide insight of processes at other scales, suggesting that a multiscale approach may be fruitful.

Traditionally the role of local factors such as competition, predation and parasitism have been emphasised in ecological research (e.g., MacArthur 1972, Cody 1974, Connell 1975), and local interspecific interactions were stressed as a key for understanding species diversity and co-existence in biological communities. Consequently, species have almost invariably been considered as acting to inhibit each other's existence in communities. Nevertheless, it is well known that the nature of interspecific interactions varies depending on local biotic or abiotic conditions (see Thompson 1988, Travis 1996 and references therein) and species are not always antagonistic to one another. Furthermore, prior to entering a stage of a local community numerous factors at different spatial and temporal scales have influenced the actors or individuals within the community. Thus, in addition to the effects of local factors, the community structure may also hold the imprint from larger scales as well. Reciprocally, local processes may also express themselves at broader levels.

Of the contemporary processes, geographical variation in climate or primary production affect regional species pools from which the species are selected into local assemblages. For example, the amount of available energy has been shown to explain the decrease in species number with increasing latitude (e.g., Turner *et al.* 1988, Currie 1991, Wright *et al.* 1993). The influence of geographical factors is often difficult to perceive at a local scale because all species are similarly influenced. However, among boreal and temperate breeding bird assemblages, which are presently considered, this is not always the case. Boreal and temperate breeding bird assemblages consist basically of resident and migrant birds, each being affected partially by different geographical variables. Resident birds must cope with conditions at their breeding areas on a year-round basis whereas migrant birds share the same circumstances only for part of the year. The direct consequences of this difference are clear on local assemblages as the proportion of migrant birds in breeding assemblages increases with increasing latitude (MacArthur 1959, Willson 1976, Herrera 1978a, Helle & Fuller 1988). This has been attributed to the harshness of winter conditions and the seasonality of food resources (MacArthur 1959). If residents are affected relatively more by winter conditions than by summer carrying capacities, this may also have indirect implications on the local scale as well as influencing variation in species interactions.

Habitat selection is the link between regional or landscape-level and local species assemblages (Ricklefs & Schluter 1993a). Habitat selection is also the first level in the hierarchy at which the individual-choice matters and the decisions are of importance for the local assemblage composition. The selection of profitable habitat for reproduction has also strong evolutionary consequences. Many passerines breed only once or twice during their lifetime and thus, their reproductive output is partly dependent on a few decisions made during the sampling and selection process. Therefore, it is not surprising that habitat selection has both strong genetic and individual based experience components (see Svärdson 1949, Hildén 1965, Partridge 1978, Jaenike & Holt 1991). On this level, individuals also experience intra- and interspecific contact. Svärdson (1949) was the first who explicitly described the mechanism and consequences of intra- and interspecific competition. Theoretically, species are suggested to hold an innate picture of the optimal habitat and competition within species tends to push individuals to suboptimal habitats whereas interspecific competition is the counterforce restricting species into the optimal habitat (Svärdson 1949). An individual's perceptual range is also of importance. Fretwell's (1972) ideal free distribution habitat selection model assumes that animals are able to measure the density of individuals from which indirectly they can infer habitat quality. Habitat selection of birds is usually considered to be connected to certain habitat components or floristics (e.g., Wiens & Rotenberry 1981, Rotenberry 1985). However, the implications of animal cognition on habitat selection may be of importance as well. For example, evidence suggests that using of intraspecific (Stamps 1988, Smith & Peacock 1990, Reed & Dobson 1993) or interspecific (Mönkkönen *et al.* 1990, 1997, Danielson 1991, Elmberg *et al.* 1997) cues in the habitat selection may have profound consequences on the composition of assembly.

Before migrating individuals reach the local scale, where their preferences are the only thing that matter, however, they must pass through a larger dimension for habitat selection that can have substantial effects on local assemblages, i.e., the landscape level. A landscape consists of different habitats embedded in a larger area constituting the basis for habitat selection among individuals. Therefore, the landscape can be considered as an intermediate scale between regional and local dimensions (Urban *et al.* 1987). At this intermediate level both landscape-structure and species-specific preferences may affect decision or selection processes. Theoretical evidence suggests that the interplay between the composition of the landscape, interspecific interactions, and the cognitive abilities of individuals may have profound effect on the final result of community composition

(Pulliam 1988, Pulliam & Danielson 1991, Danielson 1991, 1992, Bowers & Dooley 1991, Dunning *et al.* 1992).

Once breeding habitat is selected, individuals have entered into the stage where longer-term intra- and interspecific interactions take place. Interspecific competition is undoubtedly a common interaction among animals (see Connell 1983 and Schoener 1983 for reviews). In birds, both interference and exploitative interspecific competition has been shown to occur (e.g., Slagsvold 1975, Dhondt 1977, Högsted 1980, Minot 1981, Pimm *et al.* 1985, Gustafsson 1987, 1988, Sasvari *et al.* 1987, Merilä & Wiggins 1995). However, it has been strongly argued that under certain conditions the intensity and importance of competition may be unimportant (see Wiens 1977, 1989). In northern areas where environmental unpredictability is suggested to be large and turn-over rates in species assemblages are high (Järvinen 1979, 1981), interspecific interactions are assumed less important. Thus, northern assemblages are suggested to result from more purely individualistic preferences (e.g., Enemar *et al.* 1984, Haila & Järvinen 1990, Morozov 1993, Haila *et al.* 1996).

1.2. Theoretical and historical background

The coexistence of species within ecological communities has long intrigued ecologists. Before Hutchinson (1959) addressed his classical question about high numbers of co-occurring species, rivalling philosophical hypotheses about the nature of communities already existed. Both Clements (1916) and Gleason (1926) made inferences from plant communities in North America, but their conclusions were quite different. Gleason (1926) emphasised that the occurrence and abundance of species is dependent mostly on species-specific tolerances and preferences. Species coexist because their requirements and preferences for the habitat characteristics are similar. By contrast, Clements (1916) argued that coactions among species constitute the chief bounds in the community. He suggested that interspecific interactions within communities are so strong that they resemble the function of cells and organisms. The Clementsian super-organism view of communities was also later adopted by Allee and his co-workers (see Allee *et al.* 1959).

The importance of interspecific interactions in the Clementsian-community view was reflected strongly in later community concepts. The competition-mediated species coexistence concept adopted the tight interspecific relationships from the super-organism view, even though the original model also emphasised other relations between species such as exploitation and mutualism (Allee *et al.* 1959). A well established theoretical framework (Volterra 1926, Lotka 1932) and controlled experimental laboratory studies (e.g., Gause 1934, 1935) were the cornerstones of the theory of interspecific competition and competitive exclusion. This led to the competition paradigm, which was later applied to many natural systems and extrapolated over scales (see MacArthur 1972, Diamond 1972, Cody 1974, Schoener 1982). After the foundations of the ideal habitat selection theory were laid by the works of Brown (1969), Fretwell and Lucas (1970) and Fretwell (1972), several theoreticians started to work on Hutchinson's dilemma in greater detail, i.e., examining the conditions permitting species co-existence (e.g., Rosenzweig 1979, 1991, Pimm & Rosenzweig 1981, Pacala & Roughgarden 1982, Morris 1990, Brown

1990, see also Mclaughlin & Roughgarden 1993, Holt 1993). It was quite soon observed, however, that not all patterns fit the competition paradigm. It was noticed, for example, that environmental stochasticity (e.g., Wiens 1977, 1983) or other processes such as predation (Hairston *et al.* 1960, Connell 1975, Strong 1984), may overrule the effects of interspecific competition. It has also been observed in birds that nest predation can produce patterns similar to those predicted by the competition theory. Birds nesting in similar microhabitats may avoid each others company in order to decrease the risk of nest predation (see Martin 1988a,b, 1993). Nowadays ecologists hold a much more balanced and holistic view about the processes shaping communities (see e.g., Martin 1986, Wiens 1989, Cornell & Lawton 1992, Ricklefs & Schluter 1993b).

In northern boreal regions, interspecific interactions are not believed to play an important role in determining the composition of breeding bird assemblages (see Haila & Järvinen 1990) because of high annual population fluctuations (Järvinen 1979, Enemar 1984). On the other hand, seasonal environments have been suggested to promote competition between residents and migrants (Herrera 1978a, Morse 1989, O'Connor 1990). Herrera (1978a) inferred from a geographical comparison that migrant birds are inferior competitors to residents fitting into assemblages only if there are resources available after the preoccupation of the resident birds (see also Herrera 1978b). Mönkkönen *et al.* (1990) tested this hypothesis and found, by contrast, that experimentally augmented resident bird (*Parus* spp.) abundances were associated with increased migrant bird densities. They suggested that migrant birds may use residents as a cue for finding profitable breeding sites. This process, coined as heterospecific attraction by Mönkkönen *et al.* (1990), suggests that northern breeding bird assemblages may have more interactive 'community' nature than previously believed.

1.3. The aim of the study

This thesis investigates the structure of forest passerine breeding bird communities at several spatial scales. In particular, I focus on heterospecific attraction and how it manifests itself in the selection of habitat by migrant birds and in interspecific interactions during breeding. First, I make a geographical over-view of the European breeding bird assemblages by investigating the influence of abiotic factors such as location and climate on the density and relative proportion of resident birds (*Parus* and *Aegithalos* spp.; I). If geographical variation exists in the relative decreasing effect of harsh winters on densities of resident populations, it may indirectly cause geographical variation in the association between resident and migrant birds. The possibility of geographical variation in interspecific associations is explored in the first paper. The next two papers (II, III) examine the heterospecific attraction as a method of habitat selection. First, I present results from an experiment in which the density of resident birds (*Parus* spp.) was manipulated to examine whether migrant birds use titmice as a cue in the selection of breeding habitat (II). In addition, I also investigated the relative influence of food abundance on migrant density (II). In the third paper, both biotic and abiotic conditions were theoretically examined to determine when heterospecific attraction would be a beneficial habitat selection method (III).

The next theme in the thesis concerns heterospecific attraction among community members during breeding. Species interactions were examined by studying the spatial distribution of individuals in relation to predation risk. First, I measured the spatial distribution of forest birds with respect to interspecific individuals in relation to an experimentally increased perceived risk of predation (IV), and then I examined community composition and avian species distribution in relation to predator nests in the landscape (V).

2. Materials and methods

2.1. Bird assemblages in Europe

Data from breeding bird censuses were used to examine the composition of European bird assemblages (I). Census materials covered the whole of Europe from Spain to north Finland, and from Great Britain to western Russia. Since the structure of breeding bird assemblages in European mature forests are rather similar (Blondel & Farré 1988, Mönkkönen 1994), only the mature forest censuses were included in order to minimise heterogeneity of data. The densities of strictly resident titmice (*Parus* and *Aegithalos* spp.), total density of passerine species, and four different migratory bird groups (*Phylloscopus*, *Fringilla* and *Turdus* spp. and hole nesters) were extracted from census materials. In addition, titmice were divided into two groups on the basis of hoarding behaviour. A set of eleven different geographical and climatic variables were chosen to describe both winter and breeding time temperatures and precipitation conditions in each of the census locations.

The first goal in the study was to examine the influence of climate on the density and relative proportion of resident titmice in breeding assemblages (I). This was done by an ANOVA model in which forest type and altitude were used as discrete factors and geographical and climatic variables were included as continuous covariates. However, geographical and climatic variables are highly inter-correlated. Therefore, a principal component analysis was used to reduce the number variables into orthogonal principal components. Principal component scores, describing the variability of the original climatic variables in each census location, were entered into the models as covariates.

Bird censuses were also used to explore whether any qualitative geographical variation exists in the association between resident titmice and migrant bird groups (I). *Turdus*-species were used partly as a control group while the other three migrant groups were considered putative competitors with titmice, since they overlap in resource use with resident birds (e.g., Alatalo 1981). The basic approach was to explain, within each census location, the variation in the density of migrant birds by the density of titmice and vice versa. Before the densities of species were regressed however, the effects of climate, geographical location, forest type and altitude were removed from the standardised densities of both titmice and migrant birds by an ANOVA model. These procedures equalise the density differences resulting from different primary productivity of localities and remove the effect of habitat type on density. The remaining variation in density is assumed to result from the densities of other species. The residuals of the ANOVA were then applied to survey the quality of species associations in four different subregions in Europe. This approach follows the procedure introduced by Fox and Luo (1996) and Luo, Monamy and Fox (1998). They have used this method successfully on the local scale to infer estimates of competition coefficients between rodent species.

2.2. Experimental and theoretical approach to heterospecific attraction in habitat selection

Heterospecific attraction as a method for habitat selection among migrant birds was studied both experimentally (II) and theoretically (III). The experimental portion was conducted in Meltaus in northern Finland (66° 55′ N, 25° 25′ E) where eight forest fragments surrounded by clear-cuts and bogs were chosen as study sites. The experiment consisted of two treatment groups, one with an increased and another with a decreased abundance of resident titmice (*Parus* spp.). The experiment lasted for two years and each study plot received both treatments. This procedure enabled comparisons between treatments within each study plot. In addition, the relative arthropod abundance of study plots was assessed by sweep-net sampling. Samples were collected in both years along the same transects.

We used theoretical tools to examine the relative benefits and costs of using other species as cues in selecting habitat as well as the effect of interspecific competition (III). An imaginary landscape consisting of three types of habitats was considered containing a source habitat where reproduction exceeds mortality, a sink habitat with mortality exceeding reproduction and an inhospitable matrix habitat. The sink habitat may be of lower quality for example due to lower amount or quality of food or because of a high density of predators. Both source and sink habitats consist of patches, which provide enough resources for individuals to attempt reproduction (see Danielson 1992). Two species of animals live and reproduce in this world. One species is a resident and the other is a colonising (i.e., migrating) species which occupies the landscape seasonally. Both species prefer the same kind of habitat type. The resident species occupies patches before the arrival of the colonists and they are always in the source patches. Two types of colonising species were used; "cue-users" have better cognitive abilities and use the presence of residents as cues to the quality of a patch and "samplers" are individuals that always directly sample in assessing the quality of a patch.

The relative superiority of the two strategies was compared via reproductive output of the colonising species under different biotic and abiotic conditions. Conditions examined were firstly, the relative proportion of each patch type in the landscape and secondly, the intensity of competition between resident and colonising species. The latter had important consequences especially for the behaviour of the cue-user. The relative difference between the intensity of competition and the benefits gained by choosing the patch with resident bird determines the qualitative difference between an occupied and an unoccupied source patch. If competition between the individuals of colonising and resident species is intense and exceeds the benefits of aggregating with a resident, the fitness in an unoccupied patch is better. If competition is low and the benefits of choosing an occupied patch are high, an occupied patch is better. Because the cue-user is capable of detecting the difference between an occupied and an unoccupied patch, we also assumed that it can perceive the relative difference between competition and the benefits of aggregating with residents. Thirdly, the relative proportion of occupied patches was also varied in order to compare the effect of resident abundance on heterospecific attraction. Last, the cost of assessing the quality of a patch may also have profound effects on the benefits of habitat selection strategies. Both samplers and cue-users have the same assessing costs in the empty source patch and in the sink. Cue-users perceive the residents in the landscape and therefore we assumed that their cost for assessing occupied sources was always lower than that of samplers which comparatively always pay the same cost independent of patch type.

Colonisers use the sequential comparison tactic as a sampling strategy (Wittenberger 1983) in which the best of the assessed patches is selected. This strategy should be advantageous when colonising animals face a risk of possible patches for reproduction being filled quickly by intra- or interspecifics (Wittenberger 1983).

2.3. Heterospecific attraction and predation risk

The role of heterospecific attraction in the spatial distribution of individuals and species in their breeding assemblages was studied using both experimental (IV) and comparative (V) approaches. If the distribution of heterospecific individuals is even, it may refer to interspecific competition (see Pielou 1977). Random distributions may be a sign of weak interactions, whereas aggregate distributions may indicate active interactions between individuals. In the last case however, the possibility of passive aggregation (e.g., due to a patchy distribution of food) must be excluded before active interactions between species can be suggested (Pielou 1977).

In papers IV and V we studied the spatial distribution of heterospecific forest birds in relation to predation risk. If the distribution changed with respect to predation risk, it was assumed that the change was due to an active choice by birds. In paper IV the perceived risk of predation by birds was manipulated experimentally while in paper V we examined aggregations in relation to the proximity of nesting predators. These studies were conducted near Oulu, northern Finland (65°N, 25° 30′E). The area consists of a patchwork of coniferous, mixed and deciduous forest areas interspersed by a large number of clear-cuts, bogs and plantations (for further details see Orell & Ojanen 1983 and Lahti *et al.* 1997).

In the experimental work (IV) we measured the change in the spatial distribution of birds in relation to heterospecifics before and after increasing the perceived risk of predation. The experiment was carried out on eight study plots. First, all areas were censused on the first day with the location of each observed bird accurately noted onto study maps. Half of the study plots were randomised as experimental plots and the rest were control plots. During the next three days the perceived risk of predation by birds was increased by playing back the mobbing calls of birds and by showing stuffed avian predator models. On the fifth day of the experiment the study plots were censused again. The person who carried out the census did not know the treatment of the plots. The response of birds to each treatment was controlled by measuring the distance to the first and second nearest heterospecific bird (Krebs 1989). A condensed spatial distribution of birds in experimental plots relative to control plots would suggest that birds may actively aggregate as a countermove to increased predation risk.

In the last paper (V) we studied the effect of predation risk by examining the influence of a nesting, forest-hunting avian predator, the sparrowhawk (*Accipiter nisus*), on the community composition of prey and species interactions. All sparrowhawk nests in the study area (ca. 30 km^2) were first located. Breeding birds were censused using a one-hectare plot (100 × 100 m) as a sampling unit. The plots were located at different distances (range 50 - 1000 m) from the hawk's nest. The number of censused plots around thirteen hawk nests during two study years was 206 and they were located within four different forest types. The risk of predation was assumed to increase with decreasing area around the nest. Therefore, we used the inverse of the squared distance to the hawk's nest ($1/r^2 \times 1000$) as a measure of predation risk.

An ANOVA model was applied to analyse the community composition (the number of species and density) with respect to predation risk. Forest types and study years were used as factors and predation risk was included as a continuous covariate. The level of species aggregation within each plot in relation to predation risk was measured by dividing the plots into four subplots (50 × 50 m) and measuring the distribution of individuals among them. Only plots including two or more species were included in this approach. A variance to mean ratio was used to describe the level of aggregation (see Krebs 1989). Variation in aggregation with respect to predation risk was analysed by the same ANOVA model as above. Prey species were also divided into preferred and unpreferred prey on the basis of their body mass (≥ 20 g and < 20 g, respectively). This division was based on a study by Rytkönen *et al.* (1998) in eastern Finland in which they found that among forest birds species weighing about 20 g or more are over-represented in the sparrowhawk's diet (see also Götmark & Post 1996). Both density and the level of aggregation of the both prey types were studied in relation to predation risk.

3. Results and discussion

3.1. European bird assemblages in a biogeographical perspective

On the European scale, variation in climate and geographical location had a strong influence on the composition of local breeding bird assemblages (I). As expected, the low densities of resident birds were associated with increasing harshness of winter climate. The density and proportion of titmice was invariably low in NE Europe but increased quite linearly with decreasing latitude and increasing mildness of winter toward western and central Europe. In central and western Europe the maximum densities of titmice were up to 40 times greater than in northern Europe with associated increases in variance. Similarly, the relative proportion of titmice in breeding assemblages varied from a few percentages in northern Europe to a maximum of almost 50% in western Europe.

These results supported earlier indirect suggestions of an increase in the proportion of migrant birds with increasing latitude ascribed to the limiting effects of winter climate on resident populations and not to increasing migrant densities (MacArthur 1959, Willson 1976, Herrera 1978a, Helle & Fuller 1988). MacArthur (1959) suggested that the proportion of migrants is largest where the difference between summer and winter food supply is the greatest. For resident birds the most restricting factor for the density of populations and survival is quite likely the balance between winter temperatures and food supply. Increasing latitude, in addition to an increase in the harshness of winter, is coupled with a decrease in the primary productivity of the environment (see Currie 1991, Begon *et al.* 1996) and a decrease in the density and proportion of titmice is quite likely a result of their combined effect. The variance in titmice density in northern Europe was quite even and small compared with the situation in southern Europe. This suggests that northern titmice populations may be below summer basic productivity levels relative to their southern counterparts.

At the local scale, experimental approaches examining the importance of food on the survival of birds have yielded mixed results: in some cases supplemental food has been shown to increase survival or density (e.g., Krebs 1971, van Balen 1980, Jansson *et al.* 1981, Källander 1981, Hogstad 1988, Verhulst 1992, Lahti *et al.* 1998) whereas in others, it has not (Krebs 1971, Yom-Tov 1974, Källander 1981). However, as Lahti (1997) pointed out, the results suggesting the relative minor importance of food come from southern areas with mild winters and in the north (Lahti *et al.* 1998) food may play a relatively more important role than in the south. Hoarding behaviour might also influence the sensitivity of resident individuals to winter and food resource levels (Lahti 1997). Hoarding titmice may have a more balanced and safer food resource throughout the whole winter whereas non-hoarding titmice (great tit, *Parus major*; blue tit, *P. caeruleus*; long-tailed tit, *Aegithalos caudatus*) may be more dependent on the spatial and temporal variation of food. The present results support this hypothesis (I). In northern Europe the densities and variances of both groups were equally low, whereas in southern Europe (south from 60°N) the variance of non-hoarding titmice was larger than that of hoarders (I). This pattern may stem from two reasons. First, non-hoarders may track local summer resource conditions more closely than hoarders. Second, the temporal and spatial variation in food resources during winter may compel non-hoarders to emigrate more readily during winter (Lahti 1997). This would result in large density differences between locations.

In addition to direct effects, different abiotic conditions may also have indirect effects causing variation in species interactions. Species interactions vary and often in association with abiotic conditions (Thompson 1988, Travis 1996, Meserve *et al.* 1999). Traditionally, harsh and fluctuating conditions have been argued to decrease the importance and intensity of species interactions such as competition (see e.g., Wiens 1977, Dunson & Travis 1991) although it has been suggested that theoretically severe conditions per se do not necessarily enhance species coexistence (Chesson & Huntly 1997). However, there is rather convincing evidence from communities in stressful environments, such as intertidal shores (see e.g., Bertness & Shumway 1993, Bertness & Callaway 1994, Bertness & Leonard 1997, Bertness 1999, Menge 2000), suggesting that the proportion of negative (competition), neutral and positive (facilitation) species interactions in the community vary with respect to environmental stress.

Is it be possible to generalise and extrapolate the short-range variation in species interactions observed for example in intertidal shores to larger geographical scales? Associations between resident and migrant birds might provide useful and relevant groups for that kind of comparison. The abundance of resident and migrant birds in breeding assemblages are affected partly by different abiotic factors. Resident birds are also considered superior competitors to migrants (Herrera 1978a, Morse 1989, O'Connor 1990). The average titmice densities in northern Europe were about 1/6th of those in other parts of Europe, whereas the average total densities of breeding passerines in the north were between one half and one third of those in the south. This suggests that titmouse populations are perhaps not as dense as expected on the basis of summer productivity. Therefore, geographical variation may exist in the resource base or availability for migrants. This may produce differences in the quality of associations between resident and migrant birds, especially between northern and southern latitudes.

The observed index of associations between resident (titmice) and migrant birds in local assemblages supported this reasoning (I). In northern Europe the index of associations were positive and relatively strong among some species groups whereas in more southern regions the associations were often weaker or negative (I). The observed positive and strong indices of associations in northern Europe between titmice and Fringilla-species and between the titmice and thrushes, and neutral association between titmice and Phylloscopus-warblers matched well with the results of experimental studies conducted in northern Finland (Mönkkönen *et al.* 1990, II). This suggests that geographical comparisons may provide reasonable hypotheses for experimental testing at the local scale, although they do not prove competition to be relatively stronger in bird assemblages further south.

3.2. Heterospecific attraction in habitat selection

An increased abundance of resident titmice (*Parus* spp.) had a consistent effect on the number of migrants in local breeding bird communities. Considering the most common migrant species, both the number of species and the total abundance of migratory birds were higher when the density of titmice was augmented to that of reduced density conditions (II). At the species level, the redwing (*Turdus iliacus*) and the brambling (*Fringilla montifringilla*) showed the clearest positive response (II). This result provided support for the hypothesis of Mönkkönen *et al.* (1990) suggesting that in northern forests migrant birds use resident birds as cues in habitat selection. In addition, migrant abundances were not associated with relative arthropod abundance in the study plots (II). Further experiments have shown heterospecific attraction to resident birds as a common phenomenon in the process of habitat selection among forest birds (Timonen *et al.* 1994, Mönkkönen *et al.* 1997) and it has also been shown among dabbling ducks (*Anas* spp.; Elmberg *et al.* 1997).

The observation that birds may aggregate with hetero- or intraspecific individuals is not new. It is well known that many ducks and shorebirds breed within gull colonies probably due to lowered nest predation (Durango 1947, Koskimies 1957, Hildén 1964, 1965). Further, some passerines are known to breed in higher abundances near the nests of avian predators than farther away (e.g., Durango 1947, White & Springer 1965, Wiklund 1978, Ueta 1994) receiving the benefits of indirect nest protection from predator presence (Wiklund 1982, Norrdahl *et al.* 1995, Larsen & Grundetjern 1997). Using intraspecific cues in habitat selection is also common in birds (e.g., Svärdson 1949, Cody 1981, Alatalo *et al.* 1982, Mikkonen 1985, Muller *et al.* 1997, Ramsay *et al.* 1999; see Stamps 1988, Reed & Dobson 1993, Danchin *et al.* 1998, Doligez *et al.* 1999 for further references). The benefits of heterospecific attraction, however, are not as well-known or obvious. Resident titmice, for example, do not provide any direct form of protection from the predation.

3.3. Why use heterospecific cues?

3.3.1. Empirical suggestions

For each and every organism settling into a new area for reproduce means finding a good quality place as quickly as possible. The ideal location would probably be predator-free and provide large amounts of high quality food and other resources necessary for successful reproduction. For heterospecific attraction to evolve the presence and/or abundance of residents must honestly reflect habitat quality, be it the availability or quality of resources or the abundance of predators (III). In areas where resident populations are depressed by external factors below summer carrying capacity, which is probably the case in northern areas (I), this precondition quite likely holds because low population densities enable individuals to choose relatively good quality habitats.

Intuitively, the relative abundance of resident birds in the landscape might be a quick way to roughly compare the relative quality of habitat patches. After all, titmice provide living proof that a certain patch is capable of sustaining at least that population density of resident birds over the winter. In early spring, direct assessment of patch quality is difficult because the ground is generally covered by snow when the first migrants arrive. Neither is patch assessment easier for later-arriving species, since arthropod abundances do not peak until late summer (Veistola *et al.* 1995). Furthermore, the relative quality of forest patches varies annually in arthropod abundance as suggested from arthropod sampling (II).

Empirical evidence suggests that the time invested in the habitat sampling is beneficial in terms of increased fitness (Badyaev *et al.* 1996). However, intra- or interspecific competition for territories (e.g., Krebs 1971, Reed 1982, Fonstad 1984, Mönkkönen 1990) may compel birds to select territories as quickly as possible. Early start to breeding has been shown to positively affect breeding success (Alatalo & Lundberg 1984, Harvey *et al.* 1985, Barba *et al.* 1995). At least in the pied flycatcher, this is probably due to competition among males for good quality territories, which has been shown to be important, if not crucial, for mate choice by females (Alatalo *et al.* 1986, Slagsvold 1986). If resident birds reflect the relative quality of a habitat patch, then this would assist males in assessing the most attractive territories.

Nest predation has been shown to be an important factor determining microhabitat selection and species coexistence in birds (Martin 1988a,b, 1993). Theoretically, the abundance of resident birds may also reflect the distribution of the risk of nest or direct predation. There is evidence suggesting that nest predation rates vary in the landscape (e.g., Zimmermann 1984, Andrén *et al.* 1985, Wilcove 1985, Marini 1997; but see Angelstam 1986, Huhta *et al.* 1998) and often with respect to landscape structure (Robinson *et al.* 1995) or habitat type (Sieving & Willson 1998). In addition, the abundance of many mammalian nest predators follow the rodent cycles in northern areas (see Hansson & Henttonen 1988). These fluctuations bring about more temporal and spatial variation nest predation rates (see Schmiegelow & Hannon 1999), and further complicate selection of habitat for northern migratory birds (see Järvinen 1985). As well, nest predation can be considerable among hole-nesting birds (Nilsson 1984) and resident abundance may reflect the safety of a habitat associated with the lack of predation on resident birds.

The impetus of heterospecific attraction probably varies according to species and local conditions. In North America, the strongest attraction to resident birds was observed among the species that belong to the same foraging guild as titmice (Mönkkönen *et al.* 1997). Elmberg *et al.* (1997) also suggested that the teal (*Anas crecca*) uses the mallard (*Anas platyrhynchos*) as a cue to food rich breeding lakes. These results emphasise the importance of food. However, the results from northern Finland (II) are not as apparent. Of the species showing a positive response to addition treatment, the redwing does not share foraging habits with the titmice and the brambling does belong to the same foraging guild. Interestingly, these two species have been observed to aggregate in fieldfare (*Turdus pilaris*) colonies (Slagsvold 1980a) where nest predation is lower than in adjacent surroundings (Slagsvold 1980b).

3.3.2. Theoretical perspectives

In most conditions a cue-user's strategy was more beneficial than a sampler's strategy where comparatively the quality of a patch is always directly assessed (III). Samplers may gain better fitness only if the difference in the quality between an occupied and an unoccupied source patch is not large (competition nor the benefits are not large) and if the differences in the cost of assessing occupied source patches between the two strategies are low. Direct sampling is the better with lower proportions of occupied source patches (the abundance of resident species) in the landscape (III). In this case, the cue-user's more complicated selection strategy begets costs.

The reason why the cue-user's strategy was better in most cases, assuming equal costs for both sampling strategies, was the cue-user's capability to recognise the difference in quality between an occupied and an unoccupied source patch (competition vs. benefits of aggregation). How realistic is this assumption? The direct empirical evidence is scarce. However, some evidence of the cognitive abilities of birds exist to strengthen this point. Hogstad (1995) suggested that fieldfares adjust their nest dispersion behaviour to breed solitarily or in colonies according to the risk of nest predation, most likely on the basis of small mammal density. Both breeding strategies occur in the population but their relative frequency varies annually. Reed (1982) studied interactions between great tits and chaffinches, which varied from neutral to aggressive along a productivity gradient. Catchpole's (1978) results also showed that the putative congeners learn to know each other and avoid the places occupied by the other species. The point here is that birds have the ability to inspect the environment or the presence or abundance of other species and alter their behaviour on the basis of this information.

The individuals of the colonising species were assumed to use a sequential-comparison tactic in which the best of the sampled patches was selected (III). This does not result in an ideal distribution of animals because the best available patch is not necessarily selected. Traditionally, theoretical habitat selection models are based on variants of an ideal distribution of individuals. In the ideal free distribution, individuals are free to choose among all available patches whereas in the ideal despotic distribution there are dominance relationships among individuals (Fretwell 1972). In the ideal pre-emptive distribution applied by Pulliam and Danielson (1991), the occupied patch was no longer available for others. However, these models are rather unrealistic with respect to the amount of the information an individual must have regarding the habitats in the landscape. If we consider, for example, a juvenile bird selecting a habitat for the first time, the quality of information regarding available habitats is probably relatively low. Therefore, the capabilities to perceive cues of the quality of the habitats should be advantageous. The result of the analytical model indicated that given a better perceptual range is, i.e. the more information one can get with an equal cost from the landscape, an individual is relatively better suited to make comparisons between possible breeding patches (III). Empirical evidence also indicates that animals gather information and its value is important. For example, many birds have been observed to prospect breeding success of conspecifics in order to gather information for future habitat selection (Eadie & Gauthier 1985, Zicus & Hennes 1989, Danchin *et al.* 1998, Doligez *et al.* 1999). Poorer cognitive abilities, without any balancing capability, are often disadvantageous. For example, samplers might end up choosing an occupied source even though competition with residents was intense (III).

The results of the empirical (II) and theoretical (III) works suggest that the composition of a local community may be the sum of many factors. Species specific characteristics such as attraction to other species and perhaps the sensitivity of the selecting species relative to predation risk or food resources may be important factors. Although the role of individual behaviour in habitat selection models has not received much attention (Lima & Zollner 1996, Fryxell & Lundberg 1998) individual behaviour may have profound consequences for population dynamics. For example, theoretically, conspecific attraction may decrease the amount of occupied patches in a metapopulation system, which may increase the risk of local extinction (Smith & Peacock 1990, Ray *et al.* 1991). The abundance of other species may also be important. For a cue-using individual the most beneficial condition in relation to a sampler was if half of the habitat patches in the landscape consisted of source patches occupied by residents whereas the low abundance of residents in the landscape incurred costs for individuals using heterospecific cues (III). Purely abiotic factors such as landscape structure may also affect local species composition. Reciprocally, extrinsic factors may affect interspecific interactions at a local scale. Danielson (1991, 1992) showed that species interactions may vary from competition to mutualism depending on landscape structure.

3.4. Heterospecific attraction and predation risk

Birds became more aggregated in distribution with an increasing risk of predation (IV, V) suggesting that they aggregate to gain protection and enhance their survival. However, the effect of predation risk on prey is not always straightforward. Only large forest birds (≥ 20 g), which are preferred more as a prey by the sparrowhawk than smaller birds (<20 g) (Rytkönen *et al.* 1998, see also Götmark & Post 1996), seemed to aggregate with other species. In addition, the level of clumped dispersion was apparent only in the immediate vicinity of the nest and only in thickets, which is preferred nesting habitat and quite likely the hunting habitat of the sparrowhawk (V).

Numerous studies indicate that flocking or aggregated distributions are a general phenomenon among animals and that benefits may accrue in terms of either predator protection or enhanced foraging efficiency, or both (e.g., Morse 1970, 1977, Hamilton 1971, Krebs *et al.* 1972, Krebs 1973, Caraco *et al.* 1980, Pulliam & Millikan 1982, Pulliam & Caraco 1984, Clark & Mangel 1984, Munn 1986, Turchin & Kareiva 1989, Pöysä 1992, 1994, Hodge & Uetz 1996, Thiollay 1999). An increase in the level of aggregation in relation to increased predation risk (IV, V) indicates that the presence of a mutual predator is one reason for heterospecific attraction among breeding birds. The spatial distribution of aggregations and contact to other individuals are not as coherent and intensive as during the non-breeding season but the benefits are probably the same. For example, an aggregated distribution may help birds to better utilise vigilance or warning calls of other individuals. Birds may also practise collaborative mobbing against a detected predator, after which the predator often abandons a particular area (pers. obs.).

It is quite likely that an attempt to decrease the risk of predation is not the sole factor behind aggregated distributions and heterospecific attraction during breeding. Mönkkönen *et al.* (1996) observed that the dispersion of boreal forest birds was clumped and about a one half of all foraging bouts occurred with heterospecific birds. The benefits of participating in foraging groups are various. For example, learning of foraging techniques and potential food locations (local enhancement; see e.g., Krebs 1972, 1973, Pulliam & Caraco 1984, Clark & Mangel 1984, Pöysä 1992). Some birds may also take advantage from the presence of other species in terms of feeding on the arthropods, which are flushed out by group members (Swynnerton 1915, Rand 1954, Munn 1986). Mönkkönen *et al.* (1996) also conducted a playback experiment, showing that the birds were able to recognise the song of willow tits (*Parus montanus*) and were actively attracted to the song. Resident birds, and especially titmice (Morse 1970), are often nuclear species in mixed-species flocks determining the direction and speed of the flock. Resident birds probably know the best foraging areas in their territory and by following them, migrant birds can gather information on the area. Titmice also readily give alarm calls after perceiving a predator, which is utilised by other group members (Sullivan 1985).

There are however, costs involved in joining aggregations and the amount of cost may vary in relation to species characteristics or individual phenotype. Theoretically, the relative proportion of information producers (producers) and exploiters (scroungers) in a group influence the benefits of group foraging (see Vickery *et al.* 1991, Ranta *et al.* 1996). Theoretical models and empirical studies on fish also suggest that individuals usually do best in groups with individuals sharing similarities in terms of competitive or foraging ability (Lindström & Ranta 1993, Ranta *et al.* 1993, 1995). In heterospecific groups the asymmetric investment in food and predator scanning may be even more pronounced because species foraging substrates and heights in the flock or aggregation usually differ markedly. Birds that join heterospecic flocks often change their foraging niche (Hino 1998), which has been suggested to be more costly for some species than others (Hutto 1988). A species different capability and specific role in mixed-species aggregations may also allow for some species to heavily parasitize others (see Munn 1986). Sometimes, however, the benefits of aggregation compensate for the possible costs. Some orb-weaving spiders for example, form heterospecific aggregations in which prey capture rates are better than when living as solitary individuals, although the participants face an enhanced risk of predation by other spiders (see Hodge & Uetz 1996).

3.5. Implications of heterospecific attraction for interspecific interactions

Interactions between species take place primarily between individuals of species within a community. Even when considering only direct interactions, the web of interplay becomes quickly very complex with an increase in the number of species and individuals. Determining the net sum of interactions for an individual in a community is laborious, let alone in attempting to determine the evolutionary consequences of those interactions. However, the variation in individuals' interactions from one location to another provides information about the range of interactions and may also allow for generalisations about the nature of interactions within the members of community.

Migrant birds are actively attracted to resident birds (Mönkkönen *et al.* 1990, 1997, Elmberg *et al.* 1997, II). In general, this suggests that at least migrant birds are not competitively displaced to qualitatively poorer habitats by residents as earlier believed (Herrera 1978a, O'Connor 1990). Thus, interspecific competition is unlikely an important factor structuring northern breeding forest bird communities. Whether the importance and intensity of competition varies geographically (I) is a more open question. Since heterospecific attraction results in aggregated distributions of birds in the landscape (Mönkkönen *et al.* 1990, 1997, II, III) potentially having negative effects on resident birds. Numerous migrants share food resources and higher abundances may even attract predators. There is also evidence suggesting that migrants settle close to the nest sites of tits than would expected by chance (Timonen *et al.* 1994). However, this may have a positive net effect on fitness because aggregated nest dispersion may enhance protection against predators in terms of increased vigilance.

The present results (IV, V) suggest that interspecific interactions change with respect to an ultimate factor such as the risk predation. The more aggregated distribution of birds after experimentally increasing the perceived risk of predation (IV) indicates that positive benefits would accrue to all birds involved via aggregated distribution (see e.g., Morse 1977). However, that a more clumped response was higher near hawk nest's only when the plots with preferred prey were included (V) changes the picture. This may indicate that the benefits from aggregating vary according to vulnerability to predation. Theoretical and empirical evidence suggests that animals should be sorted into aggregations on the basis of their size since larger individuals face a greater risk of predation than smaller individuals (Landeau & Terborgh 1986, Theodorakis 1989, Ranta & Lindström 1990, Peuhkuri 1997). According to this hypothesis, the level of aggregated response should have increased within size classes (small and large birds) in relation to predation risk. But then which species would approach the heterospecifics, small or large? This question needs a diffrent approach, but it raises interesting questions about species interactions. One could speculate that for small birds, mixed-species associations would be beneficial because in mixed-sized groups larger individuals increase their vigilance most (Peuhkuri 1997). However, although the risk would be distributed asymmetrically in relation to body size or other phenotypic characteristics, the benefits could still compensate the possible costs.

Predation or the risk of predation near a hawk's nest decreased quite likely the number of species and their density as compared to areas at a greater distance (V). Furthermore, the preference of sparrowhawks' for larger prey (Rytkönen *et al.* 1998) seemed to manifest itself in the neighbourhood of the nest and changed the relative density of species (V). In this kind of situation it is possible that indirect interspecific interactions such as apparent competition (Holt 1977, 1984), become further involved and complicate interactions. To summarise, the presence of predators and the distribution of predation risk can be considered a biological component of the landscape resulting in variability in the quality of habitats among species. Interspecific interactions may further vary according to relatively short temporal (IV) and spatial (V) scales.

4. Questions for further studies and concluding remarks

In this thesis, some questions were answered but new posers were born. The interplay between landscape and local scale factors, seasoned with species interactions affecting the composition of a local community, offers a complex challenge. For an animal selecting a habitat, previously or early arriving species provide cues regarding the quality of habitats in the landscape. To what extent and how frequently these cues are used is unknown. Another focal question also remains unanswered: the evolution of heterospecific attraction. Do migrant birds really gain fitness benefits by using residents as a cue in habitat selection and are the benefits of aggregations really asymmetrical in relation to body size as suggested. The interactions between preferred and unpreferred prey under high predation risk also require closer examination.

Human perception is often restricted to concentrating on a local scale, and the results of this thesis suggest that it may be useful to adopt a broader scale perspective. Spatial and/or temporal variation in abiotic and biotic factors may bring about variation in interspecific interactions and local communities, which may otherwise be difficult to discover without proper context and comparison. The individuals and species, which eventually coexist in a local community, have been influenced and affected at a variety of levels or scales. The northern breeding bird community proved to be more interactive than earlier believed with species interacting in the process of habitat selection and also during breeding season. In its entity, the generality of this work and that of others (Mönkkönen *et al.* 1990, 1996, 1997, Timonen *et al.* 1994) suggest that interations between heterospecific individuals may be more positive than antagonistic at least when compared with the traditional view of communities being characterised by a prevalence for diffuse competition. However, heterospecific interactions and their variation appear finely tuned and dependent on local or prevalent conditions.

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ORIGINAL PAPERS

Titmice in European breeding bird assemblages: the role of climatic conditions and associations with migrant birds

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Summary

1. Resident and migrant birds are affected by different abiotic factors during non-breeding time. The harshness of winter probably depresses resident populations thus affecting in what proportions they contribute to breeding time assemblages. In the north, residents may be depressed further below breeding time carrying capacities by the winter conditions than in southern areas. This may have implications for the structure local of assemblages.
2. We studied how the densities and relative proportions of resident birds (*Parus* and *Aegithalos* spp.) vary along geographic location and climatic variables in Europe. Titmice were divided into hoarding and non-hoarding titmice. We also explored whether there is geographical variation in the nature of association between resident and migrant birds. Data was extracted from forest bird censuses.
3. We predicted that increasing harshness of winter would negatively affect the density and relative proportion of titmice. Non-hoarding titmice were expected to respond more readily to the increasing harshness of winter than hoarding titmice. Because of depressed densities of titmice in the north we expected the nature of association between titmice and migrant bird groups to be positive in northern Europe, whereas relatively more negative associations were expected in southern areas.
4. The density and relative proportion of titmice were found to correlate most strongly with variables that described latitudinal gradient and the harshness of winter. Both density and proportion were lowest in northern Scandinavia and highest in western and central Europe. The variance of the density of non-hoarding titmice was higher than hoarders' in regions other than in northern Europe. The associations between titmice and migrants were stronger and positive in northern Europe whereas elsewhere in Europe they were either weakly positive or negative.
5. The results suggest that geographic location and the harshness of winter strongly affect the density and relative proportion of titmice in Europe. The effect is most obvious in northern Europe. This may lay ground for geographical differences for variation in interspecific associations. The observed associations between titmice and migrant birds were consistent with information from the local scale.

Key-words: abiotic factors, forest birds, latitude, geographical scale, *Parus* spp.

Introduction

Latitudinal gradients of species diversity were first recognised a long time ago (e.g., Dobzhansky 1950, Fischer 1960, MacArthur 1972, Tramer 1974). Since then the continuously accumulating evidence have shown the decrease in species number from low to high latitudes to be almost universal feature of natural assemblages and several explanations have been proposed to explain this pattern (see e.g., Pianka 1988, Rohde 1992, Huston 1994, Begon, Harper & Townsend 1996 for reviews). The question of to what extent the abundance of species follows the same geographical pattern, however, has received much less attention than species' richness. Furthermore, if some abiotic factors affect species differently and change the relative abundances of species, this may have interesting implications to the geographical variation of the structure of local assemblages.

In birds, the two basic strategies to cope with the non-breeding season, to remain resident or to migrate, provide an interesting background in which to compare the relative contribution of these two groups to breeding assemblages geographically. Resident and migrant birds in local/regional assemblages are affected by the same breeding time conditions but during non-breeding time they face totally different circumstances. Studies made in the Northern Hemisphere indicate that the relative proportion of the abundance of migrant birds in local assemblages (MacArthur 1959, Willson 1976, Herrera 1978a, Helle & Fuller 1988) as well as the proportion of migrant species (Newton & Dale 1996) increases with increasing latitude. This pattern has been suggested to be attributable of both severe winter conditions faced by the residents and summer time food-supplies (MacArthur 1959, Willson 1976, Herrera 1978a). So far, however, this phenomenon has been studied only through the abundance patterns of migratory birds (MacArthur 1959, Willson 1976, Herrera 1978a, Helle & Fuller 1988), although the winter has been suggested to play a role in the survival of birds in temperate areas (Fretwell 1972). Some local population studies have found covariation between winter conditions and population density (Kluijver 1951, Gibb 1960, von Haartman et al. 1967, Slagsvold 1975a) whereas in some other studies the effect has been relatively small (Lahti et al. 1998) or negligible (Perrins 1965, Lack 1966, Loery & Nichols 1985).

At the local scale, however, a weak association between population density and winter conditions may partly be explained, if winter climate and food resources are relatively predictable and if species' abundances are, at least to some extent, affected by those conditions. More insight into the effects of winter conditions on resident bird populations could perhaps be gained from a larger scale approach in which densities of birds are examined against the variation of climatic variables. The observed increasing proportion of migrant birds with increasing latitude in breeding assemblages (MacArthur 1959, Willson 1976, Herrera 1978a, Helle & Fuller 1988) suggests indirectly that the density of resident birds is probably affected negatively by the harshness of non-breeding season. In this study, our first goal is to examine the effects of geographical location and a set of climatic variables on the density and relative proportion of strictly resident bird group, titmice (*Parus* spp.) including the long-tailed tit (*Aegithalos caudatus*), in the breeding forest bird assemblages of Europe.

If the winter conditions do affect the abundance of resident birds in breeding assemblages, this may also have indirect effects. It has earlier been suggested that residents are competitively superior over migrants, which can fit into breeding assemblage only if there are resources available after the prior occupation of resident birds (Herrera 1978a, Morse 1989, O'Connor 1990, see also Herrera 1978b). However, depending on the difference in the primary productivity of the environment in summer and the magnitude to which winter affects resident populations, there may be variation in the relative amount resources (food, space, nest sites etc.), which are available for exploitation by migrants after resident birds have taken their slice from the pie. In northern Europe, for example, harsh winter conditions may depress resident bird populations below the carrying capacity in summer whereas the flush of summertime arthropod fauna probably provides plentiful food resources for birds. On the other hand, in southern Europe the seasonal variation in climate and food resources is most likely not as large as in the north allowing resident bird populations to be relatively more close to summer-time carrying capacity. This may produce geographical variation in the nature of the association between resident and migrant birds.

It is well known that the intensity and importance of interspecific interactions vary according to local environmental conditions (see e.g., Thompson 1988, Wiens 1989, Travis 1996). An experimental approach is the only reliable way to assess the true nature of interactions. However, experiments encompassing large geographical areas are often infeasible. A comparative approach on the relationship between densities of potentially interacting species over large geographical areas provides information about geographical variation in the quality of interactions. In this study we use bird census data and associated climatic information from all over Europe to tentatively explore the nature of interactions (both competitive and positive) between resident and migrant birds.

We first examine the effect of both geographic location and climatic variables on the density and the relative proportion of resident birds (*Parus* spp. and long-tailed tit) in breeding bird assemblages. We hypothesise that the density and relative proportion of titmice will decrease with increasing harshness of winter. We also divide titmice species into two groups on the basis of their hoarding behaviour. Non-hoarders are expected to respond more readily to the climatic conditions than hoarding tits, because hoarding buffers against seasonal variation in food supply. Variation in the relative effect of climate on titmice may lay ground for geographic variation in the quality of interactions between resident and migrant birds. High relative density of residents in relation to carrying capacity during the breeding season may result in qualitatively dissimilar interactions with migrants compared with low-density areas. We therefore predict that in the south competitive interactions may prevail resulting in negative correlations between densities of migrant and residents. In the north positive associations are more likely to occur.

Methods

Census data and geographical variables

Bird census data were collected from published and one unpublished census results (see Appendix 1). To keep the data set as homogeneous as possible, we selected only those censuses which were made in the mature forests. Tree height (> 20 m) and/or the age (> 100 years) of the forest were used as criteria. Bird assemblages of the mature forests provide a uniform set of species because species composition is very similar across Europe (see Blondel & Farré 1988, Mönkkönen 1994). On the basis of the information given on habitat, censuses were categorised into three broad forest types: coniferous, deciduous and mixed forests. If the census was carried out over several years, the average densities of species were calculated.

We extracted from the censuses the densities (pairs/10 ha) of *Parus*-species (Siberian tit, *Parus cinctus* (Boddaert), marsh tit, *P. palustris* (L.), willow tit, *P. montanus* (Conrad), crested tit, *P. cristatus* (L.), blue tit, *P. caeruleus* (L.), great tit, *P. major* (L.), coal tit, *P. ater* (L.) and including long-tailed tit, *Aegithalos caudatus* (L.)). Titmice apply hoarding except: blue tit, great tit and long-tailed tit (see e.g., McNamara, Houston & Krebs 1990, Cramp & Simmons 1993). We also calculated the total density of passerine forest-associated species (excluding starling, *Sturnus vulgaris* (L.)) and of the following migratory species groups: *Phylloscopus* spp. (willow warbler, *Phylloscopus trochilus* (L.), wood warbler, *P. sibilatrix* (Bechstein), bonelli's warbler, *P. bonelli* (Vieillot), greenish warbler, *P. trochiloides* (Sundevall), chiffchaff, *P. collybita* (Vieillot)), *Fringilla spp.* (chaffinch, *Fringilla coelebs* (L.), brambling, *F. montifringilla* (L.)), hole nesters (pied flycatcher, *Ficedula hypoleuca* (Pallas), collared flycatcher, *F. albicollis* (Temminck) and redstart, *Phoenicurus phoenicurus* (L.)) and *Turdus spp.* (redwing, *Turdus iliacus* (L.), mistle thrush, *T. viscivorus* (L.), song thrush, *T. philomelos* (C. L. Brehm), fieldfare, *T. pilaris* (L.) and blackbird, *T. merula* (L.)).

Censuses were made using four different census methods: mapping (Enemar 1959), line transect (Merikallio 1946, Järvinen & Väisänen 1983), point count (Blondel, Ferry & Frochot 1970) and single visit study plot (Palmgren 1930) methods. Kruskal-Wallis tests were used to compare whether the total density of passerine species, the density of titmice and the relative proportion of titmice varied among census methods. Comparisons were made within four different geographical areas (see below). None of the tests were significant (see also Helle & Fuller 1988) and, therefore, we pooled the censuses over the methods.

Species belonging to genus *Parus* and *Aegithalos* were chosen as indicators of the effects of climate on populations. Titmice species are a coherent group of birds, strictly year-round residents and show relatively little variation in species composition in bird assemblages across Europe. In northern Scandinavia, titmice are almost the only small-sized forest passerine birds present year-round at their breeding areas. In the western and southern Europe, however, the group of residents birds is much more diverse including species that are migratory further north. All birds other than titmice and long-tailed tit were regarded as migrants in this study.

In this study the density of migratory birds was related to the density of titmice to examine the possible geographical variation in interactions between resident and migrant birds. Species belonging to *Phylloscopus* spp. and *Fringilla* spp. belong to the same feeding guild of arboreal insectivores as the titmice do. Hole nesters exploit similar breeding sites as most titmice species do. These three groups thus have some overlap in resource use with titmice, which is a precondition for interspecific interactions. *Turdus*-species are included as a control group. As ground feeders they do not interact with titmice while foraging. In addition, differences between body sizes and other ecological characteristics between thrushes and titmice are so large that negative interactions are very unlikely. In experimental works conducted in northern Finland we have found positive associations between densities of titmice and two *Fringilla*-species (see Mönkkönen, Helle & Soppela 1990, Timonen, Mönkkönen & Orell 1994, Forsman et al. 1998a) but also between titmice and the redwing (Forsman et al. 1998a).

The total number of the selected censuses was 86. They covered Europe from Spain in the south to Finnish Lapland in the north and from Great Britain in the west to West Russia in the east. We gathered from each census location the geographical co-ordinates (latitude and longitude) and a set of climatic variables. Mean temperature of the coldest (January) and the warmest (July) month as well as the average temperature of the whole year describes the thermal conditions of both breeding and winter time. In addition, we calculated the temperature range of the year from the mean temperatures of January and July and the number of the months with mean temperature below zero to depict the seasonality and the harshness of climate. Precipitation during the main breeding time in Europe from April to June and the total annual precipitation were chosen to portray moisture conditions. Temperature and precipitation data were extracted from the Climatic Atlas of Europe (1970). Altitude may also locally influence densities of birds and, therefore, we divided censuses made in either under or above 500 m above sea level. In our data, the great majority of the censuses from above 500 m a.s.l. were from the Central and South Europe, where that level can be regarded as a rough dividing point for highland area (see Walter & Breckle 1989). If accurate altitude was not reported, it was estimated from the Climate-diagram Maps (Walter, Harnickell & Mueller-Dombois 1975).

Statistical analyses

The eleven chosen geographical and climatic variables are very strongly intercorrelated. Therefore, we performed a principal component analysis (PCA) in order to condense the variation in the eleven geographical and climatic variables into a few uncorrelated principal components. PCA was performed on the correlation matrix because the scale on which variables were measured varied. We used an unrotated principal component solution. The location of each census locality on the principal component axes was used in statistical analyses to reveal the association between bird densities and abiotic factors.

We used ANOVA to build a statistical model to explain the variation in the density and relative proportion of the titmice. Forest type and altitude may have an impact on local densities of birds and, therefore, they were also included in the model as factors. Forest type had three levels (coniferous, deciduous and mixed forest) and altitude had two (< 500 m and ≥ 500 m a.s.l.). Principal component scores extracted from the PCA were included in the model as a continuous covariate. We included in every model all the main effects and all two-way interaction terms. A statistically significant interaction term between a covariate and factor would indicate that the effect of covariate (PC score describing geographical/climatic condition) is not parallel among forest types or altitude levels. We transformed the densities of titmice ($\log(x_i+0.5)$) and angular transformation ($\arcsin\sqrt{x_i}$) was used for the relative proportions of titmice. The univariate homogeneity of error variances was tested each time and they were found to be equal across groups in all analyses.

Census results were also used to analyse the association between resident and migrant densities. We first removed the effects of the geographical and climatic variables on the densities of titmice and migrant birds. After that the residual variation of the densities were related to each other, i.e., the residual density of titmice was used to explain the residual density of migrant birds and vice versa. We assumed that if interspecific interactions are strong enough among birds occurring locally, it may reflected to densities of birds. We used the same ANOVA model as earlier to remove the effects of the geographical and climatic variables on the densities of titmice and migrant birds. In this analyse, however, we used standardised densities of birds (see Fox & Luo 1996). We standardised the densities of titmice and the four migratory species groups by subtracting from the density of each census the average density of that species group calculated over the whole data and dividing it by the standard deviation. Standardisation scales the density of both titmice and migrants in each location to the general geographical density. Because the geographical location is one component in the covariate of the ANOVA model, it will remove the effects of different primary production levels on the densities. Thus, the residuals of both titmice and migrants are scaled to the primary productivity of each census location and are commensurate across locations.

To study geographical variation in species associations, Europe was divided into four subregions. The area north from latitude 60° formed northern Europe and the area south from latitude 45° was regarded as Mediterranean region. Western Europe consisted of Great Britain and western France (west from 2° E). The area, which fell between northern Europe and Mediterranean region, excluding western Europe, was considered central Europe. Within each of these four regions, the residual variation of each bird group was regressed separately between titmice and each migratory bird group. Regression coefficient indicates the quality of the association between titmice and migrants. Negative coefficient refers to possible competitive association and positive suggests that the increasing density of other bird group is enhancing the density of the other. Because asymmetrical interactions are common (e.g., Connell 1983), both titmice and migrant bird groups were both in turn as an independent and dependent variable.

This procedure follows the method introduced by Fox and his co-workers (Fox & Luo 1996, Luo, Monamy & Fox 1998, see also Pfister 1995). They have successfully used this method in determining competition coefficients among species in local rodent communities. Fox and Luo (1996) improved the method originally proposed by Schoener (1974) and Crowell & Pimm (1976) and managed to remove the statistical artifact between species' competitive ability and population variance (see Rosenzweig et al. 1985). Simply standardising the densities of species can solve the artifact. We tested this possibility using the method in Rosenzweig et al. (1985). First, the variances of residual densities of all bird groups were calculated for each four geographical areas. The ratio of variances between the dependent bird group and the variance of the independent group was then regressed against the index of association (α). We included all comparisons irrespectively of the direction or statistical significance of the association. The ratio of the variances of interacting species groups did not explain the variation of the index of association (regression analysis, d.f. = 1 ; 30, MS = 0·39, F = 0·76, P = 0·39). This suggested that the observed patterns were not confounded by the artefact between the census variance and the association coefficients (see also Fox & Luo 1996, Luo, Monamy & Fox 1998).

The regression method has in local communities provided consistent estimates of species interactions with manipulative experiments (see Fox & Luo 1996 and Luo, Monamy & Fox 1998). In this study, however, the scale is much larger and local habitat variables are replaced by geographical variables. We assumed that the effect of local habitat variables on the composition of bird assemblage is rather equal in different parts of Europe. This assumption is quite well-founded because bird assemblages of mature forests in Europe are very similar (see Blondel 1987, Blondel & Farré 1988, Mönkkönen 1994). It must be noted that interspecific interactions take place between individuals of different species and not between groups of species or guilds. The groups of species used here are, however, ecologically very coherent. Pooling species into reasonable ecological groups reduces the number of comparisons and also the amount of ecological noise involved in individual species densities on large geographical scale. In addition, our intention is not to determine the local processes structuring communities, but to explore whether it could be possible to get cues of qualitatively dissimilar interactions in separate geographic regions. The results of this survey can be compared with local scale experimental works already done and they can be used as hypotheses for future studies.

Results

Effects of climate

Geographical variation in the density and relative proportion of titmice varied a lot within Europe. The average densities of titmice in northern Europe were about seven times lower than elsewhere in Europe and the range varied from less than one pair/10 ha in northern Finland close to thirty pairs/10 ha in western Europe (Table 1 and Fig. 1). Relative proportions varied from almost a zero in the north up to almost 50% in western and central Europe (Fig. 2). Both the density (Fig. 1) and the proportion (Fig. 2) of titmice were most clearly correlated with geographic location and variables describing winter conditions. Increasing latitude and longitude and variables depicting increasing harshness of winter such as, mean temperature in January, temperature range or the number of months with average temperature below 0°C, were associated with low density and proportion. In the areas where the conditions are the most extreme (in northern Europe), it is notable that the variance of densities and relative proportions were very low whereas in milder conditions variance increased considerably. For example, if the average January temperature is below –8°C, densities are invariably low (see Fig. 1). Precipitation seemed to be of minor importance affecting the density and relative proportion of titmice.

Table 1. *The average densities of five bird groups and forest associated passerine species in four regions in Europe. The values in the brackets indicate the standard deviation of the mean. For further explanations see the text.*

Species group	Locality Northern Europe		Central Europe		Mediterranean		Western Europe	
Titmice	1·94	(2·21)	11·85	(7·0)	12·18	(6·60)	14·22	(11·29)
Fringilla spp.	6·15	(5·10)	11·87	(4·97)	5·93	(2·77)	3·86	(3·02)
Turdus spp.	2·66	(3·94)	6·18	(5·50)	3·91	(2·35)	2·76	(2·30)
Phylloscopus spp.	3·38	(3·30)	7·56	(7·03)	1·21	(1·57)	4·23	(3·95)
Hole nesters	1·07	(0·88)	2·11	(2·61)	0·33	(0·87)	1·73	(4·18)
Total density	22·93	(19·95)	69·17	(34·30)	49·25	(20·68)	48·33	(21·35)

The principal component analysis extracted two principal components from the original eleven variables eigenvalues larger than 1·0. Together they explained 82·35% from the total variance, of which 61·89% was accounted for by the first principal component. Negative loadings on the PC 1 were characterised with high latitude, high longitude, cold January and the high number of months with the average temperature below 0°C and large annual temperature range (see Table 2). Positive scores on PC 1 refer most strongly to high overall temperature and high precipitation. Thus, PC 1 depicts the main climatic axis in Europe ranging from SW Europe to NE Fennoscandia. The PC 2 assigned census locations along the mean annual and July temperatures and precipitation axis. Negative scores indicate high average temperature of the year and in July and relatively high precipitation (Table 2.)

Table 2. *Factor loadings of the original variables on the two principal components extracted by the principal component analysis.*

Variables	Factor loadings PC 1	PC 2
Latitude	-0·94	0·03
Longitude	-0·89	0·01
Temperature in January	0·90	-0·39
Temperature in July	0·40	-0·73
Mean annual temperature	0·80	-0·53
Annual temperature range	-0·86	0·04
# of months below 0ºC	-0·91	0·33
Precipitation in April	0·77	0·46
Precipitation in May	0·82	0·46
Precipitation in June	0·44	0·66
Yearly precipitation	0·71	0·58

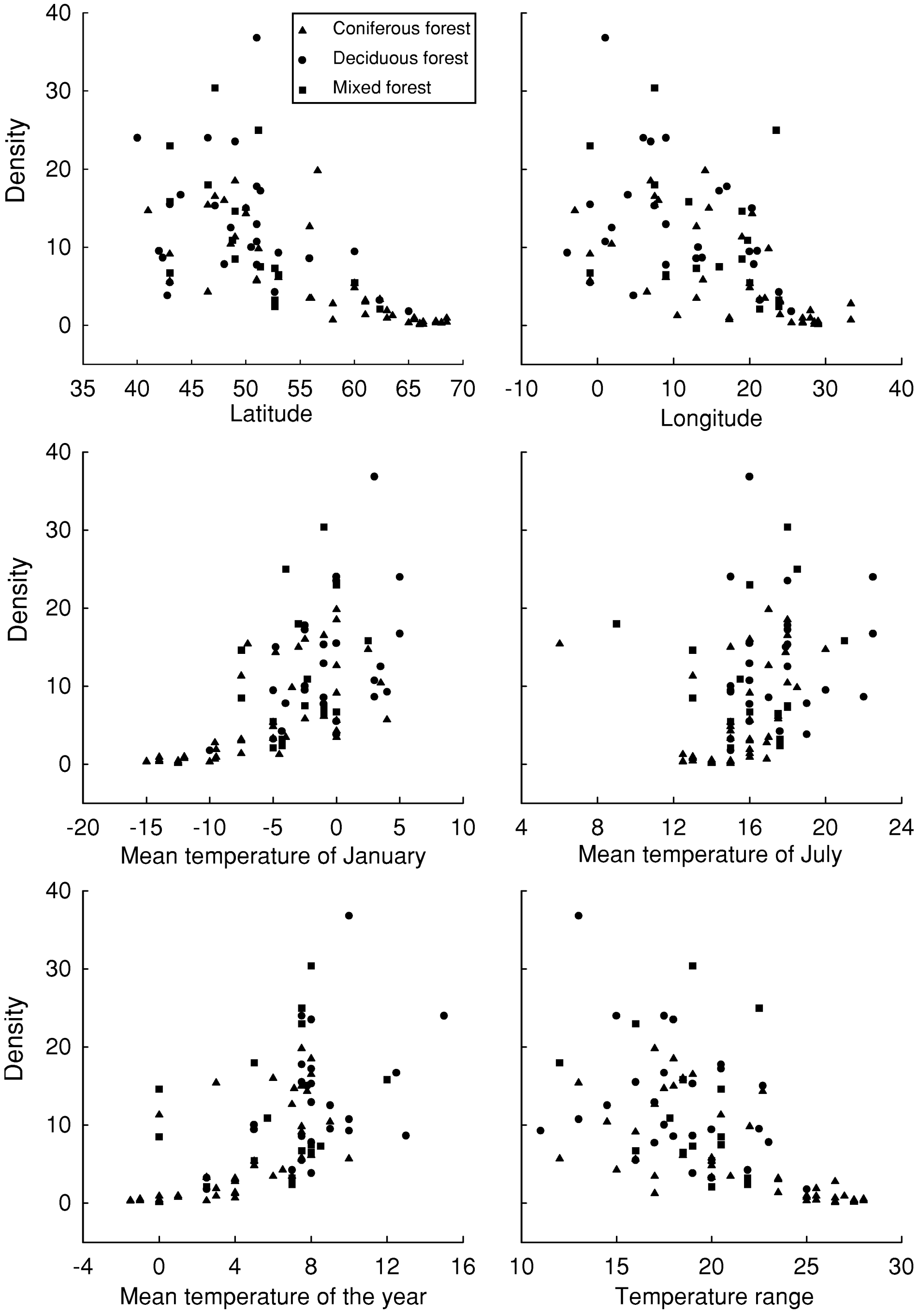
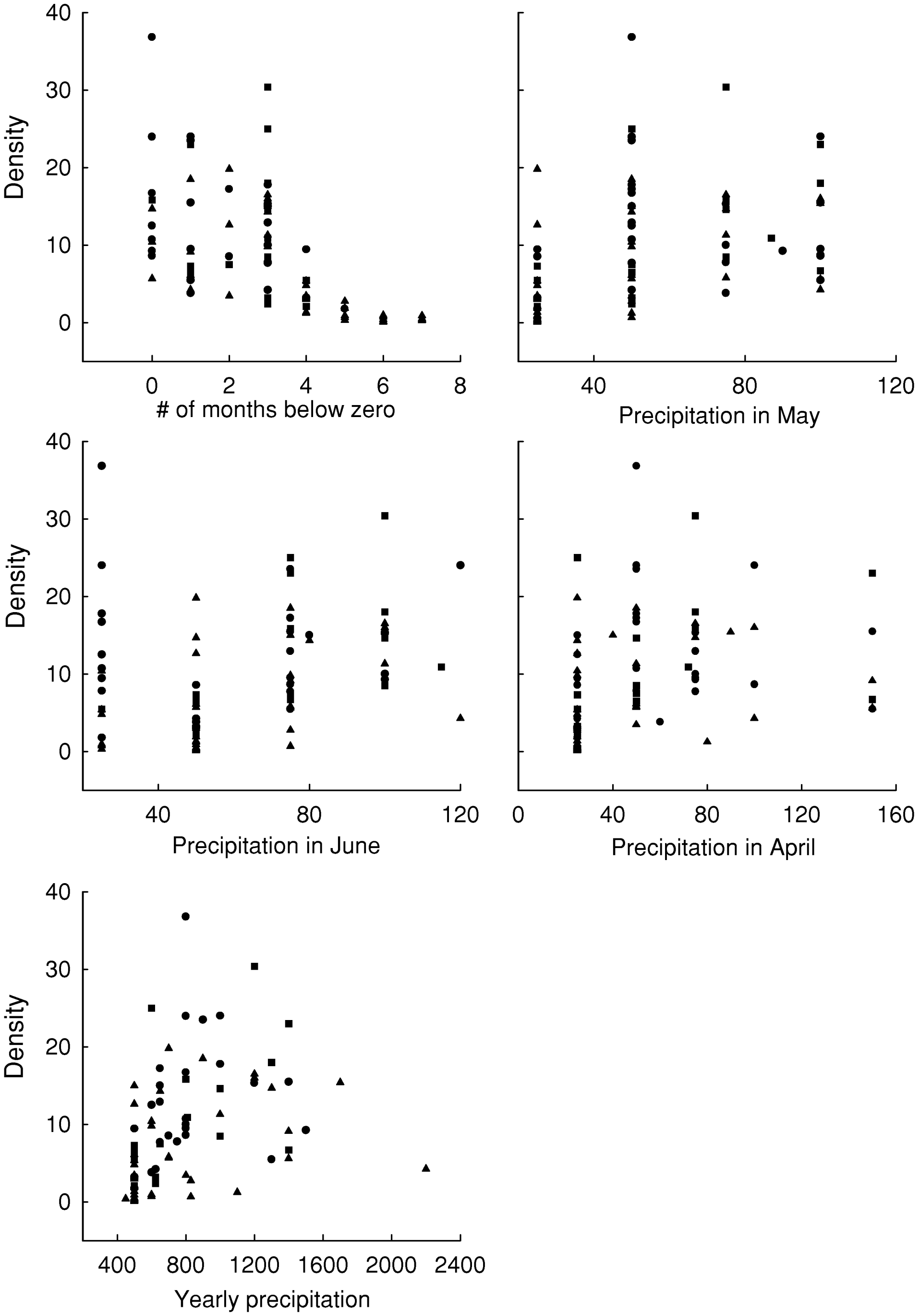


Fig. 1. The relationship between the original geographical and climatic variables and the density of the European titmice in three forest types.

Fig. 1. Continued.



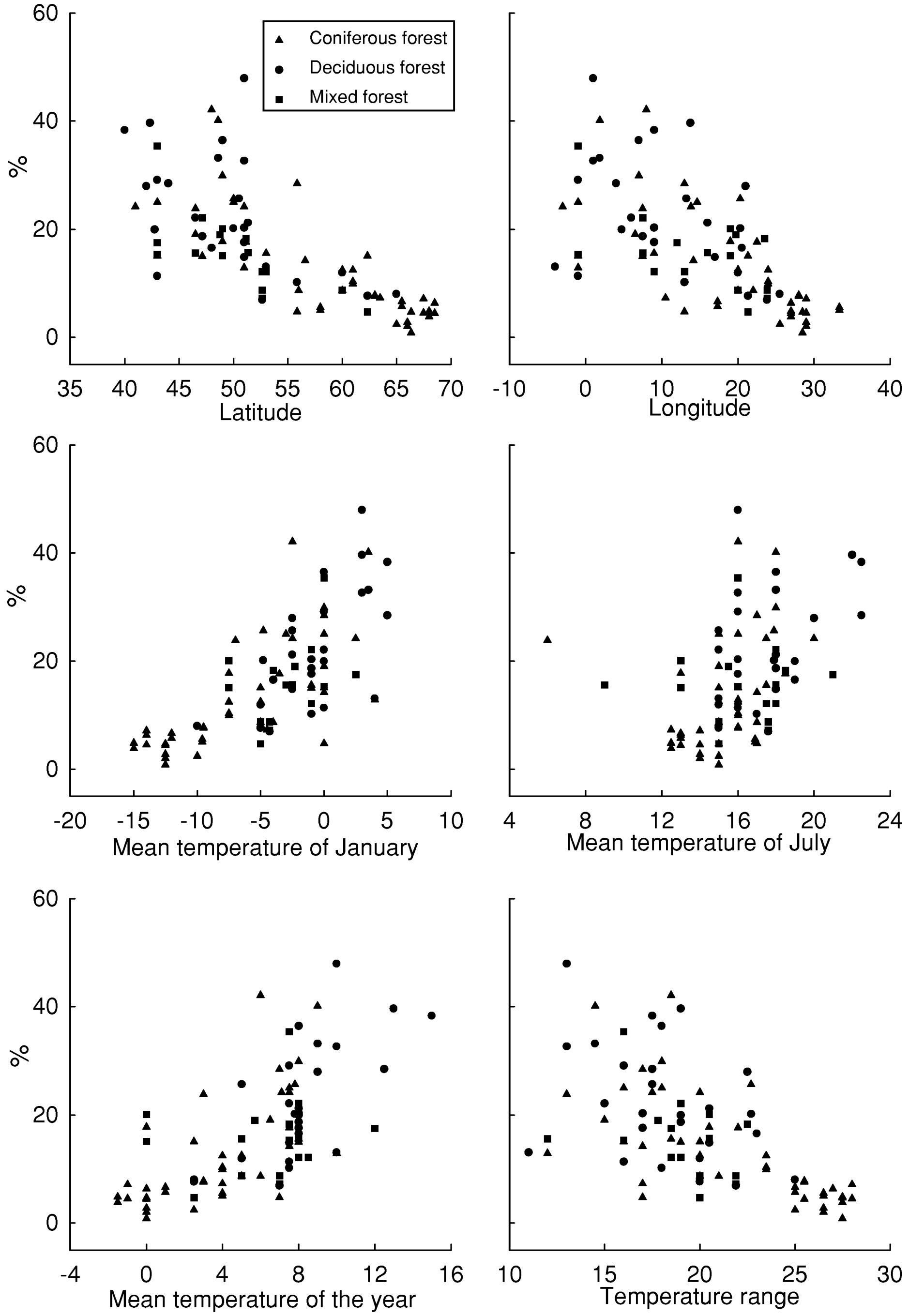
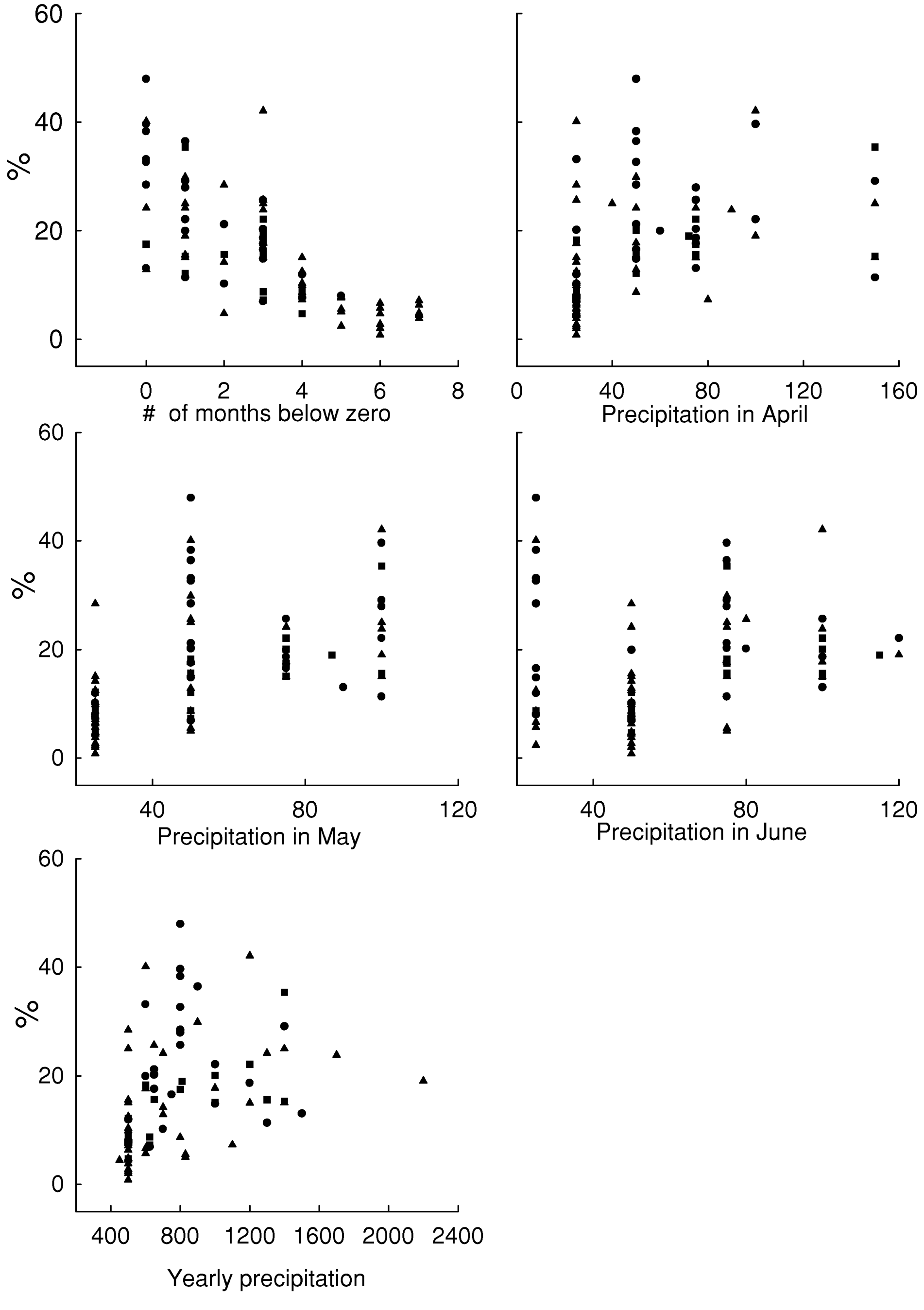


Fig. 2. The relationship between the original geographical and climatic variables and the relative proportion of titmice in the European breeding bird assemblages in three forest types.

Fig. 2. Continued.



The ANOVA model on the PC scores as covariates and forest types and altitude as categorising discrete factors explained significantly the observed variability of density and relative proportion of titmice (see Table 3). The PC 1 was overwhelmingly the best single variable in the model explaining the variance of both the density and relative proportion (Table 3) of titmice. There was a clear positive correlation between both the density (Fig. 3) and the relative proportion (Fig. 4) of titmice with the scores on PC 1. This suggests that on this scale the density and the proportion of titmice are affected most strongly by climatic factors. Northern location, cold January and long winter with seasonal climate are associated with the low density and the proportion of titmice. Moving along PC 1 to more benign conditions (southern geographical location, mild and short winters and moister climate) is coupled with increasing densities and proportions of titmice (see Figs. 3 and 4). The variance in the density and the proportion of titmice increased considerably with increasing mildness of the climate as well. PC 2 did not explain the density and the proportion of titmice significantly (see Table 3 and Figs. 3 and 4).

Table 3. *Geographical variation in the density and relative proportion of European titmice explained by the ANOVA model. Scores on PC 1 and PC 2 were used as covariates. The model explained 74·4 % and 67·3% of the total variance of density and proportion, respectively. D.f. are the same in both models.*

	Density				Proportion		
Source of variation	d.f.	MS	F	P	MS	F	P
Model	13	0·83	16·13	< 0·000	0·09	11·40	< 0·000
Forest type	2	0·18	3·56	0·034	0·01	0·83	0·442
Altitude	1	0·03	0·54	0·466	0·01	0·17	0·682
Forest type × Altitude	2	0·02	0·47	0·626	0·01	1·65	0·200
Forest type × PC 1	2	0·10	1·87	0·162	0·00	0·09	0·908
Forest type × PC 2	2	0·01	0·09	0·916	0·03	3·16	0·048
Altitude × PC 1	1	0·45	8·73	0·004	0·04	4·40	0·040
Altitude × PC 2	1	0·15	2·86	0·095	0·00	0·51	0·477
PC 1	1	1·48	28·89	< 0·000	0·24	29·24	< 0·000
PC 2	1	0·01	0·21	0·645	0·01	0·99	0·324
Error	72	0·05			0·08		

There were a number of significant interactions terms between the covariates and main factors. They arise mainly for two reasons. First, within some factor classes there were not enough geographical variation in the census locations. There were only a couple of highland censuses in northern Europe. This provides not enough geographical dispersion for the analysis and resulted in a significant interaction between altitude and the PC 1 both in the density and in the proportion of titmice (Table 3). Second, highland censuses also confounded analyses because of their peculiar climate. In highland areas the climate is coupled with high precipitation and rather low annual temperatures, which is the

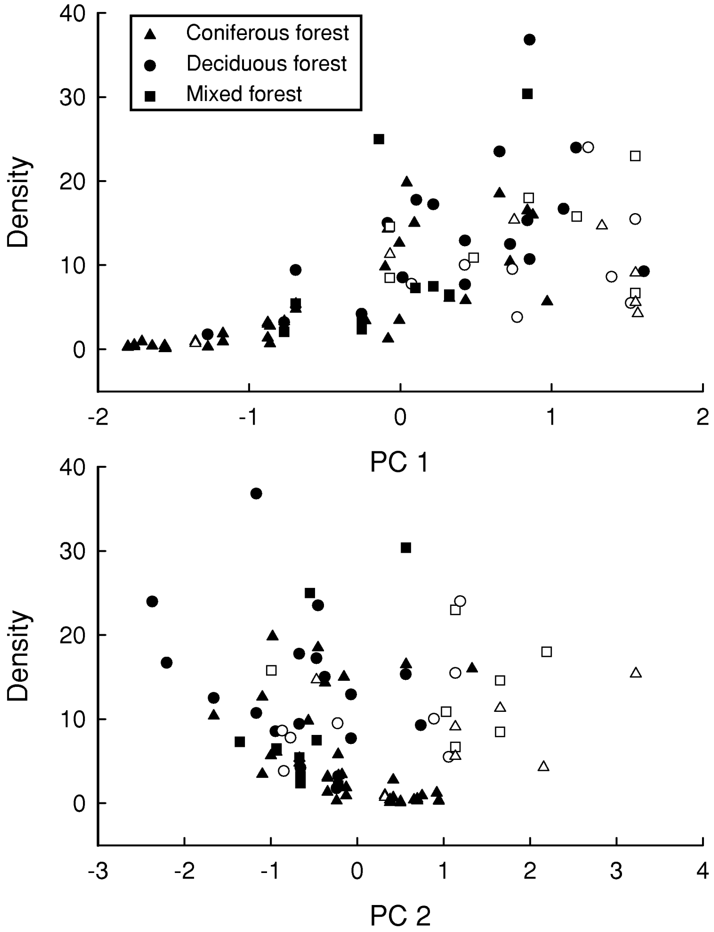


Fig. 3. The variation of titmice density (pairs/10 ha) in three forest types along the first and second principal component factors. Open symbols refer to highland censuses and filled symbols indicate lowland census. The correlation coefficients between the density and the PC 1 and the PC 2 were 0.63 ($P < 0.000$) and - 0.09 ($P = 0.391$), respectively.

reverse situation occurring in the lowland areas in central and southern Europe. Those highland locations formed the cloud of observations in which the proportion of titmice was exceptionally high in relation to the location on the PC 2 (Fig. 4) and are responsible for the significant interaction term between forest type and the PC 2 in the proportion of titmice (see Table 3). Within coniferous and deciduous forests there is negative relationship between the proportion of titmice and the PC 2. The relationship is negative in mixed forests as well but the statistical program cannot reveal that. This is because

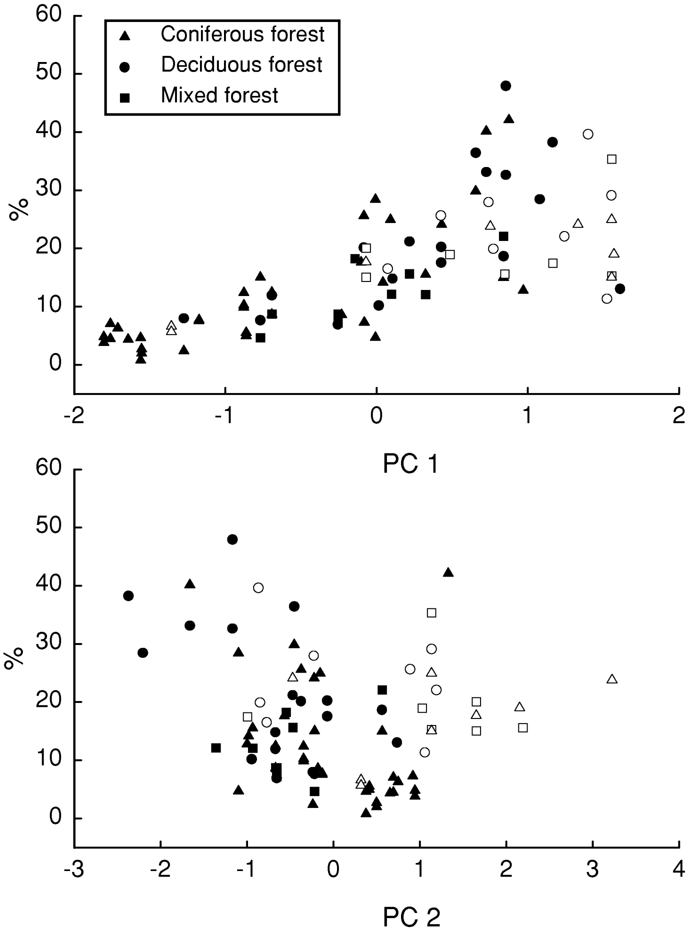


Fig. 4. The variation of the relative proportion of titmice from breeding bird assemblages in three forest types along the first and the second principal component factors. Open symbols refer to highland censuses and filled symbols indicate lowland census. The correlation coefficients between the proportion and the PC 1 and the PC 2 were 0.71 ($P < 0.000$) and - 0.18 ($P = 0.100$), respectively.

highland and lowland censuses in mixed forests form two parallel and uniform negative slopes with respect to the PC 2, but which are interpreted as a one positive slope by the statistical program (see the distribution of mixed forests in Fig. 4). There were not big differences in the ANOVA solution between the density of hoarding and non-hoarding titmice (see Table 4). The model explained significantly the density variation of both groups. However, there were some differences among individual variables of the model.

Forest type and altitude were important variables explaining the density of non-hoarding titmice. For hoarding titmice, PC 1 was the most important variable whereas for non-hoarders its explanatory power was not as obvious (Table 4). The density of hoarding titmice also behaved more steadily in the model than that of the non-hoarding titmice did. The non-hoarding titmice had a number of significant interaction terms between covariates and factors whereas hoarders did not have any (Table 4). Although PC 2 did not explain significantly the densities of either group (Table 4), there was a qualitatively difference between the hoarding and non-hoarding titmice with respect to PC 2. Density of hoarding titmice was positively correlated with PC 2 (Fig.5) whereas in non-hoarders the correlation was negative (Fig. 6). This means that the density of non-hoarders is positively correlated with high summer and annual temperature and with relatively high precipitation. By contrast, the density of hoarders is positively correlated with cooler and dryer climate.

Table 4. *The geographical variation in the density of hoarding and non-hoarding titmice in European breeding assemblages explained by the ANOVA model. Scores on PC 1 and PC 2 were used as covariates. The model explained 64·0% and 72·5% of the total variance of hoarding and non-hoarding titmice, respectively. D.f. are the same in both models.*

	Hoarding titmice				Non-hoarding titmice		
Source of variation	d.f.	MS	F	P	MS	F	P
Model	13	0·50	9·83	< 0·000	0·97	14·60	< 0·000
Forest type	2	0·22	4·22	0·019	1·24	18·91	< 0·000
Altitude	1	0·05	0·94	0·336	0·94	14·42	< 0·000
Forest type × Altitude	2	0·09	1·68	0·194	0·36	5·53	0·006
Forest type × PC1	2	0·08	1·55	0·219	0·10	1·46	0·239
Forest type × PC 2	2	0·00	0·07	0·937	0·07	1·10	0·354
Altitude × PC 1	1	0·06	1·15	0·287	1·21	18·42	< 0·000
Altitude × PC 2	1	0·00	0·05	0·823	0·36	5·46	0·022
PC 1	1	1·04	20·36	< 0·000	0·68	10·37	0·002
PC 2	1	0·11	2·11	0·150	0·12	1·84	0·180
Error	72	0·05			0·07		

The density of hoarding titmice seemed to increase rather linearly along PC 1 (Fig. 5) whereas the density and the variance of non-hoarding titmice increased sharply after a certain limit on PC 1 (Fig. 6). We splitted data into two parts on PC 1 (-0·5 < PC 1 ≤ -0·5) to study those two areas more closely. Geographically that line goes approximately along 60th latitude. On the northern side of that line, the average density of hoarding titmice seemed to be higher (1·20 pairs/10 ha) than that of non-hoarders (0·76 pairs/10 ha) but the difference was not statistically significant (t = 1·24, df = 54, P = 0·219). In the southern area, densities of hoarders and non-hoarders were rather even (5·48 and 6·86 pairs/10 ha, respectively) and they did not differ (t = 1·24, df = 101, 0·217). However, the variance of non-hoarding titmice in the southern area was larger than that of hoarders (Levene's test, F = 4·65, $n_1 = n_2 = 58$, P = 0·033). In the north the variances did not differ (Levene's test, F = 0·20, $n_1 = n_2 = 28$, P = 0·889). In other words, the abundance and variance of both groups was evenly low in NE Europe where winters are cold and long. Moving along PC 1 to more benign climate (central and southern Europe), the density of hoarding titmice increased rather steadily (see Fig. 5) whereas there seemed to be a threshold level for non-hoarders after which the variance increased more rapidly (Fig. 6) compared with hoarding species.

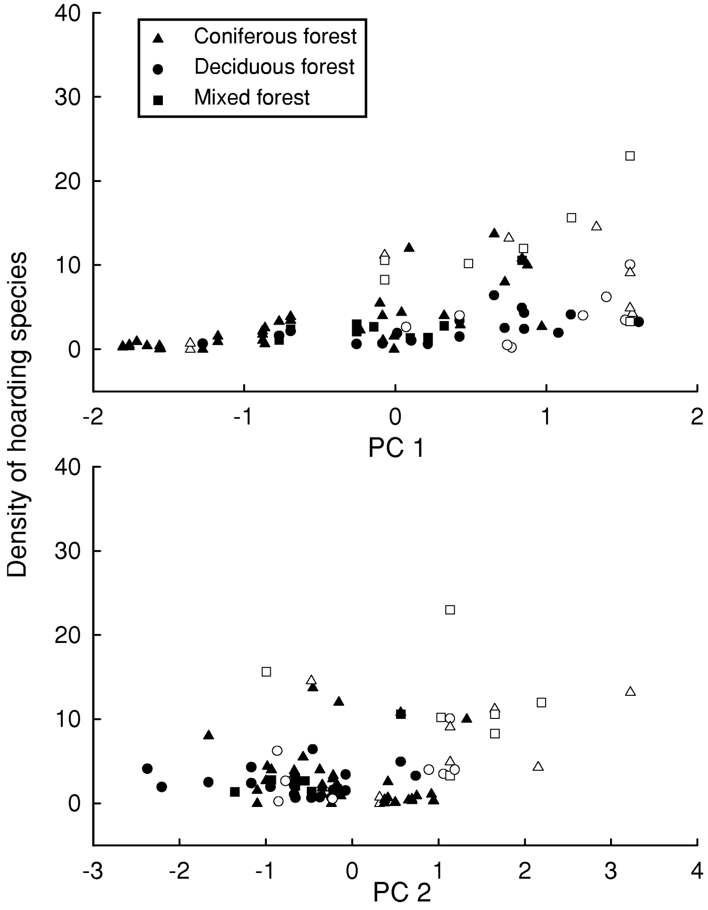


Fig. 5. The relationship between the density (pairs/10 ha) of hoarding titmice and the two first principal component factors in three forest types. Open symbols refer to highland censuses and filled symbols indicate lowland census. The correlation coefficients between the density and the PC 1 and the PC 2 were 0.56 (P < 0.000) and 0.31 (P = 0.003), respectively.

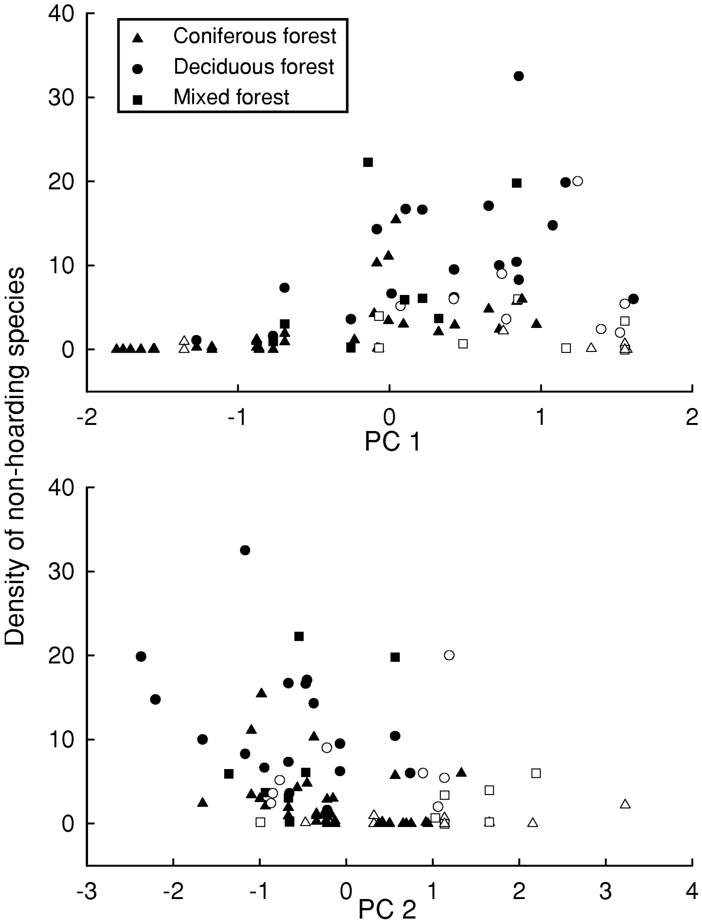


Fig. 6. The relationship between the density (pairs/10 ha) of non-hoarding titmice and the two first principal component factors in three forest types. Open symbols refer to highland censuses and filled symbols indicate lowland census. The correlation coefficients between the density and the PC 1 and the PC 2 were 0.37 ($P < 0.000$) and - 0.33 ($P = 0.002$), respectively.

The association between titmice and migrants

In general, the same ANOVA model, which we have used throughout this study, explained significantly the standardised densities of all migratory bird groups and titmice species (see Table 5). The proportion of the variance explained by the model was highest in the titmouse species (53%). Among migrant bird groups the model explained about 25-35% of the total variance (Table 5). There was, however, variation in the explanatory power among individual variables of the model and species groups. The clearest difference between resident and migrant birds was that the PC 1 (latitude, longitude and

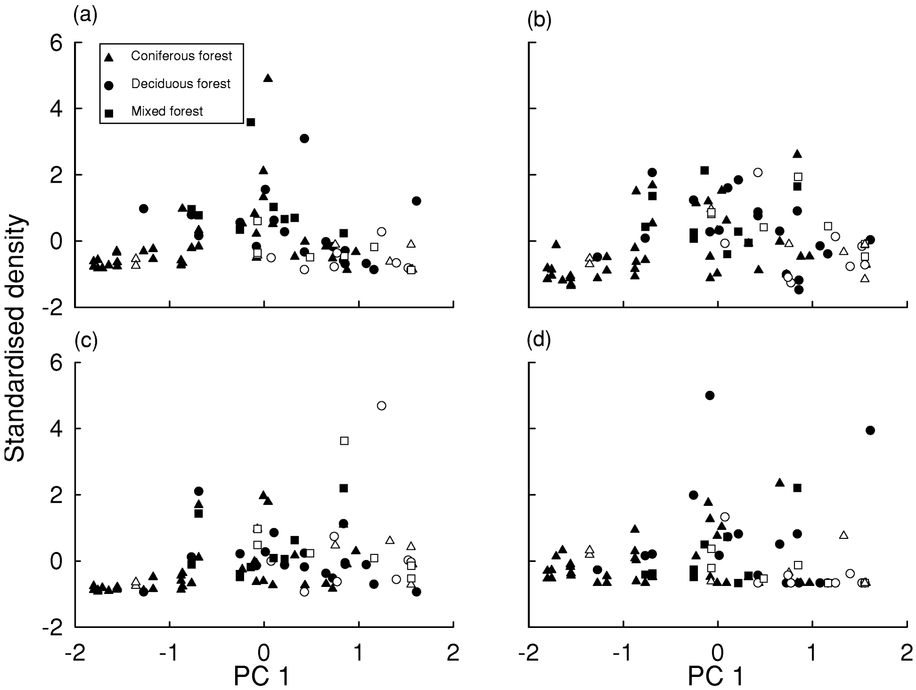


Fig. 7. The standardised densities of (a) *Phylloscopus* spp., (b) *Fringilla* spp., (c) *Turdus* spp. and (d) hole nesting species in relation to first principal component factor. Open symbols refer to highland censuses and filled symbols indicate lowland census.

the harshness of winter) was very significant variable explaining the standardised densities of titmice, whereas it was not associated with the density of any migrant bird groups. This would indicate that geographical location did not have any effect on migrant densities. However, there were several unimodal distributions of standardised densities among migrant bird groups in relation to PC 1. The density of *Fringilla* spp. and *Phylloscopus* spp. reached their peak densities in the central and western Europe, decreasing from there to both south and north. The abundances of *Turdus* spp. and hole nesters increased more linearly with decreasing latitude and harshness of winter, though the variances were high (see Fig. 7). This pattern, in addition with the confounding effect of mountain censuses (see above), may partly explain the statistically significant interactions between covariates and factors. The PC 2, indicating breeding time and annual temperatures and moisture conditions, explained significantly the standardised densities of *Fringilla* spp. and *Turdus* spp. (Table 5). This suggested that breeding time temperatures and precipitation had an impact on the abundance of those species. Except in *Fringilla* spp., forest type and altitude were of minor importance.

Table 5. *ANOVA table for the standardised densities of titmice and four groups of migratory birds. Scores on PC 1 and PC 2 were used as covariates. R^2 is the proportion of variance explained by the ANOVA model. D.f. are the same in all groups.*

	Titmice				*Phylloscopus* spp.			*Fringilla* spp.			*Turdus* spp.			Hole nesters		
Source of variation	d.f.	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Model	13	3·46	6·22	<0·000	2·19	2·68	0·004	2·22	2·85	0·002	1·87	2·22	0·017	1·68	1·92	0·042
Forest type	2	0·42	0·75	0·750	1·11	1·40	0·255	3·63	4·65	0·013	1·15	1·37	0·262	0·70	0·80	0·456
Altitude	1	1·88	1·88	0·070	2·30	2·89	0·093	0·70	0·90	0·346	0·55	0·66	0·421	1·91	2·18	0·144
Forest type × Altitude	2	0·12	0·22	0·806	0·15	0·19	0·828	0·04	0·06	0·941	0·94	1·11	0·334	2·10	2·40	0·098
Forest type × PC1	2	0·63	1·14	0·327	1·56	1·96	0·148	3·36	4·31	0·017	0·83	0·98	0·380	0·26	0·30	0·743
Forest type × PC 2	2	0·45	0·82	0·446	2·72	3·42	0·038	1·33	1·71	0·188	2·06	2·44	0·094	3·15	3·59	0·033
Altitude × PC 1	1	2·13	3·83	0·054	0·17	0·22	0·642	3·21	4·12	0·046	0·11	0·13	0·721	1·81	2·06	0·155
Altitude × PC 2	1	0·33	0·60	0·442	0·61	0·76	0·386	0·15	0·19	0·668	1·85	2·20	0·143	3·53	4·03	0·048
PC 1	1	11·97	21·51	<0·000	1·38	1·74	0·192	1·23	1·57	0·214	0·26	0·31	0·582	0·00	0·00	0·928
PC 2	1	0·83	1·48	0·227	0·08	0·11	0·745	4·48	5·75	0·019	5·08	6·03	0·016	2·21	2·53	0·116
Error	72	0·56			0·80			0·78			0·84			0·88		
R^2 (%)				52·90			32·60			34·00			28·60			25·70

After removing the effects of the geographical and climatic variables from the standardised densities of birds, the density of titmice seemed to explain the densities of some migrant bird groups. In general, the associations between titmice and migrants tended to be positive (Table 6). Only in western Europe negative associations prevailed, excluding the control group of *Turdus* spp., but they were rather weak (low α) (see Table 6). The strongest positive associations (large α) between titmice and migrants were in *Fringilla* spp. and *Turdus* spp. in northern Europe. The magnitude of the index of association is very relevant because it indicates the relative change of the dependent variable when the level of the independent variable increases one unit. In central Europe positive associations were also statistically significant in *Phylloscopus*-warblers and *Fringilla* spp., but the indices of associations were relatively weak (Table 6). The association between the titmice and the control group of *Turdus* spp. was negligible measured both by statistical significance and by the strength of the index of association except in northern Europe. It is notable that in most cases hole nesters were positively associated with titmice. However, the determination of coefficients (R^2) were not very high suggesting that the density of titmice did not succeed in explaining the variance of hole nesters very well. The standard error of the coefficient estimates the variation of the dependent variable after the effect of the independent has been removed.

When we changed the roles of independent and dependent variables between titmice and migrant birds so that the density of migrant bird groups were in turn explaining the densities of titmice, only regression coefficients (α) and standard errors changed. Other values remained the same. This is because the axis along which the difference between the predicted and the observed values are calculated is different. The quality of the associations among migrant birds and titmice within geographical locations did not change from the reverse comparison: weak negative coefficients prevailed mainly in southern and western Europe and positive weak associations elsewhere (see Table 6). The most striking difference was that in western Europe the density of *Fringilla*-species was rather strongly and negatively associated with the density of titmice (Table 6). By contrast, the index of association between these groups was much weaker when the standardised density of titmice was the independent variable (Table 6). In other words, chaffinch would affect more negatively on the density of titmice than vice versa.

Table 6. *Index of associations (α) in four geographical areas between titmice and four different migratory bird groups. The values within brackets refer to situation when the standardised density of migrant bird groups is independent variable explaining the density of titmice. In all other values the dependent variable is the density of migrant birds and independent variable is the density of titmice. The values of the P and R^2 are the same for both comparisons. R^2 (%) is the determination of the coefficient. All the values used in the analyses were residuals from the ANOVA model (see Table 4) of standardised densities of titmice and migratory birds.*

	Phylloscopus spp.				*Fringilla* spp.				*Turdus* spp.				Hole nesters			
Geographical area	α	P	R^2	Std. error	α	P	R^2	Std. error	α	P	R^2	Std. error	α	P	R^2	Std. error
Northern	0·03	0·874	0·10	0·20	1·75	0·001	34·30	0·48	1·04	0·050	14·60	0·50	0·58	0·091	11·00	0·33
Europe	(0·03)			(0·20)	(0·20)			(0·05)	(0·14)				(0·19)			(0·11)
Central	0·59	0·012	15·60	0·22	0·38	0·039	10·70	0·18	0·35	0·108	6·70	0·21	0·46	0·059	9·10	0·23
Europe	(0·27)			(0·10)	(0·28)			(0·13)	(0·19)				(0·20)			(0·10)
Mediter-	-0·10	0·556	3·20	0·17	0·23	0·337	8·40	0·23	0·49	0·107	21·90	0·28	0·15	0·078	25·60	0·07
ranean	(-0·32)			(0·53)	(0·36)			(0·36)	(0·45)				(1·77)			(0·91)
Western	-0·07	0·824	1·40	0·30	-0·16	0·164	42·00	0·10	0·16	0·478	13·30	0·20	-0·37	0·421	16·70	0·41
Europe	(-0·20)			(0·83)	(-2·57)			(1·51)	(0·83)				(-0·46)			(0·41)

Discussion

To summarise the main results of this study, increasing latitude and/or longitude coupled with increasing harshness of winter climate has a depressing effect on the density and relative proportion of European resident titmouse species in forest breeding bird assemblages. The density and proportion of titmice increases from NE Europe with decreasing latitude and longitude and peaks in western and central Europe. Especially the variance of density is much lower in the north than in the rest of Europe. Our findings confirmed the negative relationship between the abundance of resident birds and harshness of winter climate, which has earlier been indirectly suggested through the relative proportions of migrant birds in Europe by Herrera (1978a) and Helle & Fuller (1988). The average densities of titmice in northern Europe were six to seven times lower than elsewhere in Europe whereas the difference in total passerine density was only two to three-fold. This suggested that the northern titmice populations may be suppressed relatively more below the carrying capacities of summer than in the south. This may provide more space for the migrants in the north, which was our basic argument for the differences among geographical areas in interspecific relationships. The observed associations between titmice and migrants were parallel with our predictions: the most strongest positive associations were observed in northern Europe whereas in southern and western Europe they were more neutral or negative.

As homeotherm animals birds are not directly dependent on the ambient temperature, but rather on the relationship between temperature and food resources. The clear decreasing relationship of the density and relative proportion of titmice along with increasing latitude and longitude and the harshness of the winter probably reflected the relationship between critical temperatures and food resources. Latitude and mean annual temperature are both strongly correlated with actual and potential evapotranspiration, which describe rather well the variation in primary production and atmospheric energy, respectively (see Currie 1991, Begon, Harper & Townsend 1996). Higher latitudes with colder winters pose a tricky problem for resident birds: increasing cold requires more food for heat production but at the same time food abundance decreases and the daily time to harvest it because of diminishing daylight. The variation in the available energy along with latitude sets the basic limits for the abundance of species. However, at high latitudes where low primary production is coupled with harsh winters the climate may be relatively more important agent affecting the abundance of species than in the south. The result that in the SW and western Europe the variances of the titmice density were higher than in the northern Europe supports this view. In the south, the abundances may track more closely the local resource conditions, whereas in the north, the densities and variances were quite even over large areas, quite likely because of the winter climate. MacArthur’s (1959) hypothesis of the tight relationship between the large amplitude of summer and winter time food resource seasonality and the high proportion of migrants is supported by these results. Increasing harshness of the winter coupled with the decreasing amount of primary production are quite likely affecting to the decreasing abundance of resident titmouse species.

At local scale, however, evidence for the impact of temperature during non-breeding time on survival and population density is contradictory. Lack (1966) concluded that winter cold does not affect the population fluctuation of great tit at Marley Wood (see also Loery & Nicholls 1985). By contrast, Kluijver (1951) and Slagsvold (1975a) have found evidence that winter temperatures may affect the fluctuations of titmice. Especially young birds seem to have lower winter survival than adults (Ekman 1984, Koivula & Orell 1988). The role of the food for the regulation of populations and the survival of birds is more coherent than the importance of winter temperatures. Gibb (1960) concluded that the coal tit population in East Anglia was ultimately limited by food shortage, especially in late winter. Experiments with providing supplemental food for resident birds usually have increased the survival of the birds (van Balen 1980, Jansson, Ekman & von Brömssen 1981, Lahti et al. 1998, but see Krebs 1971). It has been suggested (e.g., Kluijver 1951, van Balen 1980, Lahti et al. 1998) that strong deviations to colder from the average temperature and, especially, if they are coupled with food shortage, have the most negative effect on resident populations. For example, in southern Finland the mortality of the goldcrest (*Regulus regulus*) can vary from 30% up to over 90% depending on the severity of the winter (Hildén 1982). This supports the view that bird populations are adapted to local average conditions and only deviations from that may be detectable at local scale. The depressing effect of climate is more pronounced in the context of geographical variation of densities and climate factors. These results suggest that populations of titmice are strongly affected by the winter climate, especially in the north.

Different life-history traits between hoarding behaviour of titmice also appeared in the geographical context. The density and variance of both hoarders and non-hoarders were equally low in northern Europe. Elsewhere in Europe, however, the variance of the non-hoarding titmice was larger than the hoarding titmice did. In addition, forest type explained significantly the density of non-hoarders whereas for hoarders it did not have any importance. In other words, the density of non-hoarding titmice can vary a lot regionally and locally, probably along with local resource conditions. The possible explanation for the difference is that the hoarding titmice can stabilise the energy gain better than non-hoarders and are perhaps better prepared for environmental unpredictability. Uneven distribution of food during winter may affect to the distribution of non-hoarding titmice, which are reflected in the breeding time distribution too. This can be seen as large density variances. The trends between hoarders and non-hoarders also differed in relation to PC 2. Non-hoarders were more negatively associated with low average temperature of the July and the whole year (PC 2) whereas hoarders had reverse relationship with PC 2.

After the standardisation of the densities, the ANOVA model fitted best to the titmice density but the model explained well the densities of migrant birds as well. The models explained relatively equal proportions of variance among the migrant groups. This was quite surprising because *Phylloscopus*-warblers and hole nesters are all tropical migrants whereas *Fringilla*- and some *Turdus*-species are intra-European migrants. There were, however, differences among migrant groups in relation to geographical location (PC 1). The densities of *Phylloscopus*-warblers and *Fringilla* spp. peaked in central Europe and decreased from there to the west, and even more radically to the north and the south. By contrast, the densities of *Turdus* spp. and hole nesting species increased more linearly from NE Europe to SW Europe. Helle & Fuller (1988) have observed that the average density of migrants is highest in the Central and Western Europe. The unimodal distribution probably reflected the contact zone of coniferous and southern temperate forest in central Europe, which also corresponds to the peak in the species diversity of forest associated passerines in Europe as well (Mönkkönen 1994). Apparently the low abundances in the Mediterranean area also are partly due to the high elevation of the census locations; in lowland area mature forests at that area are rare. In general, however, the effects of geographical location and climate on the breeding grounds were rather equal among different migratory groups.

The relative proportions of titmice from the breeding time passerine bird assemblages varied from almost a zero in the north Scandinavia up to almost 50% in the western Europe. This variation seemed to be associated with the quality of the association between titmice and migrants in the predicted way. In northern Europe the associations were more positive and often relatively stronger than in the southern areas. The strongest positive associations (high α) between the titmice and migrants were observed in *Fringilla*- and *Turdus*-species. This result matches well with the results of our experimental studies carried out in Finland, where we have found that *Fringilla* spp. and thrushes respond positively to augmented densities of *Parus* spp. (Mönkkönen, Helle & Soppela 1990 and Forsman et al. 1998a, see also Timonen, Mönkkönen & Orell 1994 and Mönkkönen et al. 1997). In the experiments (Mönkkönen, Helle & Soppela 1990, Forsman et al. 1998a), the *Phylloscopus*-warblers did not respond to experimentally altered titmice abundance. Likewise the result of this study suggested neutral association between titmice and *Phylloscopus*-warblers in northern Europe. Mönkkönen, Helle & Soppela (1990) coined the process as a heterospecific attraction referring to habitat selection process where other species are used as cues to productive and/or safe breeding places. This process is more likely in a seasonal system where the settlement of resident individuals preceeds the arrival of colonising (migrant) species, and the density of residents honestly reflects the quality of the habitat (Mönkkönen et al. 1999).

The associations between titmice and the control group of thrushes, measured in both ways, were rather weak in all areas except in north Europe. The observed values were parallel with the expected neutral association between titmice and thrushes suggesting that this method may give reliable estimates of the true quality of the interspecific associations. In western Europe, where the proportion of titmice was high, negative associations, though weak, were more common than elsewhere. Especially high negative index of association was observed when the density of *Fringilla*-species (i.e. the chaffinch) explained the density of titmice. This association accounted for 42% of the variance in residual densities suggesting strong interactions between titmice and the chaffinch in western Europe. Reed's (1982) playback and removal experiments in Scotland showed that interactions between the chaffinch and the great tit can vary from neutral to aggressive depending on the local conditions. Moreover, great tits quickly refilled the empty space that was created by the removals of the Chaffinches suggesting that those two species might compete (Reed 1982). It must be noted that in western Europe the breeding chaffinch population is resident year-round. This enables longer-term interactions between the chaffinch and titmice.

The association between titmice and hole nesting birds was also negative in western Europe but positive, though quite weak, in other areas. Positive associations probably reflect same habitat preferences. This result also provides good example for comparison of patterns extracted from different scales and by different methods. Several studies have shown that the competition between titmice and the pied and collared flycatcher may be severe (Slagsvold 1975b, Sasvári, Török & Tóth 1987, Gustafsson 1987, 1988, Merilä & Wiggins 1995). Densities of competitor species have been also observed to be negatively correlated (e.g., Gustafsson 1988). Those studies, however, involve nest-box breeding populations in which densities were usually high and strong conclusions concerning natural densities are not feasible. For example, in the long-term study in the Bialowieża forest, Wesolovski & Tomialojć (1997) did not find any relationship between densities of secondary hole nesting species and found no evidence for the shortage of nesting holes. These contradictory results indicate that a great care must be taken when making strong inferences from single studies, whether they were experimental or correlational (see also Sherry & Holmes 1988).

To conclude, the geographical variation in the abiotic factors affect the density and relative proportion of resident titmice in European breeding bird assemblages and may depress them to relatively lower level in northern Europe compared with southern Europe. This may in turn cause geographic variation in species interactions in local communities. Our results predict distinctive differences among geographical locations, most likely between northern and western Europe. Positive associations between migrants and titmice are more likely to occur in northern Europe whereas relatively more negative associations would be expected in western Europe. The question of whether the observed associations between titmice and migrants reflect real patterns is awaiting future experimental works.

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Appendix 1. The used census results in this study. Forest type C refers to coniferous, M to mixed and D to deciduous forest type. In the census method, M indicates mapping, L line transect, P point count and S single visit study plot, respectively. Altitude divides censuses into two classes: H refers to highland census (≥ 500 m a.s.l.) and L to lowland area (< 500 m a.s.l.).

Locality and co-ordinates	Forest type	Census method	Altitude	Reference
Northern Europe				
68°N, 27°E	C	S	L	Inkeröinen 1995
68°N, 27°E	C	L	L	Virkkala 1989
67°N, 29°E	C	L	L	Virkkala 1987
66°N, 28°E	C	L	L	Virkkala 1987
66°N, 29°E	C	L	L	Helle 1985
66°N, 28°E	C	L	L	Virkkala 1987
65°N, 25°E	C, D	M	L	Forsman et al. 1998b
65°N, 17°E	C	L, M	H	Enemar 1964
63°N, 28°E	C	L	L	Mönkkönen 1984
63°N, 10°E	C	M	L	Hogstad 1993
62°N, 21°E	C, M, D	M	L	Nordström 1953
61°N, 24°E	C	L	L	Haapanen 1965
60°N, 20°E	C, M, D	L	L	Haila 1980
Central Europe				
63°N, 12°E	C	M	L	Socher 1983
58°N, 33°E	C	M	L	Morozov 1992
56°N, 22°E	C	M	L	Matiukas 1992
56°N, 14°E	C	M	L	Nilsson 1980
56°N, 13°E	D	M	L	Enemar 1966
55°N, 13°E	C	M	L	Svensson 1975
53°N, 9°E	C, M	M	L	von Dierschke 1973
52°N, 24°E	C, M, D	M	L	Tomialojć et al. 1984
52°N, 13°E	M	M	L	Witt 1974
51°N, 9°E	D	M	L	Jedicke 1996
51°N, 23°E	C,M	M	L	Cieslak 1984
51°N, 17°E	D	M	L	Tomialojc & Profus 1977
51°N, 16°E	M, D	M	L	Tomialojć 1974
50°N, 20°E	C	M	L	Glowaciński & Weiner 1980
50°N, 20°E	D	M	L	Glowaciński 1979
50°N, 15°E	C	M	L	Exnerova, unpubl.
50°N, 13°E	D	M	H	Stastny 1985
49°N, 7°E	C, D	P	L	Muller 1981
49°N, 20°E	M	M	H	Kropil 1996
49°N, 19°E	C, M	L	H	Saniga 1995
48°N, 8°E	C	M	L	von Vidal 1975
48°N, 20°E	D	P	H	Moskat & Szekely 1989
47°N, 8°E	C, M, D	M	L	Christen 1983
46°N, 7°E	C, M	M	H	Luder 1981
46°N, 6°E	C	M	H	Catzeflis 1979
46°N, 6°E	D	M	H	Zollinger 1976
Western urope				
53°N, 4°W	D	M	L	Jones 1972
51°N, 1°W	C	M	L	Williamson 1973
51°N, 1°E	D	M	L	Fuller & Steel 1990, Fuller & Henderson 1992
49°N, 2°E	C, D	M	L	Le Louarn 1970
Mediterranean				
44°N, 4°W	D	P	L	Blondel 1981
43°N, 5°W	D	L	H	Suarez & Santos 1988
43°N, 12°W	M	L	H	Lapini & Tellini 1990
43°N, 1°W	C, M, D	L	H	Purroy 1974a, b
42°N, 21°W	D	M	H	Micevski 1983
42°N, 12°W	D	M	H	Papi 1996
41°N, 3°W	C	L	H	Potti 1985
40°N, 9°W	D	P	L	Blondel 1981

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Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest

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Abstract We studied experimentally how heterospecific attraction may affect habitat selection of migrant passerine birds in Finnish Lapland. We manipulated the densities of resident tit species (*Parus* spp.). In four study plots residents were removed before the arrival of the migrants in the first study year, and in four other plots their densities were increased by releasing caught individuals. In the second year the treatments of the areas were reversed, allowing paired comparisons within each plot. We also investigated the relative abundance of arthropods in the study plots by the sweep-net method. This allowed us to estimate the effect of food resources on the abundance of birds. The heterospecific attraction hypothesis predicts that densities of migrant species (especially habitat generalists) would be higher during increased resident density. Results supported this prediction. Densities and number of the most abundant migrant species were significantly higher when resident density was increased than when they were removed. On the species level the redwing (*Turdus iliacus*) showed the strongest positive response to the increased abundance of tits. Migrant bird abundances seemed not to vary in parallel with relative arthropod abundance, with the exception of the pied flycatcher (*Ficedula hypoleuca*) which showed a strongly positive correlation with many arthropod groups. The results of the experiment indicate that migrants can use resident tit species as a cue to a profitable breeding patch. The relationship between the abundance of the birds and arthropods suggests that annual changes in food resources during the breeding season probably do not have a very important effect on bird populations in these areas. The results stress the importance of positive interspecific interactions in structuring northern breeding bird communities.

Key words Heterospecific attraction · Positive interactions · Competition · Habitat selection · Food resources

Introduction

Factors regulating species populations and structuring ecological communities obviously vary geographically. Changing abiotic and biotic conditions can cause considerable variation in species interactions (see e.g., Thompson 1988; Travis 1996) ranging from competition to mutualism (e.g., Wilbur and Fauth 1990; Warner et al. 1991). Most experiments in bird community ecology that have detected interspecific competition were conducted in temperate regions. For example, Reed (1982), Garcia (1983), and Sherry and Holmes (1988) have shown that interspecific competition can affect habitat selection by the birds (but see Brawn et al. 1987). By contrast, experiments carried out further north have often indicated that interactions between species are either neutral (Enemar and Sjöstrand 1972; Fonstad 1984) or positive (Mönkkönen et al. 1990, 1997; Elmberg et al. 1997; but see Hogstad 1975; Sæther 1983). This apparent discrepancy may be because variable and unpredictable northern conditions provide a different selective environment for interspecific interactions than those of more southern latitudes.

Forest bird communities in the north have some characteristics which differ from those of more southerly bird assemblages. First, distinction between resident and migrant birds is very clear. Resident passerine birds in Europe consist mainly of different species of tits (*Parus* spp.). Severe winters regulate the densities of resident birds (Herrera 1978; Lahti et al. 1998) below the carrying capacity of their environment and the proportion of

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tits relative to the total density of the breeding passerine community can be low. For example, in north Finland tits make up less than 10% of the total pair numbers (Virkkala 1987a), whereas in southern areas the proportion of tits can reach a third of the total breeding density (e.g., Zollinger 1976). Another typical feature is a high year-to-year variability (e.g., Järvinen 1979, 1981; Haila and Järvinen 1990; Morozov 1993; Haila et al. 1996). This instability is probably because of the unpredictability of the physical environment (Järvinen 1979) which can lead to an unsaturated community structure (e.g., Enemar et al. 1984).

This suggested north versus south difference matches well with more theoretical considerations. For example, Bertness and Callaway (1994) predicted that positive interactions between species should be common in communities under high physical stress, which is certainly obvious in the north (Järvinen 1979; Enemar et al. 1984). They also suggested that increased predation pressure may lead to positive interactions. Predation is undoubtedly an important factor in modifying species interactions, for example enhancing species coexistence (see e.g., Connell 1975) and promoting individual aggregation (e.g., Morse 1977; Forsman et al. 1998) as well as communal nesting and predator protection (Slagsvold 1980). Dodds (1988) showed in his model that in temporally variable habitats (boom and bust environments) both positive and negative species interactions can be selected for. According to Dodds (1988) a sudden increase in the abundance of insect food for insectivorous birds in the north is one example of this kind of environment.

One form of positive species interaction is heterospecific attraction, an idea introduced by Mönkkönen et al. (1990). They found that experimentally increased densities of resident birds (*Parus* spp.) were associated with an increase in migrant densities, even if it was assumed earlier that resident and migrant birds compete over food or space and residents are superior in this competition (Herrera 1978; Morse 1989). This result gave rise to a new hypothesis: migrant birds may use residents as a cue for a suitable breeding patch in the northern forest environment.

In the present study, we provide an independent test of the predictions of the heterospecific attraction hypothesis. We conducted a manipulative experiment, following the scheme of Mönkkönen et al. (1990), but in more northern and harsher conditions. We manipulated the numbers of resident birds in the study plots and monitored responses of migrant birds by bird censuses. The hypothesis predicted that increased migrant abundances would be associated with increased resident abundances, and that habitat generalists, especially, would be expected to have a positive response to an increased abundance of resident species. In addition, we estimated the relative arthropod abundances in each study plot to control for the effects of food resources on bird densities.

Materials and methods

Study plots and manipulations

The experiment was conducted in Meltaus, Finnish Lapland (66°55′N, 25°25′E), approximately 40 km north of the Arctic circle. Eight distinct woodlots (range 7–30 ha) isolated by clearcuts or open bogs were chosen as study plots (see Table 1). The shortest distance between two study plots was 3 km and the longest 40 km. All plots were dominated by spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*); birches (*Betula* spp.) were also present in small numbers in both shrub and tree layer. In all other plots, except Kaarremaa, the average tree height was 15–20 m, and the age of the forest was 150 years or more. Kaarremaa forest is less than 100 years old, comprising a rather dense planted Scots pine stand with average tree heights *c.* 15 m. In all areas the field layer was dominated by bilberries (*Vaccinium myrtillus*) and lingonberries (*V. vitis-idae*) and the shrub layer was very weakly developed, consisting mainly of single saplings. Depending on the size of the study plot four to eight nest boxes (entrance hole diameter of 35 mm) were placed in each plot in summer 1992.

In this experiment we manipulated the numbers of resident bird species (the willow tit *Parus montanus*, the Siberian tit *P. cinctus*, and the great tit *P. major*). The experiment lasted for 2 years. In all areas we provided additional food (suet and sun-flower seeds) in the previous winter in order to increase tit numbers, and to habituate them to use feeders which make them easier to be caught. In the removal plots we captured tits in mist-nets and removed them immediately by car for 30–40 km. Removals were started in March and terminated before the arrival of the first migrant birds at the beginning of May. In the addition plots tits were allowed to breed and some removed pairs were introduced there. In 1993 removals were made in four study plots (Kaarremaa, Kiristäjäjärvi, Kotkanpesämaa, and Kaunismaa) and the four other areas acted as a addition plots. In 1994 the treatments of the study plots were reversed so that we could control for the possible effects of different habitat quality between areas. The treatment of the areas was determined as follows: we formed four pairs out of eight plots (see Table 1) so that the size of the plot and the forest structure were as similar as possible for each a pair. After that the treatment for the first study year was determined within a pair by flipping a coin.

The response of migrants to the manipulation was measured by censusing the number of breeding birds by the territory mapping method (Koskimies and Väisänen 1988). During censusing each plot was walked through along parallel lines 50 m apart. Censusing was repeated four times between 24 May and 21 June. Each bird observed was located accurately on a map. We interpreted observations as a pair if a singing, foraging or alarm calling individual was observed within a 100 m distance during at least two visits. Observations where a female was seen with a singing male were interpreted as a breeding pair.

Arthropod sampling

Relative arthropod abundances in the study areas were assessed by using the sweep-net method (net diameter 37 cm). The sweep-net method is perhaps most suitable for sampling field layer arthropods (see Veistola et al. 1995), but it is probably appropriate for assessing relative differences in arthropod abundance between study plots and years. In each study plot we chose the two longest diagonals as sampling lines. We took samples from ten spots along the sampling line so that the first and the last spot were at the edge of the plot and the distance between all sampling spots in the line was even. Each study plot thus had 20 sampling spots. Each sampling spot covered a circular area with a radius of 10 m, and within that area we took sweep-net samples from field, shrub and tree layer, five hits in each. Vegetation 0–0.3 m high was considered as field layer, bushes and saplings 0.3–1.8 m were defined as shrub layer and samples taken from adult trees 1.8–3.0 m high were considered as tree layer. Arthropod sampling was done by the same

Table 1 Number of the breeding pairs of tit and migrant species in the study plots during addition (ADD) and removal treatment (REM) of tits. Species present in at least four study plots included. A line connects the study plots which formed a pair in the treatment lottery. Abbreviations: *Parus* spp. *Parus montanus*, *P. cinctus*, *P. major*; *F mon Fringilla montifringilla*, *P tro Phylloscopus trochilus*, *M str Muscicapa striata*, *A tri Anthus trivialis*, *T ili Turdus iliacus*, *F coe Fringilla coelebs*, *C spi Carduelis spinus*, *T vis Turdus viscivorus*, *F hyp Ficedula hypoleuca*, *P pho Phoenicurus phoenicurus*

		Study plots								Total
		Kaarremaa	Kolmikanta	Kiristäjärvi	Namalikkoselkä	Kaunismaa	Karvaslehto	Räihänmutka	Kotkanpesämaa	
Size (ha)		30	24	20	25	14	7	15	12	
Species	Trmnt.									
Parus spp.	ADD	4	1	3	2	1	1	4	1	17
	REM	1	–	–	–	–	–	2	–	3
F mon	ADD	8	7	6	9	5	4	5	6	50
	REM	5	6	6	6	5	2	6	5	41
P troc	ADD	7	4	5	7	2	4	3	3	35
	REM	8	5	4	3	2	3	5	4	34
M str	ADD	1	4	2	2	–	3	2	1	15
	REM	1	1	5	2	–	–	–	1	10
A tri	ADD	1	2	2	2	1	2	–	1	11
	REM	2	2	1	1	1	1	1	–	9
T ili	ADD	–	1	2	2	1	1	1	–	8
	REM	–	–	2	–	–	–	–	–	2
F coe	ADD	–	1	–	2	–	–	1	–	4
	REM	–	1	–	1	1	–	–	–	3
C spi	ADD	–	1	–	1	–	1	1	–	4
	REM	1	–	1	–	–	–	–	–	2
T vis	ADD	1	–	1	–	–	–	–	–	2
	REM	–	1	–	–	–	1	–	–	2
F hyp	ADD	13	3	2	1	2	2	3	4	30
	REM	9	5	2	3	1	4	4	4	32
P pho	ADD	3	3	2	4	3	–	1	2	18
	REM	4	2	2	3	2	–	2	4	19
Others	ADD	–	–	1	–	–	1	4	–	6
	REM	–	2	2	–	–	–	1	2	7

person. The contents from each sampling spot were put into plastic bags and frozen. Samples were taken between 26 June and 7 July, from the same sampling spots, in both years. Sweep-netting was done only when the weather was warm (20°C or higher) and dry. Arthropods were identified basically to order level. The number of individuals in samples were calculated and individuals were assigned into two length classes (<5 mm; >5 mm). We also measured the total arthropod biomass (fresh weight) of each sampling spot, with an accuracy of 10^{-4} g (scale type: Sartorius-Werke GMBH, type 2402).

Statistical treatment

Manipulation may affect community structure and abundances of single species as well. To analyze community structure effects, we performed a factor analysis on log-transformed ($x+1$, natural base) densities of migrant species (pairs/10 ha) with a varimax rotation. The densities of each species and study plot during both treatments were used as variables, and analysis was performed during one computer run. Factor analysis uses the covariance of variables to create factors and the original total variability is compressed into a few factors. This method can be used for grouping variables and each factor refers to a new rearrangement of the variables (species) along the factor (Table 2). The eigenvalue of the factor describes the factor's ability to explain the original variability, and it is calculated from the sum of the squares of the species factor scores. Varimax rotation helps the interpretation of factors by modificating the species factor scores to be either as large or small as possible. In short, factor analysis was used to describe the structure of the bird communities during both treatments and consistency of changes in community composition in response to treatments. The analysis calculates factor scores for each community and factor. These scores can be used in testing the effects of the manipulation by comparing community factor scores within each plot between treatments by a paired *t*-test. We included in the analysis only those species which were present at four or more study plots (see Table 1), because chance may have considerable effects on the results for species which are rare or have low abundances (see Helle and Mönkkönen 1986).

Because each study plot was both experimental and a control area for itself, we used a paired *t*-test to see how manipulation

Table 2 Eigenvalues and coefficients of determination (R^2) of the first three factors and the factor loadings of the ten most abundant migrant species (present on four or more study plots). For species abbreviations see Table 1

	Factor 1	Factor 2	Factor 3
Eigenvalue	3.37	2.71	1.35
R^2	33.7	27.0	13.7
Bird species			
C spi	0.842	−0.328	−0.066
M str	0.784	−0.386	0.087
T ili	0.702	−0.495	−0.139
A tri	0.683	0.335	−0.193
P tro	0.631	0.583	0.298
F mon	0.493	−0.090	0.594
F hyp	0.036	0.833	0.306
T phi	−0.017	0.789	−0.472
F coe	−0.129	−0.490	−0.495
P pho	−0.652	−0.448	0.531

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affected abundances and species richness of migrant species. Because earlier results (e.g., Mönkkönen et al. 1990, 1997) have shown that heterospecific attraction between migrants and residents is possible, our testable prediction was logical and one-tailed. Therefore our choice of one-tailed hypothesis testing was justified (see Underwood 1990, 1997; Sokal and Rohlf 1995). When we tested species' responses to manipulation, we used the Dunn-Šidák method (Sokal and Rohlf 1995) to correct the value of the critical P due to multiple comparisons (8 species).

There was also another study project going on in the same study areas and, unfortunately, there was a change in the structure of the nest boxes so that in 1994 the size of the entrance hole was bigger (65 mm diameter) than in 1993 (35 mm). This may have confounded the results, especially for hole-nesting species. Probably the effect was not very severe but, nevertheless, we excluded the pied flycatcher (*Ficedula hypoleuca*) and the redstart (*Phoenicurus phoenicurus*) from all analyses except the factor analysis and correlation analysis between abundances of arthropods and birds.

Arthropod abundance may vary between years and study plots considerably and may have an impact on the density of birds. Firstly, we tested the variation in the relative arthropod abundance (i.e., quality of the study area) between years within each study plot using Pearson's correlation coefficient. We used a pooled number of arthropod individuals of different groups and length classes, and the total weights of the arthropods collected from different vegetation layers, to analyse the predictability of the quality of the plots. The number and the weights of arthropods were all log-transformed ($x+1$, natural base). A high correlation between years would indicate a good predictability of food resources. Secondly, we controlled for the effect of relative food resources on the density of birds by testing if the abundance of the bird species/species groups and arthropods/biomasses of arthropods varied parallely between treatments within each study plot. We calculated the difference in the abundance of the most common bird species/species groups and arthropods between treatments (number of pairs of birds or individuals of arthropods during addition treatment – number during removal treatment). These differences were used in Spearman's rank correlation to survey the relationship between the annual variation of birds and arthropods. A positive and high correlation between the differences of abundance of birds and arthropods would indicate that annual changes in food resources have probably affected population sizes of birds in those areas. In spite of the multiple comparisons we did not correct the critical P value ($P = 0.05$) because of the exploratory nature of this approach. In order to reduce the number of correlations, we pooled all arthropods in three different groups, according to the method of locomotion. Walking arthropods refer to Arachnida, Hexapoda and Aphidoidea. Flying arthropods consist of all other Pterygota except Aphidoidea. Crawling arthropods include all larvae.

Some arthropod groups were clearly dominating within the three pooled groups (walking, flying and crawling arthropods). Walking arthropods consisted almost completely of Aranea, and more specifically Linyphiidae, with a minor proportion of Aphidoidea. Flying arthropods were more a heterogeneous group, but the three most numerous groups were overwhelmingly Nematocera, Brachycera and Hymenoptera. The rest of flying arthropods consisted mainly of Ephemeroptera, Plecoptera, Lepidoptera and Homoptera. Crawling arthropods included mainly the larvae of Lepidoptera, with small numbers of the larvae of Coleoptera.

All statistical analyses were made by SPSS for Windows software.

Results

The relationship between birds and arthropods

The relative arthropod abundance seemed to be quite variable between study years in the study areas. In general, most of the between-year correlations were positive, but only the biomasses in shrub and tree layer had clearly significant or almost significant positive correlations (i.e., were the most predictable food resources) between years (Table 3).

The general trend among pairwise differences of the abundances of different migrant species/species groups and arthropod groups between treatments was that they varied, independently of each other (see Table 4). Only two species, the pied flycatcher and the siskin (*Carduelis spinus*), deviated clearly from the general non-parallel relationship between bird and arthropod abundances. The abundance of pied flycatchers seemed to vary in parallel to the abundance of arthropods. In the correlation matrix there were eight statistically significant positive correlations, and seven of them were due to the pied flycatcher. On the other hand, the siskin had many negative significant correlations with arthropods. However, this was an artifact, because there were no siskins present in the study areas in 1993 (probably due to the cold spring and beginning of the summer) when the abundance of the walking and flying arthropods was higher than in 1994.

Migrants response to manipulation

We included in the final factor solution factors with eigenvalues greater than 1. The three first factors together explained 74.4% of the variance in species abundance. The first factor alone explained 33.7% of variation and most species (seven out of ten) had positive loadings along that axis (Table 2). Since most species showed a positive response to the addition treatment of the tits (see later), factor 1 was interpreted as depicting the effect of the increased abundance of tits on the bird community. Communities gained higher factor scores on the first factor during the addition treatment of tits than during the removal treatment ($t = 1.97$, $df = 7$, $P = 0.045$).

Table 3 The relationship between the number of individuals of different arthropod groups and the biomass of the arthropods in different vegetation layers between the consecutive years in each study plot. Pearson correlation coefficient (r_p) refers to the predictability of relative arthropod abundance between years. P is the statistical significance of the correlation; $df = 6$ in all cases

Arthropod group	r_p	P
Aranidae	0.295	0.479
Hymenoptera	0.613	0.106
Aphidoidea	0.336	0.415
Brachycera	0.642	0.086
Nematocera	−0.007	0.987
Larvae	0.572	0.139
Biomass in the field layer	0.068	0.873
Biomass in the shrub layer	0.805	0.016
Biomass in the tree layer	0.683	0.062
Total biomass	0.304	0.464

Table 4 The correlations between the difference in the most common migrant bird species/species groups and the difference in the number of arthropods/arthropod biomasses in three vegetation layers. Difference denotes between-treatment (addition of tits – removal of tits) differences within study plots for both birds and arthropods. A positive and high correlation suggest that arthropod and bird abundances have fluctuated parallely in these areas. Different arthropod classes are pooled to three groups according to the way of locomotion (walking, flying and crawling arthropods). Walking arthropods refers to Arachnida, Hexapoda and Aphidoidea. Flying includes all other Pterygota except Aphidoidea. Crawling arthropods consist of all larvae. In the Spearman's rank correlation matrix the upper value refer to the correlation coefficient (r_s), and the lower to the propability value of coefficient. Only *P* values that are smaller than or equal to 0.05 are shown and printed in **bold**; *df* = 6 in all cases. Foliage gleaners are marked with *F* after abbreviation, *G* refers to ground foraging, *A* denotes to aerial feeding and *S* is a symbol for seed eaters. For bird species abbreviations see Table 1

Species	Walking			Flying			Crawling			Biomass			Total
	Field	Shrub	Tree	Field	Shrub	Tree	Field	Shrub	Tree	Field	Shrub	Tree	
F mon (F)	−0.158	0.303	0.121	−0.024	−0.024	0.085	−0.133	−0.265	−0.230	−0.049	−0.061	0.012	0.061
P tro (F)	−0.061	−0.479	0.196	−0.049	−0.111	0.037	−0.270	−0.372	−0.246	−0.331	−0.589	0.037	−0.196
M str (A)	−0.536	0.077	−0.664	−0.460	−0.370	−0.460	−0.217	0.476	0.498	−0.141	−0.243	−0.460	−0.370
A tri (G)	0.000	−0.463	0.180	0.026	0.077	−0.026	**−0.746** **0.034**	−0.685	−0.077	−0.257	−0.617	0.103	−0.180
T ili (G)	−0.507	−0.169	−0.507	−0.507	−0.507	−0.507	0.169	**0.720** **0.044**	0.507	−0.056	−0.394	−0.507	−0.282
F coe (F)	−0.067	0.412	−0.674	**−0.866** **0.005**	−0.591	**−0.866** **0.005**	−0.096	0.139	−0.481	−0.481	−0.495	**−0.867** **0.005**	−0.577
C spi (S)	**−0.720** **0.044**	0.000	**−0.720** **0.044**	**−0.720** **0.044**	−0.592	**−0.772** **0.025**	0.556	0.480	0.386	−0.206	−0.566	**−0.720** **0.044**	−0.463
T vis (G)	0.463	0.232	0.463	0.309	0.309	0.386	0.386	−0.288	−0.694	0.000	0.386	0.309	0.232
F hyp (A)	**0.835** **0.010**	0.282	**0.737** **0.037**	**0.737** **0.037**	**0.712** **0.048**	**0.798** **0.018**	0.528	−0.039	−0.135	0.430	**0.798** **0.018**	**0.737** **0.037**	0.614
P pho (A, G)	−0.371	−0.642	−0.087	−0.087	−0.519	−0.111	0.235	0.211	0.297	0.111	−0.247	−0.148	0.049
Total migrant density	−0.299	0.311	−0.228	−0.467	−0.264	−0.252	0.240	0.447	−0.192	−0.347	−0.347	−0.371	−0.335
Foliage gleaners	−0.209	0.430	−0.148	−0.467	−0.074	−0.282	−0.270	−0.164	−0.602	−0.589	−0.516	−0.331	−0.479
Ground foragers	−0.136	−0.272	−0.148	−0.420	−0.210	−0.247	−0.148	−0.033	−0.482	**−0.717** **0.046**	**−0.741** **0.035**	−0.284	−0.618

This suggests that manipulation affected migrant abundances or species number. However, the trend was not very clear when all 13 migrant species, except the pied flycatcher and the redstart (see Methods), were considered. There was no difference in the species number between the treatments ($t = 1.11$, $df = 7$, $P = 0.152$), but the total abundance of migrants was nearly significantly higher when tit abundance increased ($t = 1.80$, $df = 7$, $P = 0.058$). Considering only the eight most abundant migrant species which were present at four or more study plots (once again excluding the pied flycatcher and the redstart), both the species number ($t = 2.83$, $df = 7$, $P = 0.013$) and the total abundance ($t = 2.08$, $df = 7$, $P = 0.039$) were higher during the addition treatment (see Fig 1).

Altogether we observed 15 migrant species (including the pied flycatcher and the redstart) during this experiment. We included the eight most abundant species (see Table 1) in the pairwise comparisons, but not the pied flycatcher nor the redstart. The redwing (*Turdus iliacus*) had the strongest response to the manipulation. It was more numerous during the addition treatment compared to the removal treatment (see Table 1) ($t = 3.42$, $df = 7$, $P = 0.0055$, which is smaller than the critical $P = 0.0064$ according to the Dunn-Šidák method for multiple test). The most numerous species in the area, the brambling (*Fringilla montifringilla*), also seemed to respond positively to the increased resident abundance ($t = 2.18$, $df = 7$, $P = 0.033 > P = 0.0073$, Dunn-Šidák method). The remaining responses were non-significant. Therefore, on the species level only one species, the redwing, showed a statistically significant, positive response to the manipulation. It is notable that the addition of tits had no negative effects on the migrant species. Mean abundance of the mistle thrush (*Turdus viscivorus*) was the same in both treatments, but all other species showed a positive (though non-significant) trend in response to the increased abundance of tits.

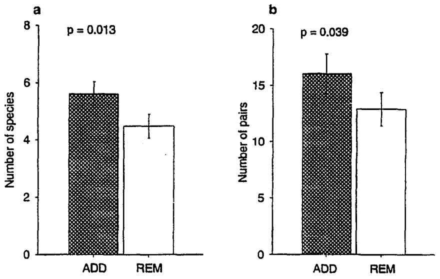

Fig. 1 Mean number of **a** migrant species and **b** migrant pairs during addition (*ADD*) and removal treatment of tits (*REM*) based on species that were present on at least four study plots. The *error bar* is the SEM

Discussion

The results of the manipulative experiment are in general agreement with our predictions. While the abundance of tits was higher the abundance and the number of the most common migrant species was higher than while it was lower. These results support the heterospecific attraction hypothesis proposed by Mönkkönen et al. (1990; also Mönkkönen et al. 1997) and emphasize the importance of positive interspecific interactions in the habitat selection of migrant birds. By contrast, food resources seemed to have no, or very little, effect on changes in bird abundances between treatments. The only notable exception was the pied flycatcher. This may suggest that birds either do not or cannot estimate the level of food resources in habitat patches, or that food resources do not restrict population sizes. This result also reduces the possibility that different amounts of food resources would have confounded the results. Thus, it is the presence of resident birds that is selected for by the migrants. Moreover, the relative quality of the plots, measured by the relative abundance of the arthropods, seems to vary annually. From the point of view of the migrants, this suggest that site fidelity may not be a very profitable strategy in the north.

The number of negative correlations between the abundance of birds and arthropods were surprisingly high. Interestingly, the pied flycatcher was the only species the abundance of which seemed to fluctuate with the arthropod abundance. Veistola et al. (1996, 1997) have found that in Kevo (*c.* 300 km north from Meltaus) the breeding success of the pied flycatcher, a new comer in Lapland, was negatively affected by harsh weather during breeding time, whereas the Siberian tit (resident species) and the redstart (native migrant species) did not suffer considerably. These results match well with suggestions that food resources during the breeding season do not limit the population sizes of birds (see e.g., Gibb and Betts 1963; Lack 1966). However, they may be important with respect to breeding success (e.g., Dhondt 1977; Högstedt 1980; Orell and Ojanen 1983).

Although species richness and abundance of the most numerous migrants were higher when tit abundance was increased, at the species level only the redwing clearly responded positively to the increased abundance of tits. This may be due to differences in behavior both between and within species. Firstly, site tenacity between species varies considerably, which affects species' habitat selection procedures (Mikkonen 1983; Enemar et al. 1984). Species that lack site tenacity may be more inclined to use different kinds of cues to a profitable breeding site (e.g., food resources, other species). Of the species breeding in the area, at least the brambling has the propensity to form loose breeding colonies (Mikkonen 1985), and the redwing and the brambling have been found to aggregate and breed in heterospecific colonies (Slagsvold 1980). Moreover, several species have been shown to form heterospecific feeding flocks during the breeding period (Mönkkönen et al. 1996). Secondly, inexperienced young individuals are probably not as site-tenacious as old ones (see Nichols 1996) which can make them more inclined to use settled individuals as cues. If there is only a small proportion of young birds in a population in a given year, the likelihood of detecting a significant response to the manipulation may be low.

Conspecific attraction (see Stamps 1988; Reed and Dobson 1993 for reviews) has been observed to affect habitat selection in many animal species. Also, heterospecific attraction may be an important mechanism in species habitat selection. When the first migrants arrive in these latitudes there is usually a thick snow cover on the ground with only a few snowless spots. It is difficult to directly estimate the abundance of arthropod food resources in different habitat patches in spring because in Lapland the peak abundances occur later in the summer (Veistola et al. 1995). Moreover, our results based on arthropod sampling suggest that the relative arthropod abundance in the study plots varies between years. Migrants are also probably time-constrained at the onset of breeding. For example, the breeding success of the great tit (Barba et al. 1995) and the pied flycatcher (Alatalo and Lundberg 1984; Harvey et al. 1985) has been observed to decrease considerably due to a couple of days' delay at the onset of breeding. Intraspecific competition for territories (Krebs 1971; Reed 1982; Mönkkönen 1990) may also create pressure for individuals to choose breeding sites as quickly as possible. The ability to use the presence of the tits as a cue of a good and/or safe breeding place could provide a quick way to roughly estimate the relative quality of the breeding sites. Different species have similar habitat preferences in these areas, because most of the breeding species (70–80%) are habitat generalists in northern Finland (Virkkala 1987b), and are therefore able to use each other as cues. Furthermore, at least some migrant species seem to be able to recognize the song of the willow tit (Mönkkönen et al. 1996) which makes detection of the occupied habitat patch possible.

Current views on the natural communities emphasize that interspecific interactions either limit the number and the abundance of the species within a community, or that they are of no importance in structuring the communities (see e.g., Wiens 1989; McLaughlin and Roughgarden 1993). However, our results suggest that interactions, and especially positive ones, between resident and migrant birds promote the species richness and the abundance in breeding bird communities in the far north. Mönkkönen et al. (1997) conducted the same kind of experiment as this study in North America, Minnesota and were also able to demonstrate the positive effect of increased resident density on the species richness and the abundance of migrant species. Parallel results from two different continents (Mönkkönen et al. 1990, 1996, 1997; Timonen et al. 1994; this study) suggest that heterospecific attraction is a wide-spread phenomenon in northern communities. Furthermore, Elmberg et al. (1997) have found that heterospecific attraction may be a potential process affecting species co-existence in dabbling duck assemblages (*Anas* spp.).

The ultimate causes of heterospecific attraction may, however, be different on the two continents. In Minnesota, the abundances of arboreal insectivores, i.e., birds that belong to the same foraging guild as the tits, were clearly higher while the abundances of resident birds were increased (Mönkkönen et al. 1997). This indicates that food may be the keyfactor resulting in heterospecific attraction. In Finland there was no such clear trend with any distinct ecological species group. However, migrants can use tits as a sign of a low predation habitat patch, too. Resident preference for low predation sites may result from active selection by tits or from direct effects of predation, and as a result resident density may reflect relative differences in predation pressure (direct and/or nest predation) at a landscape level. An interesting detail is that the redwing and the brambling, which had the two most positive responses to the addition of tits, have been found to aggregate to breed in fieldfare (*Turdus pilaris*) colonies to obtain protection against nest predators (Slagsvold 1980; see also Isenmann and Fradet 1995). An experiment by Forsman et al. (1998) showed that increased perceived risk of predation caused aggregated dispersion of individuals among breeding passerine birds. This suggests that predation may induce heterospecific attraction because aggregated dispersion of birds produces benefits through increased vigilance or mobbing abilities (see e.g., Morse 1977; Caraco et al. 1980).

We conclude that heterospecific attraction of migrant birds to residents affected migrants' breeding patch selection and the structure of the breeding bird community. It is probable that migrants use tits as a sign of a good quality or safe breeding patch. The relative importance of heterospecific attraction on community structure is probably affected by the geographical location and by the local biotic and abiotic conditions. Empirical tests based on predictions derived from theoretical analysis of the ecological conditions promoting the evolution of heterospecific attraction are needed to reveal the generality of this process.

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Evolution of heterospecific attraction: using other species as cues in habitat selection

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Abstract. We analyzed the ecological conditions that may favor a habitat selection process in which later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites (heterospecific attraction). In our model, colonists assessing potential breeding patches could select between high-quality source and low-quality sink patches. A proportion of the source patches were occupied by residents. Colonists could either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Cue-users gained benefit from lowered costs when assessing occupied source patches. The cue-using strategy is an efficient way to choose the best possible patch not only when interspecific competition is intense, but also when benefits from social aggregation exceed the effects of competition. High relative cost of sampling empty patches increases the fitness of the cue-using strategy relative to samplers. The strongest attraction to heterospecifics was predicted when the benefit from aggregating with residents exceeded the effects of competition, and approximately half of the landscape consisted of occupied, high-quality source patches.

Key words: analytic modeling, colonists, habitat selection, heterospecific attraction, landscape composition, residents

Introduction

'Heterospecific attraction' was coined by Mönkkönen et al. (1990) to describe the situation where individuals choose habitat patches by the presence of established individuals of a heterospecific species (residents). Heterospecific cues may be profitable if residents reflect the relative quality of patches or if heterospecific aggregations enhance foraging efficiency or reduce predation risk. The alternative – sampling a patch directly for its relative quality (abundance of predators, food, and other resources) – will take time and consume energy (see Danielson, 1991). If time is a limiting factor in reproduction, later-establishing species may gain advantage by using residents as cues. Numerous empirical studies suggest that heterospecific attraction is a common process, at least in birds (Timonen et al., 1992; Mönkkönen et al., 1996; Elmberg et al., 1997; Mönkkönen et al., 1997; Forsman et al., 1998a, 1998b). So, it is important to determine the ecological conditions favoring heterospecific attraction.

Heterospecific attraction will be an evolutionary stable strategy (ESS) for two species that are potential competitors only if the benefits of selecting patches occupied by another species exceed costs. The ESS requirement will be easiest to satisfy when the costs of assessing habitat suitability are high. The costs are likely to vary with landscape composition (e.g., relative amount of source and sink patches) and the abundance of resident species. In this article, we analyze how competition and the benefits gained from social aggregations and from using other species as cues affect the fitness of colonizing individuals. We also study how landscape composition and the abundance of resident species influence fitness and the potential evolutionary advantage of heterospecific attraction.

The model

We define the *landscape* as a large area within which habitat patches are embedded. A *habitat* is a combination of biotic and abiotic factors that make a certain patch more or less suitable for a species. *Patches* are areas smaller than the landscape that contain only habitat of a single type that fulfill the requirements of an individual. We assume that landscapes are composed of three different habitat types: source habitat patches where reproduction exceeds mortality, sink habitat patches where mortality exceeds reproduction, and matrix that cannot be occupied (Danielson, 1992). We assume that our colonizing organism is a good disperser with good cognitive abilities so that the dilution effects of matrix can be ignored.

We consider here the consequences for a colonizing species from interactions with a resident species. The resident species samples the landscape, settles and may start breeding before the arrival of the colonist species. The two species recognize the same source and sink habitats. Patches for the later arriving species can be further divided into those occupied and those unoccupied by the earlier-establishing (resident) species. We assume that resident populations are regulated by winter conditions to levels well below the summer carrying capacity of the environment, and that residents always settle in the source habitat patches so that their presence reliably reflects habitat quality.

Colonists encounter source patches unoccupied by a resident (u-patches), source patches occupied by a resident (o-patches), and sink patches (s-patches), with relative frequencies p, q and r, respectively, in the landscape. The quality of these three types, as measured by the expected patch-specific fecundity, are denoted B_u, B_o and B_s, respectively. We assume that B_s is always lower than B_u and B_o. The relation between B_o and B_u depends on the intensity of competition.

If the cost of competition exceeds the benefits gained by settling in *o*-patches (richer food, lower predation, benefits from social aggregation) then $B_u > B_o$, otherwise $B_u < B_o$.

We compare two strategies of sampling the landscape by the colonizing species. Strategy 1: Individuals directly sample food resources and predation risk in order to estimate the relative quality of the patches (termed samplers, hereafter). Strategy 2: individuals also use residents as a quality cue (cue-users). Both strategies impose a fitness cost which lowers the fitness that could otherwise be achieved at the selected patch. The cost may arise, for example, from the time delay in the start of breeding (see e.g., Harvey et al., 1985). Samplers incur a cost C_d for each time unit spent sampling a patch. Cue-users incur the cost C_r, in an occupied patch or C_d if the patch is unoccupied. We assume $C_r < C_d$ because using cues takes less time. Traveling costs between patches are the same for both strategies, and they are not parameterized separately.

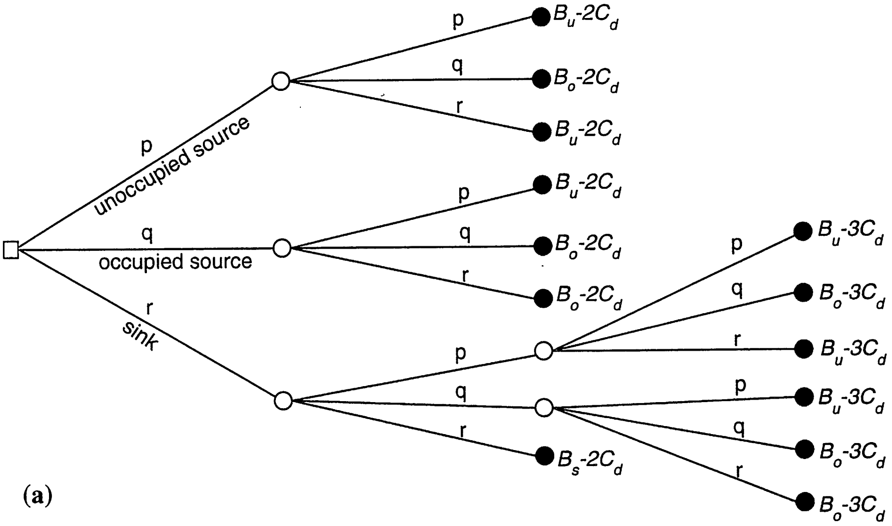
Animals may exhibit various tactics when selecting among patches (see e.g., Janetos, 1980; Wittenberger, 1983). We assume they use a sequential-comparison tactic (SCT). In SCT, animals follow the following rules:

1) Sample at least two patches.
2) Continue to sample if the current patch is better than the previous one.
3) If the current patch equals the previous one, stop and select the current patch.
4) If the current patch is poorer than the previous patch, return and select the former patch.

To analyze the fitness consequences of such a rule, we use a variant of natural decision theory (Cooper, 1981; Cooper and Kaplan, 1982) where sequences can be depicted with decision tree diagrams (Fig. 1) for both $B_u > B_o$ and $B_u < B_o$. Samplers do not assess competition nor benefits by residents, and, therefore, their decision tree is independent of the relation between B_u and B_o. SCT should be advantageous when their risk is high of being pre-empted from the best patches (Wittenberger, 1983). As the selection tactic may have a profound effect on the results, it is important to consider the alternatives. We do this in another paper (Forsman et al., in prep.).

Our model of habitat selection is similar to the ideal pre-emptive distribution of Pulliam and Danielson (1991). As in that model, potential breeding patches differ in expected reproductive success, and a patch occupied by a conspecific is no longer available. Occupation does not influence the expected reproductive success of any other patches. Our model does not result in an ideal distribution because colonists do not necessarily end up selecting the best available patch but rather the best of the evaluated ones.

The fitness equations flow from Figure 1. Going from left to right in the figure, we see that each move to a new patch *u*, *o* or *s* is associated with a probability value *p*, *q*, or *r* dependent on the proportion of each patch type in


p
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q
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sink
B_u-2C_d
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B_o-2C_d
B_u-3C_d
B_o-3C_d
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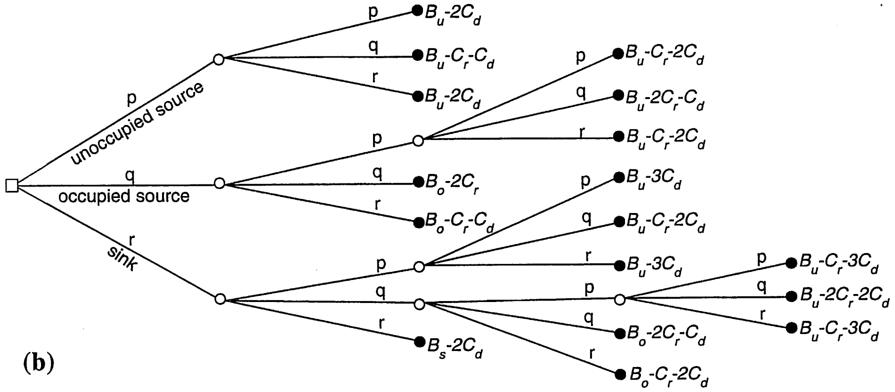
B_o-3C_d
B_s-2C_d

(a)


p
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B_u-2C_r-C_d
B_u-C_r-2C_d
B_o-2C_r
B_o-C_r-C_d
B_u-3C_d
B_u-C_r-2C_d
B_u-3C_d
B_u-C_r-3C_d
B_u-2C_r-2C_d
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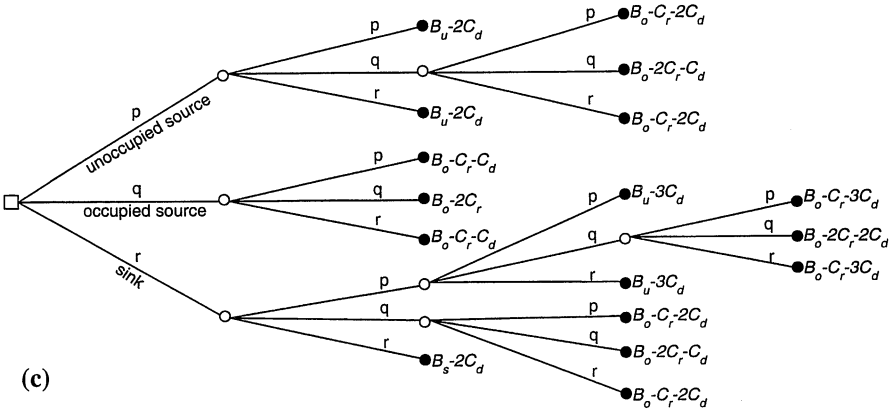
B_s-2C_d

(b)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B_u-2C_d
B_o-C_r-C_d
B_o-2C_r
B_o-C_r-C_d
B_u-3C_d
B_o-C_r-3C_d
B_o-2C_r-2C_d
B_o-C_r-3C_d
B_u-3C_d
B_o-C_r-2C_d
B_o-2C_r-C_d
B_o-C_r-2C_d
B_s-2C_d

(c)

the landscape. The fitness of an individual when each possible selection sequence has stopped is also given in Figure 1. Deriving the fitness equations of the strategies can be described as a left to right process of "averaging out" the fitness consequences of all possible selection routes (Cooper, 1981). For example, if an organism is able to use the presence of residents as a cue (Fig. 1B) and first finds an *u*-patch, the decision rule implies that it is certain to end up settling in this patch type. Thus, it will gain the fitness benefit B_u. The fitness cost for assessing will be C_d (for assessing the first *u*-patch) plus the *average* cost of assessing the second patch, where we must consider the probability of finding each of the possible patches. The expected fitness is therefore $(B_u - C_d - pC_d - qC_r - rC_d)$. Following this logic for all of the possible decision routes, we end up with the fitness equations shown in the appendix.

From the fitness equations, we can derive the conditions for cue-users to have higher fitness than samplers, assuming p, q, and r all ≥ 0 (see Appendix for details). If $B_u > B_o$ then the condition is,

$$C_r < \frac{(1+q+pq)C_d + p(B_u - B_0)}{qp+q+p+1} \tag{1}$$

and if $B_u < B_o$ then the condition is

$$C_r < \frac{(1+q+pq)C_d - p(B_u - B_0)}{qp+q+p+1} \tag{2}$$

That is, the strategy that maximizes fitness is determined by the relationship between C_d and C_r, the intensity of competition in relation to benefits of social aggregations $(B_u - B_o)$ and the composition of the landscape (frequencies p and q). To understand how each of these factors influences fitness of the individuals with different strategies of sampling the landscape, we graphically analyse these conditions and the fitness equations, looking particularly for parameter values where the optimal strategy changes.

Results

All other things being equal, intense competition (large positive value of $(B_u - B_o)$ in Condition 1 or large benefits (large negative value of $(B_u - B_o)$ in Condition 2 increase the fitness of cue-users relative to samplers (Fig. 2). Even

◄

Figure 1. Decision tree diagram for (a) samplers, (b) for cue-users when $B_u > B_o$ (competition), and (c) for cue-users when $B_u < B_o$ (benefit). The square in the left is the base node where the decision starts. Each move to another patch (to the right from this starting point) is associated with probability p, q or r. Open circles denote states where the decision sequence continues and filled circles denote when the sequence stops. The fitness of an individual when each possible selection sequence has stopped is also given in the end of each branch of the tree.

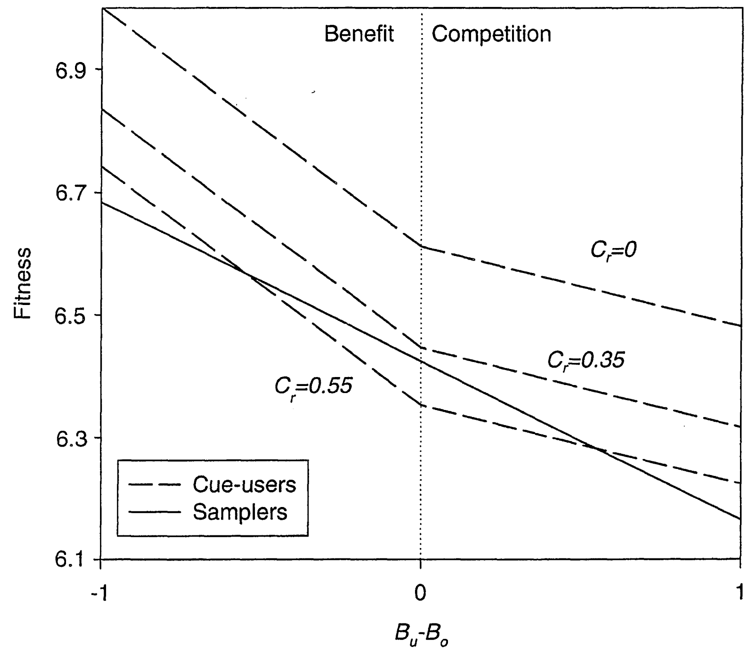

Figure 2. Fitness of cue-users and samplers in relation to the difference in quality between B_u and B_o. When $B_u - B_o$ is negative, the benefits of selecting *o*-patches exceed any costs of competition, and when $B_u - B_o$ is positive competition is more important than benefits. The graph was drawn for the values: $p = 0.5$, $q = 0.2$, $r = 0.3$, $C_d = 0.55$, $B_s = 4$, $B_u = 8$. We let B_o vary from 7 to 9. We calculated fitness curves for cue-users for three different values of C_r exemplifying the fitness effects of cost difference between cue-users and samplers.

at very moderate differences in quality between *u*- and *o*-patches, it is always beneficial to use residents as cues to high quality patches.

If there is no effect of competition and no benefits ($B_u = B_o$), the Conditions 1 and 2 change into

$$\frac{C_r}{C_d} < \frac{1+q+pq}{qp+q+p+1} \tag{3}$$

This condition implies that high relative cost of sampling empty patches ($C_d \gg C_r$) increases the fitness of cue-users relative to samplers (fig. 2). The right-hand-side expression ranges between 0.5, when $p = 1$ and $q = 0$, and 1, for all q when $p = 0$. That is, if the cost of assessing a patch by using cues is less than half of the cost of direct sampling of the patch, it is always beneficial to use cues, even if there is no difference in quality between *u*- and *o*-patches. If the cost of using cues equals the cost of direct sampling, it is never beneficial to use cues if there is no additional effect of patch quality difference (i.e. $B_u \neq B_o$).

It follows from Conditions 1 and 2 that the optimal strategy will depend on p and q. If $B_u > B_o$ there will be a change in optimal strategy when

$$C_r = \frac{(1+q+pq)C_d + p(B_u - B_0)}{qp+q+p+1} \tag{4}$$

If $B_u < B_o$ there will be a change in optimal strategy when

$$C_r = \frac{(1+q+pq)C_d - p(B_u - B_0)}{qp+q+p+1} \tag{5}$$

The quality of the sink patches (B_s) has no influence on whether a cue-using or a direct sampling strategy should be used. This is because assessing sink patches is equally costly for both strategies, and any term containing B_s is averaged out when deriving Conditions 1 and 2 from the fitness equations (see appendix). In the limiting case when there are no occupied source habitat patches ($q = 0$) in the landscape, cue-users and samplers have equal fitness, because the animals will follow the same selection paths independent of strategy (Fig. 1). When the frequency of occupied patches (q) is relatively low, a combination of patch frequencies can be found where it may be more beneficial not to use residents as cues to source patches (hatched area Fig. 3). As the frequency of occupied patches increases, at some point it will become more beneficial to be a cue-user. The location of this value depends on the effect of competition and the difference between C_d and C_r. When there are only sink habitat patches and occupied source habitat patches in the landscape ($p = 0$) it is always beneficial to use cues; Conditions 1 and 2 become $C_r < C_d$ if $p = 0$, which is true by definition. The area of frequencies of q and p when cue-using strategy is best increases with increasing difference in quality between u- and o-patches (compare rows in Fig. 3) and with increasing difference between C_d and C_r (compare columns in Fig. 3).

The fitness of cue-users is a nonlinear function of q, the proportion of occupied source patches (Fig. 4). The rate of change of fitness and the shape of the curve are determined by the relation between the costs ($C_d - C_r$), and the level of competition ($B_u - B_o$). With no competition or benefit ($B_u = B_o$), sampler fitness is independent of q (Fig. 4). In this case, samplers fitness may be higher than that of cue-users provided that the cost difference is small. More often than not, an increase in q results in an increase in the fitness of cue-users (Fig. 4).

From the decision trees in Figure 1, we can also calculate the probability that a colonist individual selects an o-patch. For samplers it is

$$q(p+q+r+pr+qr+r^2) \tag{6}$$

For cue-users if $B_u > B_o$,

$$q(q+r+qr+r^2), \tag{7}$$

and if $B_u < B_o$,

$$q(1+p+pr+r). \tag{8}$$

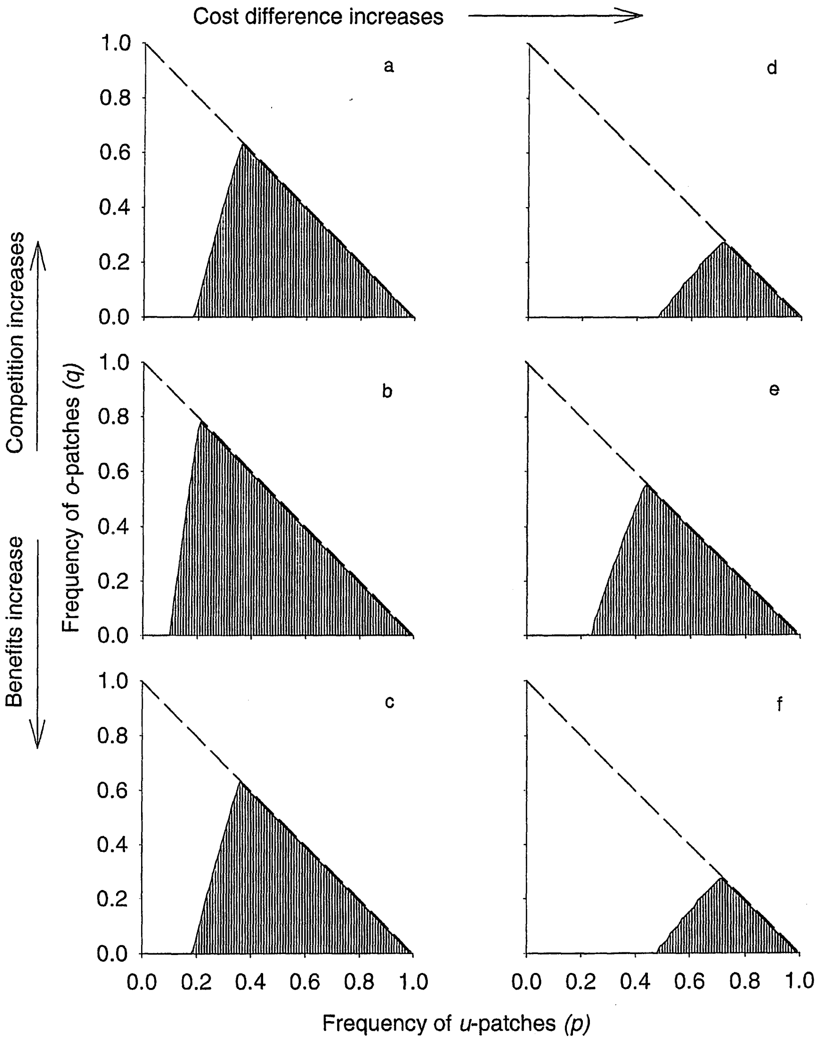

Figure 3. Frequency areas of p, q, and r where the conditions of higher fitness for cue-users than for samplers (see Condition 1 and Condition 2) either hold (open area) or do not hold (hatched area) true. Rows in the figure denote different levels of species interactions, from competition on top to benefit on the bottom, while cost difference increases from the left to the right column. All frequency combinations of p, q, and r can be found to the left of the dashed line. a) $B_u = 8$, $B_o = 7.8$, $C_d = 0.5$, and $C_r = 0.45$, b) $B_u = B_o = 8$, $C_d = 0.5$, and $C_r = 0.45$, c) $B_u = 7.8$, $B_o = 8$, $C_d = 0.5$, and $C_r = 0.45$, d) $B_u = 8$, $B_o = 7.8$, $C_d = 0.5$, and $C_r = 0.4$, e) $B_u = B_o = 8$, $C_d = 0.5$, and $C_r = 0.4$, and f) $B_u = 7.8$, $B_o = 8$, $C_d = 0.5$, and $C_r = 0.4$.

Hence, if $B_u > B_o$ and $p > 0$, a sampler is always more likely to select *o*-patches than a cue-user (Fig. 5). If $B_u < B_o$ and $p > 0$ then cue-users always have a higher probability of selecting *o*-patches than do samplers (Fig. 5). A cue-users'

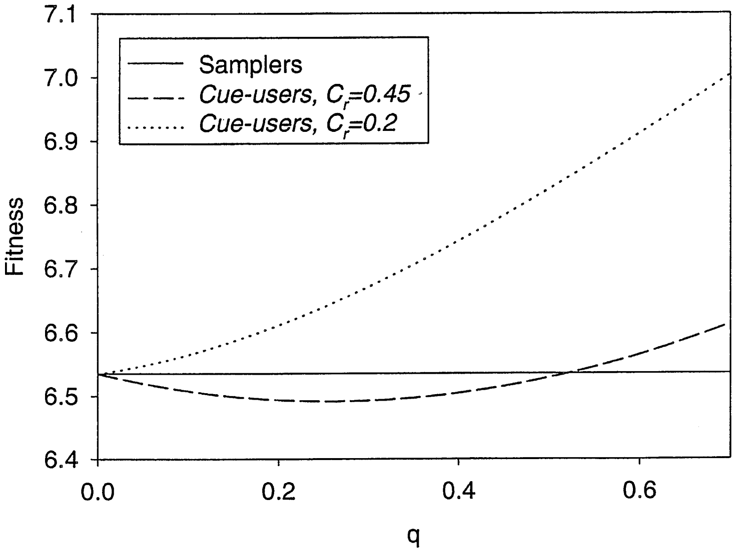

Figure 4. Fitness of cue-users and samplers in relation to the frequency of occupied source habitat, q. The graph was drawn for the values: $r = 0.3$, $C_d = 0.5$, $B_u = 8$, $B_o = 8$, and $B_s = 4$. Because there is no competition nor benefit, samplers' fitness (solid line) does not change with q. For cue-users, the dotted line shows the fitness when $C_r = 0.2$, and dashed line shows the fitness when $C_r = 0.45$.

probability of selecting o-patches is highest relative to that of samplers when $p = q = 0.5$ and $r = 0$.

Discussion

Recognizing the presence of a heterospecific individual seems to be the favored strategy in most cases. Samplers can achieve higher fitness than cue-users only if the difference in quality between occupied and unoccupied source patches is low, and the cost of assessing patch quality directly is low. The advantage to samplers is highest in a landscape with a low proportion of occupied source patches. Then, the relatively more complicated patch selection procedure of cue-users creates costs which override the benefits of avoiding the direct assessment of the patch quality. As can be seen from the decision trees in Figure 1, a cue-user usually assesses more patches before settling, and although some of the patches are comparatively cheap to assess, the higher number of patches can make this strategy less beneficial. We conclude that selection generally favors individuals capable of using other species as cues.

Recognizing the presence of a competitor, i.e., the cue-using strategy, is favored almost irrespectively of the intensity of competition. Why? Because the colonist species is time constrained and has limited ability to find the ideal

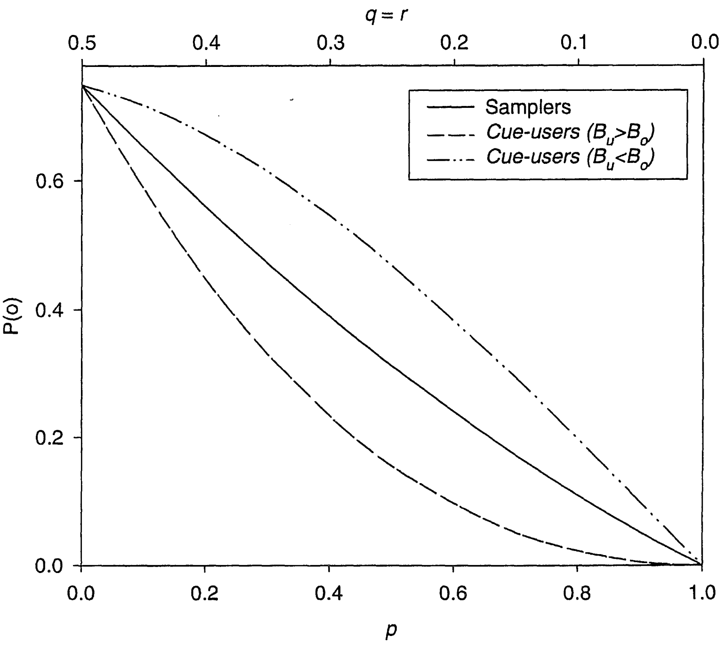

Figure 5. Probability of settling in an occupied source patch (P(o)) in relation to landscape composition for samplers and for cue-users both when $B_u < B_o$ and $B_u > B_o$. Note that only certain combinations of p, r and q are shown.

patch. So, it benefited from any increment in the ability to find the best possible patch. Cue-using strategy, conditional upon conditions, can be used both to avoid competition by and to aggregate with heterospecific individuals (see e.g., Cody, 1978; Mönkkönen et al., 1996).

Many earlier models of habitat selection have assumed that the presence of other species affects habitat selection but through an unspecified process (e.g., Rosenzweig, 1985; Morris, 1987, 1990, 1995; Brown and Pavlovic, 1992). Danielson (1991, 1992), however, explicitly assumed in his two-species model that, when species *B* occupies a patch, individuals of species *A* do not invest much time or energy in sampling that particular patch. Instead they use the resources saved to sample another patch, perhaps finding one that is unoccupied by species *B*. Our results show that such recognition is usually selected for.

Our model makes several assumptions about the two species. First, we assume that residents and colonists have shared habitat preferences. Previous work has focused more on species with distinct preferences (Pimm and Rosenzweig, 1981; Danielson, 1991, 1992) than with shared preferences (Rosenzweig, 1985). There is often considerable overlap in the habitat niches of different species, particularly among habitat generalists. Our model is, therefore, more likely to apply to habitat generalist (see also Mönkkönen et al., 1990, 1997; Forsman et al., 1998b). Dall and Cuthill (1997) suggested that, all else being equal, the generalist strategy is costly because generalists need to gather more information about their environment than do specialists. One way to avoid such costs would be to use information provided by other individuals.

Second, we assume that residents do not prevent colonists from settling in patches where residents have established themselves. This assumption seems realistic because interspecific territoriality is quite likely an exception in nature (Blondel 1985), observed only among congeners (Cody 1978, Robinson and Terborgh 1995). Indeed, there is evidence that territories of different species may overlap more than expected by chance alone (Reed 1982, Timonen et al. 1994).

Finally, we assumed that residents would be a reliable sign of patch quality. This assumption is robust. Residents, arriving sooner, are probably less time-constrained than colonists and, hence, can invest more time in assessing habitat quality. Thus, their distribution will be closer to ideal. Patches with high predation risk may lack residents because the latter have had time to evaluate the risk or because residents in risky patches have been consumed. Social aggregations may provide benefits not linked with the absolute quality of patches, e.g. mutual exploitation of resources leading to enhanced feeding efficiency and reduced predation rates (e.g., Alexander, 1974; Morse, 1977; Caraco and Pulliam, 1984; Latta and Wunderle, 1996).

We constructed our model to evaluate the fitness consequences for a colonizing organism from interactions with a resident species. It would be important to develop more general models which consider frequency-dependent strategy of using other individuals (both heterospecific and conspecific, and for both residents and colonists) as cues of habitat quality. Including density-dependence too, could easily make the model analytically intractable, but such models could be simulated.

Acknowledgments

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Appendix. The fitness equations derived from the choice trees in Figure 1.

For samplers (Fig. 1A):

$$\begin{aligned} W_1 = {} & p(pB_u + qB_o + rB_u - 2C_d) \\ & + q(pB_u + qB_o + rB_o - 2C_d) \\ & + r(p(pB_u + qB_o + rB_u - 3C_d) \\ & + q(pB_u + qB_o + rB_o - 3C_d) \\ & + r(B_s - 2C_d)) \end{aligned}$$

For cue-users when $B_u > B_o$ (competition, Fig. 1B):

$$\begin{aligned} W_2 = {} & p(B_u - C_d - pC_d - qC_u - rC_d) \\ & + qp(B_u - C_r - C_d - pC_d - qC_r - rC_d) \\ & + q^2(B_o - 2C_r) + qr(B_o - C_r - C_d) \\ & + r(p(B_u - 2C_d - pC_d - qC_r - rC_d) \\ & + q((q + r)(B_o - C_r - C_d) - qC_r - rC_d \\ & + p(B_u - 2C_d - C_r - pC_d - qC_r - rC_d)) + r(B_s - 2C_d)) \end{aligned}$$

For cue-users when $B_u < B_o$ (benefit, Fig 1C):

$$\begin{aligned} W_3 = {} & p((p + r)(B_u - 2C_d) + q((p + r)(B_o - 2C_d - C_r) \\ & + q(B_o - C_d - 2C_r))) + q((p + r)(B_o - C_r - C_d) \\ & + q((p + r)(B_o - C_d - 2C_r) + q(B_o - 3C_r))) \\ & + rp((p + r)(B_u - 3C_d) + q(B_o - 2C_d - C_r - (p + r)C_d - qC_r)) \\ & + rq((p + r)(B_o - 2C_d - C_r) \\ & + q(B_o - 2C_r - C_d - C_d - (p + r)C_d - qC_r)) + r^2(B_s - 2C_d) \end{aligned}$$

To solve the Conditions 1 and 2 from the expressions $W_1 < W_2$ and $W_1 < W_3$, we first collect all terms containing B_u, B_o, C_d, and C_r and get for the first inequality

$$\Phi C_d > \Phi C_r + \Psi C_r + \Psi B_o - \Psi B_u$$

and for the second

$$\Phi C_d > \Phi C_r + \Psi C_r - \Psi B_o + \Psi B_u$$

where

$$\Phi = qp + q^2p^2 - q^2 + q^3p - 2q - q^2p + q^3$$

and

$$\Psi = q^2p + p^2q - 2pq$$

It can be shown that

$$\Psi/\Phi = p/(1+q+pq)$$

which can be used to solve the Conditions 1 and 2 (see main text).

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Aggregate dispersion of birds after encountering a predator: experimental evidence

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Forsman, J. T., Mönkkönen, M., Inkeröinen, J. and Reunanen, P. 1998. Aggregate dispersion of birds after encountering a predator: experimental evidence. – J. Avian Biol. 29: 44–48.

Animals may join flocks to gain protection against predation. In this experiment we investigated how predation risk affects the spatial distribution of forest birds during breeding time. We manipulated the perceived risk of predation by showing stuffed avian predators and by playing the warning signals of some of the passerine species in experimental areas. The spatial distribution of the bird individuals in both experimental and control areas was investigated by censusing birds and marking the locations of all individuals on maps both before and after the simulated appearance of a predator. We predicted that the distances between heterospecific individuals would be reduced in the experimental areas compared with those in control plots because of a perceived increased risk of predation. After predator presentation individuals in experimental areas were closer to heterospecifics than in control areas. Predation risk is one possible cause of clumped distribution of species and mixed-species foraging flocks in boreal breeding bird communities.

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Mixed-species bird flocks are a common phenomenon throughout the world. Especially in tropical areas flocks can be very tight and may exist year round (e.g. Greig-Smith 1978, Munn and Terborgh 1979). In temperate and boreal areas heterospecific flocking has usually been observed outside the breeding season (Gibb 1954, Morse 1970, but see Mönkkönen et al. 1996).

Two general models have been proposed to explain why animals should join mixed-species foraging aggregations (see e.g. Morse 1977, Caraco et al. 1980, Berner and Grubb 1985, Pöysä 1992). According to the anti-predation model, individuals join flocks to gain protection against predators and to maintain their feeding effiency, whereas the feeding effiency model predicts that members of the flock can increase their foraging effiency, e.g. through copying foraging methods of other individuals or through information sharing.

Our earlier studies have shown that positive interactions between species affect the structure of boreal breeding bird communities (Mönkkönen et al. 1990, Mönkkönen et al. in press, J. T. Forsman, M. Mönkkönen, P. Helle and J. Inkeröinen unpubl.) and that mixed-species foraging flocks exist also during the breeding season (Mönkkönen et al. 1996). Our results (Mönkkönen et al. 1996) also suggested that the distribution of bird species is clearly clumped and that the observed pattern was not due to the occurrence of high quality food patches but birds more or less actively seek for heterospecific aggregations.

We made a field experiment to test if the risk of predation affects the spatial distribution of species, i.e. whether the clumped distribution we observed earlier was a response to predators. We manipulated the risk of predation that birds perceive when they see a predator. The response of birds to the experiment was measured by the distances between individuals to their nearest heterospecific neighbours. We predicted that if predation risk affects the spatial pattern of species, distances between heterospecific individuals should shorten (i.e. the distribution be more clumped) between censuses in plots where we increased the perceived risk

IV

Table 1. The sizes of the study plots, densities (pairs/10 ha) and dominance (% of total individuals, in parentheses) of the most common species in the study areas. Densities are calculated as a mean of the two censuses.

Study areas	Size (ha)	P tro (31.7)	F coe (23.8)	E rub (6.9)	C spi (6.7)	F hyp (5.5)	R reg (4.9)	P mon (3.5)	P maj (2.3)	Others (14.7)	Total density
Experimental plots											
Korpi II	14.0	6.8	1.4	0.7	–	–	–	–	–	1.8	10.7
Käärmekuru I	16.0	0.9	2.8	0.8	0.9	–	0.3	0.6	–	2.8	9.1
Kalikkakangas	13.0	1.9	2.7	0.8	0.8	0.8	1.2	0.8	–	0.4	9.4
Pyyryväiskangas	14.0	2.9	3.2	–	0.4	1.4	1.4	0.4	–	2.5	12.2
Control plots											
Korpi I	23.0	10.4	5.9	1.3	–	0.9	0.7	0.7	1.1	1.1	22.1
Käärmekuru II	17.0	2.9	2.3	1.8	1.8	–	0.6	–	0.3	2.4	12.1
Myllykoski	15.0	4.3	3.0	1.7	2.0	1.7	–	0.7	–	1.0	14.4
Toivarinaro	15.0	1.3	2.7	0.7	2.0	1.7	1.3	0.7	0.7	3.2	14.3

Abbreviations. P tro = *Phylloscopus trochilus*, Willow Warbler; F coe = *Fringilla coelebs*, Chaffinch; C spi = *Carduelis spinus*, Siskin; E rub = *Erithacus rubecula*, Robin; F hyp = *Ficedula hypoleuca*, Pied Flycatcher; R reg = *Regulus regulus*, Goldcrest; P mon = *Parus montanus*, Willow Tit; P maj = *Parus major*, Great Tit.

of predation compared with the corresponding distances in control plots.

Methods

The study areas were located near Oulu, northern Finland (65°N, 25° 30′E). The experiment was carried out in the first week of June, 1995. During that time birds' breeding cycle is at the most stable phase, the majority of species and pairs have established their territories, and most of them are laying or incubating. Eight woodlots with distinct boundaries (clearcuts, ditches, roads etc.) were chosen as study areas. We formed four pairs of plots so that forest structure was as similar as possible within each pair. The sizes of the study areas were between 13 and 23 ha (see Table 1). The forest and the vegetation structure of the plots were very much alike. In only two plots (Korpi I and II) did forest structure differ from that in the others. All the other plots were mixed spruce *Picea abies* forest, with birch *Betula* spp. and Scots pine *Pinus sylvestris*. Mean tree heights were approximately 17 m for coniferous trees and about 10 m for deciduous trees. The field layer mainly consisted of bilberry *Vaccinium myrtillus* and lingonberry *Vaccinium vitis-idaea*. In Korpi I and II the dominating tree species was birch, with small patches of spruce, and average tree height was c. 13 m. Different species of grass dominated the field layer. The forest structure in these two plots was generally more open than that in the other plots. In all plots the shrub layer was poorly developed and consisted of single saplings.

Each of the four authors was responsible for one pair of study plots. On the first day of the experiment, birds were censused by walking through the study plots along parallel lines 50 m apart. For this we had created a grid system (50 × 50 m) in each plot, marked with numbered plastic flags. The same grid system was also marked on the field maps (scale 1:2500 – 1:3200), so that the locations of individual birds could be very accurately plotted on the maps. Censuses were made between 08.00 and 15.30 hours. The exact position of each observed bird individual was marked on the map. If a bird moved during the observation, its route was marked on the map. Our walking speed was approximately 1.3 km per hour. We tried to make simultaneous observations depicting the true spatial configuration of the individuals at any one time. However, some of the relatively close observations were made during different transects, which means that there was a time lag between them.

The predator presentations were made during the next three days. One plot in each pair was chosen randomly as the experimental plot and the other acted as the control plot. In experimental plots we increased the perceived risk of predation by showing a stuffed Sparrowhawk *Accipiter nisus* (all males) and Pygmy Owl *Glaucidium passerinum* and by simultaneously playing back the warning calls of Willow Tit *Parus montanus*, Great Tit *Parus major* and Chaffinch *Fringilla coelebs*. Willow Tit and Great Tit are the most abundant resident species in the area and the Chaffinch, together with the Willow Warbler *Phylloscopus trochilus*, strongly dominates among the migrant species (see Table 1). The predator dummies were placed at the head of a stick or were tied to the branches of trees at the height of 1.5–2.0 m. The loudspeaker was placed in the immediate vicinity (c. 5 m) of the predator model. In total, the predator presentation lasted for three days, for five hours per day, between 07.00 and 16.00 hours. At each spot, the predator was presented for 10–15 min, during which the observer was settled at a distance of 15–20 m from the model and loudspeaker. To avoid habituation of the birds to the models, we presented the Sparrowhawk and the Pygmy Owl alternately at the

Table 2. Mean nearest neighbour distances (NND, in m) to the first and the second nearest heterospecific neighbour in experimental and control areas on the basis of the first and second census. The predator presentation was done between the first and the second census. The changes of the mean NNDs (d, in m) between censuses on each study plot are printed in bold. Number of observed bird individuals refers to the variation in density between censuses.

Study areas	1st NND			2nd NND			Number of obs. individuals	
	First census	Second census	d (2nd–1st)	First census	Second census	d (2nd–1st)	First census	Second census
Experimental plots								
Korpi II	75.9	52.0	**−23.9**	94.5	79.1	**−15.4**	14	16
Käärmekuru I	52.2	36.2	**−16.0**	73.0	91.7	**18.7**	16	13
Kalikkakangas	85.5	46.0	**−39.5**	130.9	74.2	**−56.7**	11	13
Pyyryväiskangas	39.3	33.1	**−6.2**	76.1	67.4	**−8.7**	18	16
Control plots								
Korpi I	47.7	41.7	**−6.0**	66.4	65.4	**−1.0**	50	51
Käärmekuru II	39.2	58.2	**19.0**	59.9	80.5	**20.6**	23	18
Myllykoski	52.7	53.6	**0.9**	71.7	69.6	**−1.8**	23	20
Toivarinaro	37.3	41.1	**3.8**	57.0	63.9	**6.9**	20	23

chosen spots. The models were kept in view while we moved between spots, but the warning calls were not played. Locations where predators were presented were distributed evenly over the study areas, and were changed daily. We made approximately one predator presentation per hectare and day. In this manner we ensured that birds did not start to avoid the surroundings of permanent presentation spots.

The study areas were censused again one day after the last manipulation day at the same time of day and by the same person as during the first census. Weather conditions did not differ between censuses. The person carrying out the census was not aware of which of the plots was the experimental plot and which one was the control.

We measured the nearest neighbour distance (1st and 2nd NND; see Krebs 1989) to the nearest heterospecific neighbours (in m). In interpreting the census maps, an individual's nearest neighbour was determined on the basis of the place where it was first observed. If an individual moved during the census it could be the nearest neighbour of someone else. We also had a 50 m wide boundary strip around the study plots in which birds could be neighbours of individuals in the study plot, but not vice versa. Our sampling unit was the mean of the all NNDs in each study area. The change in the experimental and control plots' NND between the second and the first census was calculated to measure the birds' response to the predator presentation in the experimental plots, and these values were used in the statistical treatment. We used the Mann-Whitney U-test and one-tailed significance level to test for differences between experimental and control plots. We were entitled to use the one-tailed significance level because we tested the explicit prediction that in experimental plots NNDs would be reduced compared with the changes in control plots (see Underwood 1990, 1997, Sokal and Rohlf 1995).

Results

The changes in the mean 1st NNDs between the second and the first census were clearly different in experimental plots than in control plots. The mean distances to the 1st nearest neighbour between censuses were reduced more in experimental plots compared with those in control plots ($U = 0$, $n_{experiment} = 4$, $n_{control} = 4$, $p = 0.010$) (see Table 2), indicating that individuals had moved closer to heterospecifics after the predator presentation in experimental plots. The change in the mean distance to the second nearest neighbour between censuses did not show as clear a pattern. Distances were only slightly reduced after the predator presentation in experimental plots compared to controls ($U = 3.00$, $n_{experiment} = 4$, $n_{control} = 4$, $p = 0.075$). This result was due to one experimental plot (Käärmekuru I; see Table 2), where the difference in the 2nd NND between the censuses deviated strongly from the other experimental plots.

The density of individuals has a great impact on the NND. The more individuals there are in a study area the smaller are the distances between them. Decreasing number of individuals between censuses can make NNDs longer, if their locations in respect to others are determined purely by a random process. We tested if the manipulation affected the number of observed individuals in the study plots and so may have resulted in the changes in NNDs described above. For each species we counted the number of observations on both census occasions. We then checked in which direction (increasing, stable or decreasing) numbers changed between censuses. We made altogether 41 species observations in experimental plots and 46 observations in control plots. If changes in these would be distributed purely randomly between censuses the expected value for increasing, stable and decreasing number of species observations is 13.67 for experimental areas and 15.33

for control areas. The observed values did not differ from those expected in the experimental areas ($\chi^2 = 5.02$, df = 2, two-tailed $p = 0.081$) or in the control areas ($\chi^2 = 1.22$, df = 2, two-tailed $p = 0.544$).

Furthermore, the changes in the total number of individuals did not affect the differences in mean NNDs between censuses in an expected way, i.e. when the number of observations increased the mean NND did not decrease or vice versa (sign test: 1st NND, M = 3, two-tailed $p = 0.36$; 2nd NND, M = 3, two-tailed $p = 0.36$). Therefore, it can be concluded that the results of the experiment were not statistical artifacts of changes in the number of individuals between censuses.

Discussion

The results indicate that an increased risk of predation influences the spatial distribution of species and individuals during the breeding season. In experimental plots individuals were closer to heterospecifics after predator presentations than in control plots, suggesting that species aggregate actively. Predation risk is obviously one reason for the aggregated species pattern and for the presence of heterospecific foraging flocks during the breeding season in boreal forests, as described in Mönkkönen et al. (1996). This supports our earlier suggestion (Mönkkönen et al. 1996) that aggregations are not a consequence of the clumped occurrence of rich food patches alone. Species and individuals can, of course, gather at rich food patches, but the risk of predation can increase the aggregation of birds even more. The results also indicate that birds are able to assess predation risk and change their behaviour and space use in relation to other species accordingly.

The nearest neighbour distances were, however, relatively little reduced in the experimental plots, and the relatively long mean NNDs do not entitle us to speak of flocks in a normal sense. However, regardless of the configuration of the group, the function is possibly the same. Birds may aggregate because thereby they can better utilize one another's vigilance and alarm calls. Birds' readiness for group defence or mobbing of predators may also improve. Moreover, the structure and coherence of bird flocks differs between breeding time and winter. During the breeding period foraging flocks are quite loose, and they form and dissolve frequently. In addition, the species' tendency to join flocks varies (Mönkkönen et al. 1996). Breeding activities, such as hatching and guarding of the nest, are probably the cause of the relatively long mean distances between individuals. Nevertheless, it may be possible that aggregation is profitable at this scale too.

If distances between first nearest neighbours are reduced, there is a threshold after which the distance to their *n*th nearest neighbour should increase. This threshold refers to the scale of flocking and varies according to the size of the group, density of birds and species space use. This variation may explain why changes in 2nd NNDs did not show as clear a pattern as the changes in 1st NNDs.

During the non-breeding season the influence of predation risk on flocking behaviour is better known (see e.g. Suhonen et al. 1993, Koivula et al. 1994). Increased perceived risk of predation has been observed to increase the size of mixed-species bird flocks in winter as well as the frequency of flock-foraging in some species (Székely et al. 1989). However, Yaukey (1995) observed two kinds of response of mixed-species flocks to his experiment with simulated predation risk. After the simulated presence of a predator some flocks became tighter, but in some other cases birds ceased to flock. In wintering waders the dynamics of territoriality and flocking can be very flexible. Some wader species defend feeding territories, but after detecting a predator individuals abandon their territories and form flocks (Myers 1980, 1984, Whitfield 1987). After the danger is over, birds return to their territories. In temperate and boreal forests the territory system is usually considered to restrict the space use of breeding birds. Species may, however, be less restricted to their own territories than usually thought. Hanski and Haila (1988) found that Chaffinch males were not necessarily aggressive toward other foraging males who were in their singing territory or home range. Different species also share common space because their territories often overlap (Reed 1982, Mikkonen 1985, Haila and Hanski 1987, Timonen et al. 1994). It would also be more profitable for an individual bird to aggregate with heterospecifics than conspecifics in the breeding season, because of intraspecific competition and risk of being cuckolded. Aggregation and flocking can be costly, however (see e.g. Stinson 1980, Thompson and Thompson 1984, Sullivan 1985). The costs of aggregating are probably small in the present case, because NNDs were only slightly reduced (by 6–39 m, see Table 2), and interspecific competition is not considered to be very important process in northern regions (Järvinen 1978, 1979, Mönkkönen et al. 1990).

The results suggest that predation risk is one possible reason for positive interactions between species, which have been shown to play important roles in northern bird communities (see Mönkkönen et al. 1990, Timonen et al. 1994, Mönkkönen et al. 1996, Mönkkönen et al. in press). Bertness and Callaway (1994) suggested that positive interactions should be common in communities under high physical stress and in communities with high predation pressure.

To conclude, perceived predation risk can shape the spatial configuration of individuals and species in breeding bird communities, and is probably one reason for heterospecific foraging aggregations and clumped species distributions. Our results do not exclude the importance of food or feeding facilitation, learning of foraging skills and information sharing as the basic reasons for aggregation or flocking. The relative roles of the processes involved may be difficult to discern because variation in predation pressure or food conditions can produce a continuum of possible outcomes of species interactions (Bronstein 1994). Whether the spatial variation in the relative risks of predation has more general and widespread influence on boreal bird community structure remains a challenge for future studies.

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Effects of predation on community assembly and spatial dispersion of breeding forest birds

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Abstract. In a landscape context, nesting avian predators cause variation in predation risk with respect to the distance to their nests, which may have both direct (predation) and indirect (predation risk) effects on the prey community. We studied the community assembly and spatial dispersion of a breeding forest bird community in a structurally complex forest landscape surrounding forest-hunting sparrowhawk (*Accipiter nisus*) nests. Our sampling unit was one-ha study plots, which were divided into four subplots. We used the variance-to-mean ratio of the number of species observed within a plot to determine whether the distribution of species was clumped, random or uniform. We measured the predation risk as the inverse of the squared distance to the hawk's nest. Because predation risk is higher nearer a hawk's nest than farther away, we predicted that species would show more clumped distribution within study plots near the sparrowhawks' nests than farther away. We also expected densities and community patterns to vary with respect to predation risk. The results suggest that predation and/or its risk has a complex, and local effect on the prey community. The predation risk negatively affected the number of species and densities of birds only in the first year (1996) of study. The relationship between the density of large birds (≥ 20 g, preferred prey) and predation risk was also negative in 1996, but not in 1997, whereas the density of small birds (< 20 g) was not affected by predation risk in either year. There was no relationship between predation risk and clumping for all species together. When we analysed separately plots that contained large and small birds or large birds alone, however, increasing predation risk positively affected the index of dispersion, but only in thicket (one of the forest types), which is probably the preferred hunting habitat for sparrowhawk. The observed patterns with respect to predation risk were probably attributable to the direct and/or indirect effects of sparrowhawk predation. These results are well in line with studies made in farmlands on predator-prey interactions. In those studies, however, the effect of predators on prey communities was much stronger and extended farther in the landscape from the nest of predators than in this forest study. A possible reason for this difference is higher habitat structural complexity in forests, which may mitigate the effect of predators.

Key words: Finland; predation risk; heterospecific attraction; boreal breeding bird community; sparrowhawk; *Accipiter nisus*; species interactions vs. predation risk; community structure vs. predation risk in landscape; profitable vs. unprofitable prey.

Introduction

Predation affects natural communities through direct effects, which decrease the number of prey, and indirect effects, which result from predation risk. In avian communities, for example, predation risk may affect community assembly (number of species and their relative abundance) if species have different requirements for cover or antipredator tactics such as predator scanning or escape behavior (Pulliam and Mills 1977, Lima et al. 1987, Schluter 1988, Watts 1990, Lima and Valone 1991, Suhonen 1993). Communities are also modified by variation in predation risk if prey species avoid settling areas within high predation risk when selecting their habitats (Norrdahl and Korpimäki 1998). Predation risk has also been proposed to be one factor promoting mixed-species foraging aggregations (see, e.g., Morse 1977, Caraco et al. 1980, Berner and Grubb 1985), thus affecting species interactions.

Evidence of direct effects of predation on community structure seems to be strong in aquatic systems (Connell 1975) and, especially, in marine environments (see Sih et al. 1985). In birds, however, the evidence of effects of predation on prey populations is more scarce or contradictory (see Newton 1993 for review). Perrins and Geer (1980), for example, showed severe predation pressure of sparrowhawks (*Accipiter nisus*) on tit (*Parus* spp.) populations, but did not find any obvious effects on the population density of tits. The evidence of the effects of sparrowhawk predation on forest birds is also lacking at local (Newton et al. 1997) and nationwide (Thomson et al. 1998) scales. Predation, however, may influence populations and communities of prey species at some spatial and temporal scales. Several studies have shown that nesting avian predators can considerably diminish the abundance of their prey in the vicinity of their nests compared with more remote areas. Geer (1978) suggested that the breeding success of tits is reduced near sparrowhawk nests, probably owing to predation. Meese and Fuller (1989), Sodhi et al. (1990), Suhonen et al. (1994) and Norrdahl and Korpimäki (1998) have shown that the abundance of potential prey species decreases with closer proximity to predators' nests.

Most of these studies have been made in structurally simple environments, e.g., farmland (Suhonen et al. 1994, Norrdahl and Korpimäki 1998) or tundra (Meese and Fuller 1989). Both empirical (e.g., Crowder and Cooper 1982, Fraser and Cerri 1982, Savino and Stein 1982, Gilinsky 1984) and theoretical (e.g., Murdoch and Oaten 1975, Holt 1984, McNair 1986, Sih 1987, McLaughlin and Roughgarden 1993) studies imply that a greater structural complexity of habitats has a profound and often stabilizing effect on predator-prey interactions. It is not clear whether predation or predator avoidance have such an effect in structurally more diverse habitats, such as forests.

Prey individuals, in addition to direct avoidance of predators (Norrdahl and Korpimäki 1998), may also try to reduce their probability of being preyed upon by adjusting their spatial dispersion in relation to each other according to predation risk. Under a high predation risk, individuals may aggregate as a countermove against predation, whereas a uniform distribution could reduce the probability of predators finding them. We have earlier found that bird species in boreal forests show aggregated distribution patterns both between (Mönkkönen et al. 1990, 1997, Forsman et al. 1998a) and within habitat patches (Timonen et al. 1994, Mönkkönen et al. 1996). These aggregations are probably due to heterospecific attraction (see Mönkkönen et al. 1990), suggesting that aggregative behavior of species is active (see Mönkkönen et al. 1996). Furthermore, Forsman et al. (1998b) showed in their experiment that increasing predation risk is one possible factor inducing aggregated distributions of breeding forest birds.

In this study, we investigated the effects of a generalist, forest-hunting avian predator, the sparrowhawk, on community assembly and spatial distribution of forest birds in a structurally complex forest landscape. We tested whether the community composition of prey and the aggregated distribution of species vary together with the relative predation risk in a landscape context. We used study plots of fixed size, which were situated at different distances from nests of sparrowhawks. Because the sparrowhawk prefers prey species with body mass of over 20 g (Rytkönen et al. 1998), and profitable and unprofitable prey probably respond differently to the presence of a predator (Suhonen et al. 1994), we expected the density of profitable prey species to be more dependent on the distance to the sparrowhawks' nests than the density of unprofitable prey. A higher number of encounters with a predator probably induces heterospecific aggregations (Forsman et al. 1998b). Therefore, we predicted that species distribution would be more clumped nearer hawks' nests than farther away. The forest bird species pool, however, contains species with different sensitivies to predation risk, which may lead to behavioral differences among species. Specifically, individuals of species that are more vulnerable to a predation may be more prone to aggregate with other species than individuals of species with low risk of being preyed upon. Because the benefits of heterospecific attraction between individuals of large and small birds may differ because sparrowhawks prefer large birds to small birds as prey (Rytkönen et al. 1998), we predicted that large birds would aggregate more readily with other species than small birds.

Methods

Study landscape

Our study landscape was located near Oulu, in northern Finland (65°N, 25° 30'E), and was about 30 km^2 of heterogeneous forest. Old spruce (*Picea abies*), mixed coniferous and deciduous and Scots pine (*Pinus sylvestris*) forests, young sapling stands, and dense thickets were the most common forest types. The predominant tree species were spruce, Scots pine, birches (*Betula* spp.) and aspen (*Populus tremula*). The shrub layer in the forests was usually poorly developed and consisted mainly of saplings and occasionally willows (*Salix* spp.) or junipers (*Juniper communis*). Depending on the forest type, the field layer mainly consisted of billberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*), dwarf birch (*B. nana*), labrador tea (*Ledum palustre*) or different herbaceous species. The relief of the area is flat and forest patches are usually separated by bogs, clear-cuts or sapling stands. A few human settlements with cultivated fields are also to be found. For a more thorough description of the area see Orell and Ojanen (1983).

Study design and bird censuses

The study was conducted in 1996 and 1997. In this area, the last migrant birds arrive at the end of May. The end of May and June is the main breeding season for most birds. Sparrowhawks arrive approximately at the end of April and their breeding starts in mid-May. The nests of the sparrowhawks were located and identified on maps during May. In 1996 we found 8 nests and 5 nests were found in 1997. It is unlikely that in the central study area any sparrowhawk nest went unnoticed. Because different types of forests were usually quite closely intermixed, our sampling unit for bird censuses was a one hectare plot (square shaped, 100×100 m). Censuses were started at a corner of the plot. Using a compass we first walked along the side of the plot to an other corner. After that, we walked through the study plot along parallel lines 25 m apart. Censuses were completed at the opposite corner of the starting point. Altogether, there were five walking lines, of which three were within the plot and two were along the sides of the plot. Each plot was censused once and a fixed time of 30 min was used for each plot. Each bird observed and also its movements were marked accurately onto schematic study maps. Censuses were carried out in June and early July in both years and between 0500 and 1200 hours, in fair weather. The total number of censused plots was 206. In 1996 139 plots was censused and in 1997 67. The number of plots in thickets was 51, 68 in spruce forests, 21 in deciduous forests and 66 in mixed forests.

Selås and Rafoss (1999) found the mean ranging distance of their radio-tracked male sparrowhawks to be well over one km from the nest; therefore, study plots were located from 50 m to 1000 m from the hawks' nests. The preliminary selection of study plots was done using a map and an aerial photograph. The final decision on the placement of plots was made in the field. We tried to keep the forest type and vegetation within a plot as homogeneous as possible. The selected plots were situated at least one hundred meters apart. After a plot census was complete, we wrote a rough description of the plot's habitat and vegetation. We estimated the tree species composition and the height of the forest, and wrote a brief description of the forest structure (i.e., moist or dry, dense or sparse, etc.). Based on this information we classified study plots into four general forest types (Table 1).

Table 1. *Mean tree species composition (% of number of stems), tree height and description of forest structure of the four forest types in this study. Thicket and dense mixed forest are preferred by the sparrowhawk as breeding habitats (Sulkava 1964).*

	Tree species				
Forest type	Spruce	Scots pine	Deciduous	Height class (m)	Description
Thicket	23	32	45	10-15	Dense, moist and rather young forest.
Spruce forest	74	14	12	> 20	Usually older forest with closed canopy.
Deciduous forest	12	3	85	15-20	Fairly open, ground layer consist of different herbaceous species.
Mixed forest	48	20	32	> 20	Rather closed canopy, often with well developed ground and schrub layer.

Spatial dispersion of species was calculated within each one-ha study plot. Each study plot and schematic study map was divided into four 50×50 m subplots and we counted the number of species in each of them. We used the variance-to-mean ratio (Krebs 1989) of the number of species observed within the entire plot with respect to one subplot to measure the level of species clumpedness within each study plot. Values of this ratio refer to different spatial dispersion of species. Zero indicates uniform and one indicates random dispersion. Values indicating maximum aggregation depends on the number of observed species within a plot. Because we were studying species aggregations, we only included those plots which contained at least two species.

The distribution of predation risk

The hunting habitat selection of the sparrowhawk is affected by many factors, such as the distribution of forest types around nest and the density of prey (Marquis and Newton 1981, Selås and Rafoss 1999). Selås and Rafoss (1999) have found that the mean ranging distance of a male sparrowhawk during breeding time from the nest was well over one kilometer, and males used different areas between their nests and mean ranges in approximately equal proportions. This suggests that the predation effort of a hawk does not vary much in relation to the distance to the nest, but does vary substantially with respect to predation risk per area unit. The relationship between predation risk and distance to the nest is not linear, because the area around hawk's nest increases geometrically with increasing distance. If one moves one distance unit away from the nest, the area around the nest has quadrupled, which quickly dilutes predation risk. Therefore, we assumed that predation risk increases with decreasing distance from the nest, and more importantly, with decreasing area around the nest. We used the inverse of the squared distance to the hawk's nest ($1/r^2 \times 1000$) to describe the predation risk and intensity. The predation risk will increase strongly with decreasing distance at the very

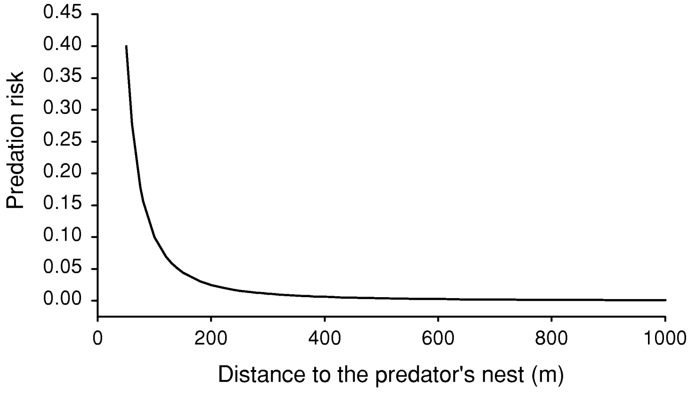

Fig. 1. The change in predation risk with respect to the distance to the nest of a predator. The risk is calculated as an inverse of a squared distance to the nest and multiplied by 1000.

neighborhood of the nest, but it is practically unchanging, roughly from 200-300 m onwards from the nest (see Fig. 1).

Statistical analyses

We used ANOVA and MANOVA when analysing the community assembly and species aggregation around sparrowhawks' nests. Forest type (see Table 1) and year (1996 and 1997) were used as factors and predation risk (risk = $1/r^2 \times 1000$) as a continuous covariate. We included in every model all the main effects of the main factors (forest type and year) and the covariate (predation risk), and all two-way interaction terms. A statistically significant interaction term between covariate and factor would indicate that the effect of predation risk is not parallel within factor levels. We tested for the univariate homogeneity of variances (ANOVA and MANOVA) and the homogeneity of covariance matrices (MANOVA) and transformed ($\sqrt{x_i + 0.5}$) values were used if needed. Because the number of observations varied among factor levels, which leads to unbalanced ANOVA-model, we used the approach suggested by Stewart-Oaten (1995). We first ran the model using Type III sum of squares (ss) to check whether there were any significant interaction terms between variables. If not, predation risk was left alone in the model and its effect was checked using Type II ss. If interaction occurred, Type II ss were not calculated. This procedure was used, because Type III sss are not very powerful for detecting main effects in an unbalanced situation. Stewart-Oaten (1995) argued that the best way to determine the true model in this situation is to simplify the model step by step and use Type II sss, if no interaction term appears to be significant.

We divided species into small birds (< 20 g) and large birds (≥ 20 g). The body masses of the species were extracted from von Haartman et al. (1963). The division between small and large birds was based on a study by Rytkönen et al. (1998). They showed that the sparrowhawk prefers more species weighing approximately 20 g or more than would be expected on the basis of their density in an area. We also tested the level of clumpedness between two types of birds based on their body mass. Therefore, we separated data into two parts, again using the body mass of species as a divide (see above). We formed two groups of plots. First group consisted of plots where both large and small birds were observed together or small birds alone (small bird plots). The second group contained plots with both small and large birds together or with large birds alone (large bird plots). We should observe a stronger relationship between the predation risk and the index of dispersion if the larger birds have a greater tendency to aggregate. This kind of division was reasonable, because the number plots that contained either only small ($n = 30$) or large ($n = 3$) birds alone were too small for ANOVA.

The distribution of sampling plots in relation to predation risk, measured as $1/r^2 \times 1000$, was very skewed with a majority of observations situated in low risk areas (risk < 0.011, distance to nest > 300 m). We therefore used a distribution-free resampling technique to further test our predictions. First, we calculated correlation coefficients of the observed values between predation risk and the dependent variables we used in ANOVA and MANOVA. We then independently resampled each variable with replacement and calculated the correlation coefficient between the resampled values of predation risk and the dependent variables. Resampling was repeated 1000 times. We then counted the number of correlations that were equal or more extreme than the observed correlation. In other words, we estimated the probability that the observed correlation arises because of chance alone. All analyses were done by SPSS 8.0. for Windows software and resamplings were done by Resampling Stats Add-in for Excel (Resampling Stats 1998).

Distribution of study plots in space and time

The predation risk index divides the data into two parts (see Fig 1). The number of plots in the neighborhood of hawk's nest (roughly 0 – 300 m from the nest), where predation risk is clearly decreasing with distance to the nest, was 48. This is much less than the 158 plots in the area of stable predation risk (300 onwards from the nest).

Temporal phase of the breeding cycle may affect birds propensity for aggregative behavior, although heterospecific foraging groups and clumped distribution have been observed throughout the whole breeding season (see Mönkkönen et al. 1996). Of the plots which were used to measure species clumpedness (157 plots, see Methods), 34 plots were within 300 m radius around the nests and 123 plots were farther away. Twenty-one of the close to hawks' nest plots were censused during the first half of June and 13 during the second half. The corresponding numbers for further away plots were 76 and 47, respectively. Thus plots were evenly distributed in time with respect to distance.

Results

Community assembly at different predation risks

Bird densities in the four forest types fell into two groups. In thickets and spruce forests, the total of the mean densities of all species were about equally low (see Table 2), whereas in deciduous and in mixed forests densities were relatively higher.

In general, there was a trend toward decreasing number of species and the density of forest birds with increasing predation risk. However, in 1996 the trend was more pronounced than in 1997 (see Fig. 2 and 3). In the ANOVA models, forest types and study years explained most of the variability in the number of species and the density of forest birds, whereas predation risk index was of minor importance (Table 3). The difference between study years was even greater when analysing bird densities. The large interaction term between predation risk and study years gave us reason to suspect that the effect of predation risk was not parallel between study years (see Table 3). Therefore, we divided data between years and we ran ANOVA for both the number of species and the density of birds.

Table 2. *Densities (pairs/1 ha) of most numerous species and their total densities in the four forest types. Average body masses of species are also given.*

Species	Forest type				Body mass (g)
	Thicket	Spruce forest	Deciduous forest	Mixed forest	
Willow warbler *Phylloscopus trochilus*	0.94	0.24	1.29	0.92	9.4
Chaffinch *Fringilla coelebs*	0.61	0.63	0.81	0.82	21.5
Siskin *Carduelis spinus*	0.14	0.35	0.14	0.25	12.6
Willow tit *Parus montanus*	0.08	0.18	0.33	0.30	11.2
Goldcrest *Regulus regulus*	0.04	0.28	-	0.21	5.5
Spotted flycatcher *Muscicapa striata*	0.16	0.12	0.24	0.15	15.4
Great tit *P. major*	0.03	0.12	0.14	0.21	17.5
Robin *Erithacus rubecula*	0.12	0.07	0.10	0.15	16.5
Pied flycatcher *Ficedula hypoleuca*	0.08	0.07	0.09	0.14	12.6
Tree pipit *Anthus trivialis*	0.02	0.10	0.05	0.03	22.1
Others	0.41	0.53	0.38	0.39	
Total density	2.63	2.69	3.57	3.59	

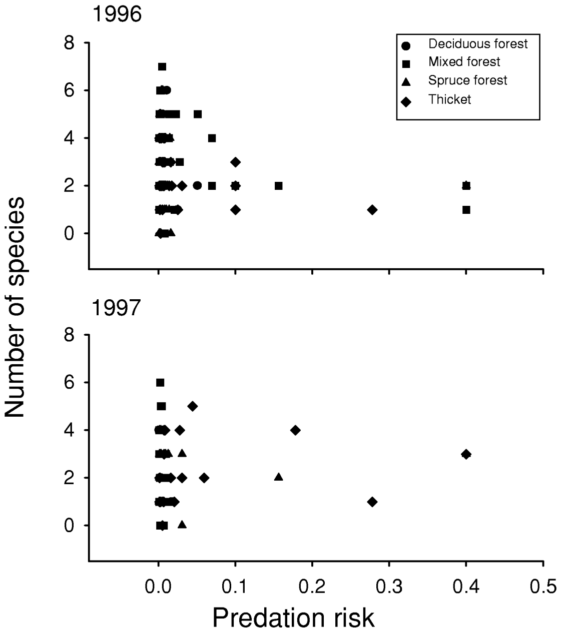

Fig. 2. The relationship of the number of species in relation to predation risk in two study years.

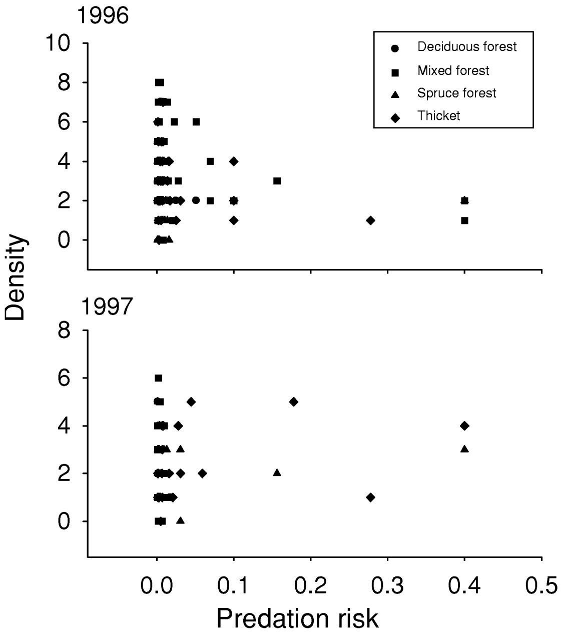

Fig. 3. The relationship of the density (pairs/ha) of forest birds in relation to predation risk in two study years.

***Table 3**. ANOVA (Type III ss) table for the the number of species and the density of forest birds. Study years and forest types were factors and predation risk (Risk, see Methods) was used as a covariate.*

Source of variation	df	MS	F	P
Number of species				
Model	12	4.17	2.07	0.021
Forest	3	7.06	3.51	0.016
Year	1	9.58	4.76	0.030
Forest×Year	3	0.78	0.39	0.762
Risk×Year	1	3.78	1.88	0.172
Risk×Forest	3	1.67	0.82	0.482
Risk	1	5.04	2.51	0.115
Error	193	2.01		
Total density				
Model	12	9.25	3.15	<0.000
Forest	3	12.08	4.11	0.007
Year	1	34.37	11.69	0.001
Forest×Year	3	1.58	0.54	0.660
Risk×Year	1	8.30	2.82	0.095
Risk×Forest	3	2.43	0.83	0.480
Risk	1	8.11	2.76	0.098
Error	193	2.94		

In 1996 the ANOVA model was significant for the number of species, and Type II ss revealed that predation risk significantly affected the number of species (Table 4). In 1997, neither the Type III ss model (df 7 ; 59, MS = 2.11, F = 1.08, P = 0.389) nor the Type II model (df 1 ; 65, MS = 0.50, F = 0.25, P = 0.618) fit the data.

The difference between years was similar in the density of forest birds as well. In 1996 the total density decreased with increasing predation risk (Table 4). In 1997 both models failed to explain variability of densities (Type III ss: df 7 ; 59, MS = 2.55, F = 1.12, P = 0.365) (Type II ss: df 1 ; 65, MS = 1.39, F = 0.59, P = 0.443).

Table 4. *ANOVA (Type III and II ss) table for the number of species and density of forest birds in 1996. Forest type was the factor and predation risk was used as a covariate. Type II sum of squares were used to determine the main effect of the predation risk.*

	Type III ss				Type II ss			
Source of variation	df	MS	F	P	df	MS	F	P
Number of speies								
Model	7	4.97	2.46	0.021				
Forest	3	7.23	3.58	0.016				
Risk×Forest	3	1.23	0.61	0.609				
Risk	1	5.22	2.59	0.110	1	9.25	4.37	0.038
Error	131	2.02			137	2.12		
Density								
Model	7	10.10	3.13	0.004				
Forest	3	15.07	4.68	0.004				
Risk×Forest	3	2.24	0.70	0.556				
Risk	1	9.47	2.94	0.089	1	19.74	5.72	0.018
Error	131	3.22			137	3.45		

Table 5. ANOVA (Type III ss) table for the multivariate and univariate solution for the density of large and small birds. Study years and forest types were factors and predation risk was used as a covariate.

Source of variation	df	Error df	Pillais value	F	P
Multivariate test					
Forest	6	386	0.074	2.47	0.023
Year	2	192	0.083	8.74	<0.000
Forest×Year	6	386	0.014	0.45	0.839
Risk×Year	2	192	0.021	2.01	0.137
Risk×Forest	6	386	0.025	0.81	0.566
Risk	2	192	0.015	1.48	0.230
Univariate tests					
Source of variation	Dependent	df	MS	F	P
Model	Large birds	12	0.34	2.48	0.005
	Small birds	12	0.44	2.10	0.018
Forest	Large birds	3	0.07	0.48	0.694
	Small birds	3	0.98	4.69	0.003
Year	Large birds	1	2.18	15.94	<0.000
	Small birds	1	0.42	2.01	0.158
Forest×Year	Large birds	3	0.05	0.39	0.759
	Small birds	3	0.11	0.54	0.658
Risk×Year	Large birds	1	0.49	3.59	0.060
	Small birds	1	0.11	0.55	0.460
Risk×Forest	Large birds	3	0.14	0.99	0.400
	Small birds	3	0.13	0.64	0.589
Risk	Large birds	1	0.23	1.64	0.201
	Small birds	1	0.30	1.44	0.231
Error	Large birds	193	0.14		
	Small birds	193	0.21		

The results of a MANOVA suggested that predation risk does not affect densities of birds of different masses, but, univariate tests between predation risk and study years in large birds suggested different responses between years (Table 5). In 1996 the relationship between densities and predation risk was negative, whereas in 1997 the pattern was less clear (Fig. 4). We therefore analysed the two years separately. Multivariate test suggested that in 1996 there might be differences in densities between bird types (see Table 6). Univariate tests (ANOVA) pinpoint variable(s) that have the strongests effect on the result of the multivariate test. The result of this analysis suggested that the effect of predation risk is not statistically very strong on either small or large birds (Table 6); however, the density of large birds was indicatively more negatively associated with predation risk than the density of small birds. In 1997 the result of the multivariate test suggested that the density of small or large birds did not vary in relation to predation risk (Type II ss: df 2 ; 64, Pillais value: 0.02, F = 0.49, P = 0.617).

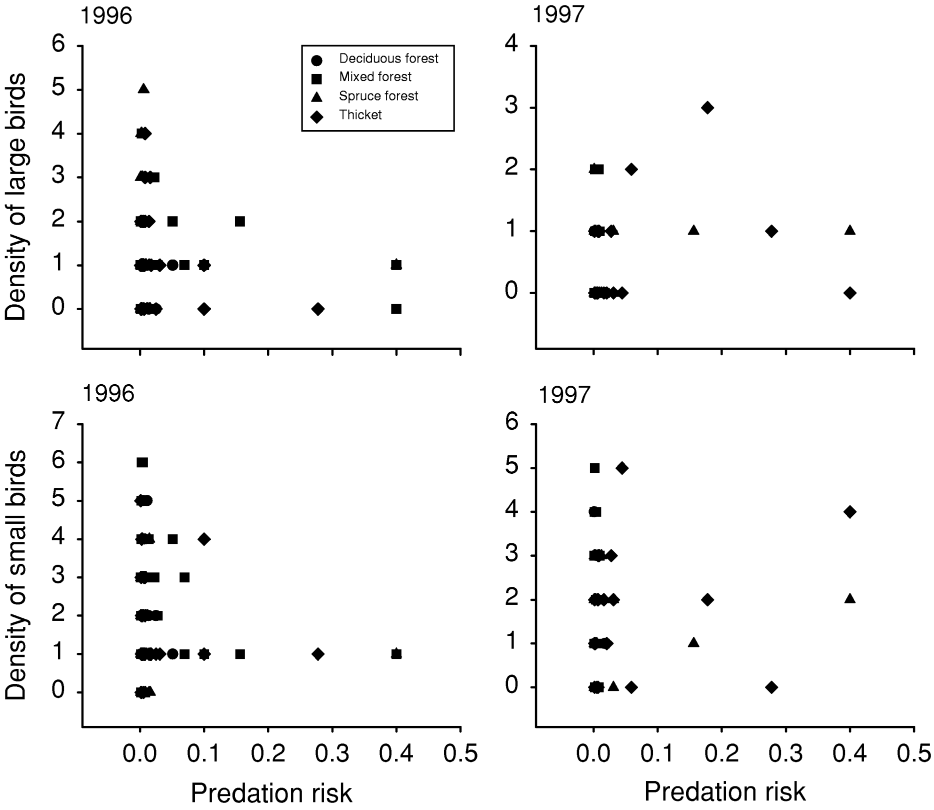

Fig. 4. Density (pairs/ha) of large (=>20 g) and small (< 20 g) birds with respect to predation risk in two study years.

Table 6. *ANOVA (Type III and II ss) table for both multivariate and univariate solutions of the density of large and small birds in 1996. Forest type was a factor and predation risk was used as a covariate. Type II ss were used to determine the main effect of the predation risk.*

	Type III ss					Type II ss				
Source of variation	df	Error df	Pillais value	F	P	df	Error df	Pillais value	F	P
Multivariate test										
Forest	6	262	0.13	3.00	0.007					
Risk×Forest	6	262	0.04	0.78	0.588					
Risk	2	130	0.02	1.67	0.207	2	136	0.04	2.63	0.076
Univariate tests										
Source of variation	Dependent	df	MS	F	P	df	MS	F	P	
Model	Large birds	7	0.18	1.17	0.326					
	Small birds	7	0.63	3.14	0.004					
Forest	Large birds	3	0.04	0.24	0.866					
	Small birds	3	1.27	6.33	<0.000					
Risk×Forest	Large birds	3	0.17	1.10	0.350					
	Small birds	3	0.10	0.47	0.701					
Risk	Large birds	1	0.30	1.95	0.165	1	0.50	3.27	0.073	
	Small birds	1	0.29	1.45	0.231	1	0.54	2.46	0.119	
Error	Large birds	131	0.15			137	0.15			
	Small birds	131	0.20			137	0.15			

The results of resamplings were consistent with the results of ANOVA and MANOVA. In 1996 all dependent variables: the number of species, total density and the densities of large and small birds correlated negatively with predation risk whereas in 1997 correlations were non-significant (Table 7). The difference between the density of small and large birds with respect to predation risk was small in this analysis as well.

Table 7. *The results of the resampling approach for the correlation coefficient between dependent variables and predation risk in both study years.* R_{obs} *refers to the observed coefficient. Significance level (P) was calculated as the number of correlations in resampled data set that were equal or more extereme than observed correlation divided by the number of repeats (1000).*

	1996		1997	
Dependent	r_{obs}	P	r_{obs}	P
Number of species	-0.095	0.014	0.062	0.705
Total density	-0.200	0.005	0.095	0.768
Density of large birds	-0.152	0.035	0.118	0.827
Density of small birds	-0.132	0.059	0.030	0.565

Spatial dispersion of species in relation to predation risk

After excluding the plots containing fewer than two species, the remaining 157 plots could be used in examining the spatial dispersion of all species with respect to the predation risk. Type III ss ANOVA model could not explain significantly the variability of the index of dispersion (df 12 ; 144, MS = 0.33, F = 0.59, P = 0.847) and there was no relationship between predation risk and the index of dispersion with Type II sss either (df 1 ; 155, MS = 0.09, F = 0.17, P = 0.684).

There were some differences in the variability of clumpedness between large and small bird plots. For small bird plots, the ANOVA model did not fit the data significantly (Type III ss: df 12 ; 141, MS = 0.32, F = 0.58, P = 0.857), and Type II ss ANOVA showed that predation risk did not have a significant effect of on the dispersion index of small birds (df 1 ; 152, MS = 0.07, F = 0.13, P = 0.717). For large bird plots, the fitted model explained significantly the variation of dispersion index (Type III ss: df 12 ; 114, MS = 1.04, F = 2.39, P = 0.009), but there was a strong interaction term between predation risk and forest types (df 3 ; 114, MS = 2.50, F = 5.77, P = 0.001), indicating that the effect of predation risk on aggregation varies among forest types. Therefore, we analysed forest types separately for large bird plots (Table 8). Among forest types, only in thickets did predation risk have a significant effect on index of species dispersion (see Table 8, Type II ss). In thickets, the values of index of dispersion at the area of low predation risk are consistently low, but increase rapidly along with predation risk (see Fig. 5). In other forest types values show more or less random or even slightly decreasing distribution with respect to predation risk (Fig. 5). However, the statistical power in this analysis was not very high because of the low number of observations in individual forest types. In thickets, there were 25 plots in the ANOVA model, and of those, eight plots were in the area near the nests (0 – 300 m from the nest).

Table 8. *ANOVA (Type III and II ss) table for the index of dispersion for plots which contained large and small birds or large birds alone in four different forest types. Year was a factor and predation risk was used as a covariate.*

	Type III ss				Type II ss			
Source of variation	df	MS	F	P	df	MS	F	P
Thicket								
Model	3	3.20	7.77	0.001				
Year	1	0.33	0.79	0.384				
Risk×Year	1	0.41	0.99	0.330				
Risk	1	5.47	13.29	0.002	1	9.09	22.88	<0.000
Error	21	0.41			23	0.40		
Spruce forest								
Model	3	0.11	0.28	0.84				
Year	1	0.18	0.43	0.515				
Risk×Year	1	0.18	0.43	0.516				
Risk	1	0.04	0.10	0.752	1	0.08	0.21	0.650
Error	34	0.41			36	0.40		
Deciduous forest								
Model	3	0.51	2.01	0.159				
Year	1	0.07	0.26	0.617				
Risk×Year	1	0.05	0.18	0.678				
Risk	1	0.03	0.12	0.732	1	0.39	1.34	0.263
Error	14	0.25			16	0.29	1.34	
Mixed forest								
Model	3	0.16	0.29	0.836				
Year	1	0.45	0.83	0.367				
Risk×Year	1	0.25	0.47	0.499				
Risk	1	0.25	0.45	0.504	1	0.01	0.03	0.871
Error	42	0.54			44	0.53		

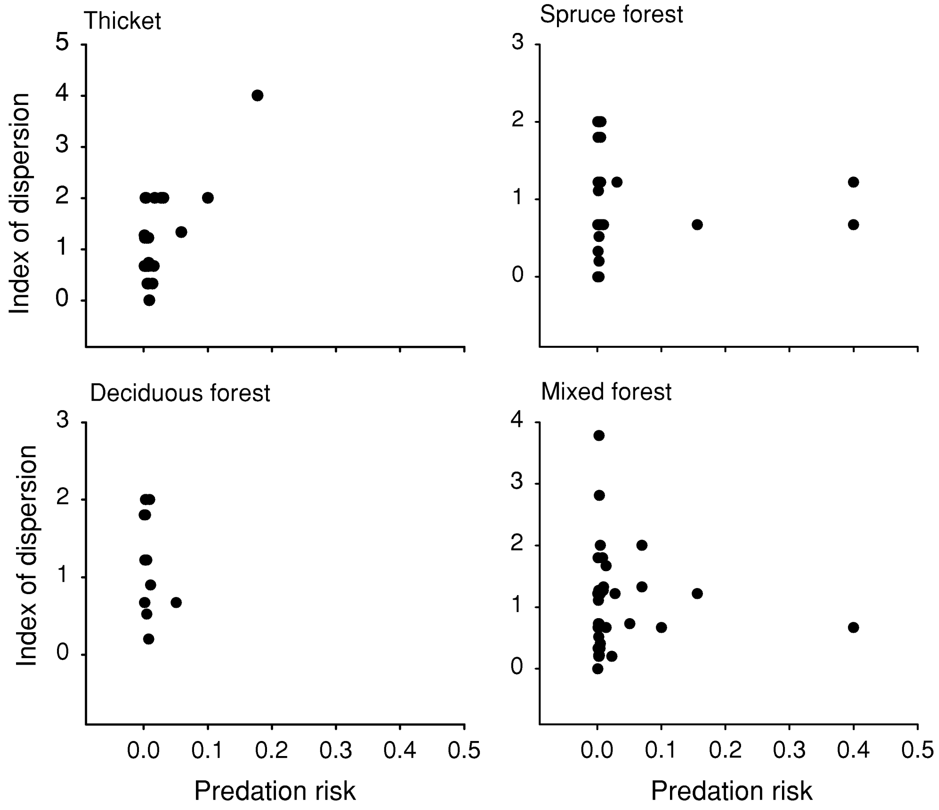

Fig. 5. The level of clumped distribution of birds in plots which contained large (=> 20 g) and small (< 20 g) birds or large birds alone in four forest types with respect to predation risk.

The results of resamplings further strengthened these results. In the thicket, the correlation coefficient between dispersion index of large bird plots and predation risk was positive and strong (Table 9). In the thicket the correlation coefficients of other bird types were positive whereas in other forest types they were negative and not statistically significant (Table 9).

Table 9. *The comparison of the correlation coefficients of the index of dispersion and predation risk between the observed and the resampled values in four forest types.* R_{obs} *refers to the observed coefficient. Significance level (P) was calculated as the number of correlations in resampled data set that were equal or more extereme than observed correlation divided by the number of repeats (1000).*

	Dependent		
Forest type	All species plot	Large bird plots	Small bird plots
Thicket			
r_{obs}	0.263	0.706	0.257
P	0.079	< 0.000	0.072
Spruce forest			
r_{obs}	- 0.070	- 0.076	- 0.074
P	0.640	0.646	0.658
Deciduous forest			
r_{obs}	- 0.301	- 0.278	- 0.301
P	0.898	0.874	0.911
Mixed forest			
r_{obs}	- 0.036	- 0.025	- 0.039
P	0.559	0.509	0.583

Discussion

The distribution of a predation risk in a forested landscape context had a strong, but very local effect on community composition and spatial configuration of breeding forest birds. The effect of hawks' presence on species richness and density was detectable only at close proximity to the nest, which was expected because of the quick dilution of predation risk with increasing distance from the nest. Our results match earlier findings of lower prey populations near predators' nests in structurally simple habitats (Meese and Fuller 1989, Suhonen et al. 1994 and Norrdahl and Korpimäki 1998), though the effect is much weaker and local than found in farmland studies. The present results suggest that predation can affect bird communities inhabiting structurally more complex forest landscapes as well (see also Sodhi et al. 1990).

Because males do most hunting at the time the study was done and they are smaller (body mass appr. 150 g) than females (appr. 260 g), the predation risk during our study was concentrated mainly on small and medium-sized songbirds, which formed the bulk of birds we censused. Therefore, it is most likely that the observed patterns are the result of direct and/or indirect effects of sparrowhawk predation. The range of detectable prey depletion around sparrowhawk nests, however, was much smaller than that found in farmland studies in Finland. In farmland landscapes the effect of kestrels (*Falco tinnunculus*) on prey density and species number extended much farther away, up to 1 km (Suhonen et al. 1994, Norrdahl and Korpimäki 1998), than was observed in our forest study. The obvious reason is that in farmlands birds can see hunting kestrels and their nest sites far away. In forests, however, both predators and prey are more hidden and responses were not as far reaching. This matches well with the results of theoretical studies (see e.g., Murdoch and Oaten 1975, Holt 1984, McNair 1986, Sih 1987, McLaughlin and Roughgarden 1993), which predict increasing heterogeneity of habitat to stabilize predator-prey interactions. Lower total densities in 1997 (2.48 pairs/ha) than in 1996 (3.33 pairs/ha) might have compelled hawks to search prey in a larger area, which could explain the observed between-year difference in the effects of predation risk on species numbers and total abundance.

Areas with fewer species and low densities in the vicinity of the hawk nest could also result from the habitat selection of prey species. Sparrowhawks settle in their territories quite early, when some prey species have not yet arrived. Late-arriving migrants can take into account the presence of a predator when selecting a profitable breeding area. The effect of a nesting predator on the habitat selection of prey species was suggested earlier by Meese and Fuller (1989), Sodhi et al. (1990) and Suhonen et al. (1994). Norrdahl and Korpimäki (1998) explicitly tested the predator avoidance hypothesis and found support for it. Avoidance of predators may also affect communities later in the breeding season. Birds that have settled in the most risky areas could move farther away from the predator’s nest for their second brood or if their first brood fails. The number of relocations of new nesting attempts due to nest predation can be considerable. For example, the nest predation rate of the chaffinch can be up to 87% of all nests, and usually a new nesting attempt is made after the predation on a nest (Hanski and Laurila 1993).

Several studies of the diet of the sparrowhawk (e.g., Sulkava 1964, Opdam 1975, 1978, Newton and Marquiss 1982) indicate that although the male and female sparrowhawk together can prey upon almost every living forest bird species, there is a clear preference for certain masses (see e.g., Selås 1993, Götmark and Post 1996, Rytkönen et al. 1998). Our results suggest that the preference of sparrowhawks for larger bird species was not very clearly reflected in the distribution of birds in the landscape with respect to the predation risk. The density of large birds (≥ 20 g) was slightly more affected by increasing predation risk than the density of smaller birds, but result was not very strong. However, the observed trend was similar to those from farmland areas (see Suhonen et al. 1994, Norrdahl and Korpimäki 1998) where only the densities of prey species profitable to the kestrel were lower near the predators' nests than farther away. In a landscape context, the areas in the immediate vicinity of hawks' nests can be special types of ecological neighborhoods where the relative proportions of species are different than in the surrounding landscape. This may have implications for the interactions between two potential competitors, if one is preferred prey and the other is not (apparent competition, see e.g., Holt 1977, 1987).

Predation risk may also directly affect the quality of species interactions. Species under high predation risk may seek protection against a mutual predator through the benefits that can be gained from aggregations (see, e.g., Morse 1977). There was no relationship between predation risk and clumpedness of all species but the pattern changed when we studied the level of aggregation separately for large and small birds. In small bird plots there was no increase in clumpedness with respect to predation risk. In contrast, in large bird plots the level of aggregation increased with the predation risk, but only in thickets. Note that the subanalyses in every forest type reduced the sample size and therefore the power of the statistical tests. Particularly the number of plots near the nest were in short supply. The distinct result in thickets from other forest types may occur, because thickets are the most preferred breeding habitat of sparrowhawk in our study area. Out of the thirteen nests in our study, nine were in thickets and four in swampy and dense spruce or mixed forests (see also Sulkava 1964 and Selås 1996). They are probably the most frequently used hunting habitats as well. The radiotelemetry studies on sparrowhawk suggest that dense and relatively young forests are preferred also as their hunting habitat (Marquis and Newton 1982, Selås and Rafoss (1999). Of the forest types in our study area, spruce and deciduous forests are relatively old or open, whereas thickets and part of mixed forests (young and dense enough) better fulfill the requirements of sparrowhawks, which hunt by ambushing prey. Therefore, it is very likely that increased clumpedness in thickets is because they are preferred nesting and hunting habitats, which results in an increased predation risk perceived by prey.

Our present results fit well with earlier studies, which showed that predation risk can induce heterospecific attraction and flocking among birds. During non-breeding season the propensity to heterospecific flocking in birds was enhanced by experimentally increasing the perceived risk of predation (Székely et al. 1989, Yaukey 1995). In the present study birds showed more aggregative pattern only at the vicinity of hawk's nest in the habitat which is probably most used by the hawk (see above). Breeding birds are probably not as free to form flocks as are non-breeding birds because of territoriality. Foraging in heterospecific flocks nevertheless also occurs during breeding season (Mönkkönen et al. 1996). Furthermore, an experiment by Forsman et al. (1998b) showed that a greater perceived risk of predation resulted in shorter nearest-neighbor distances between heterospecific breeding bird individuals within forest stands. The function of aggregation is possibly the same on all spatial scales: a higher level of aggregation provides better protection against predators.

The difference in the level of aggregation between small and large bird plots raises interesting questions about the benefits and costs of this behavior. Benefits (better protection against predation) are obviously larger than costs (e.g., increased competition) for large birds, because they are at higher predation risk and most likely dominate interspecific interactions with smaller birds. Aggregations with larger heterospecifics may confer an extra cost for small birds if this increases their risk of being preyed upon. This may result if predators more easily detect bird aggregations than alone individuals. From large birds' point of view, aggregation may spread the higher risk among larger number of individuals.

There may be other costs involved in aggregated distribution too. Hino (1998) has shown that some species that join foraging flocks change their foraging substrates and techniques in the presence of other species, which may be more costly to some species than others (Hutto 1988). Therefore, if the relative predation risk is lower farther away from a sparrowhawk nest, it may not be beneficial to join mixed aggregations. The continuous presence of a sparrowhawk around its nest would thus produce a selective environment favoring aggregated dispersion and heterospecific attraction among species, and, therefore, compensating for the possible costs. This result is consistent with the view of conditionality of community patterns and interspecific interactions (see, e.g., Schoener 1986, Bertness and Callaway 1994, Bronstein 1994). Variation in predation risk in a landscape leads to variability in interspecific interactions, and further supports the view that the intensity and importance of competition, for example, varies according to landscape structure (see, e.g., Danielson 1991). Predation risk can be seen as a factor producing heterogeneity in the landscape structure in terms of the relative quality of patches.

To summarize, our results suggest that the variation in predation risk with respect to the distance to sparrowhawk nest can locally affect the number of species and the relative abundance of prey species. The density of larger and more preferred prey seem to be slightly more affected by the predation risk than the smaller prey species. However, there was variation in the response of prey in relation to predation risk between years. Predation risk had detectable effects on species interactions, measured in the the level of heterospecific aggregation, only among large birds, in the vicinity of the nest and in the habitat which probably is most frequently used by sparrowhawk. Our results show a great variety in patterns of predator-prey interactions indicating heterogeneity and variability in the effects of predation risk among species and in different spatial and temporal scales.

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