The role of climate in limiting European resident bird populations

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Abstract

Aim To study densities of eight groups of resident forest bird populations across Europe to examine their association with abiotic (temperature, precipitation) factors.

Location Europe.

Methods Densities of residents (and migrant birds, which were used as a control group) were extracted from published breeding bird censuses. For each census location we obtained geographical co-ordinates (latitude and longitude), temperature and precipitation variables describing both breeding and non-breeding seasons. Resident densities were first examined separately in relation to co-ordinates and principal component axes, which were extracted from temperature and precipitation variables. The relative impact of each explaining factor (co-ordinates and principal component axis) on resident densities was checked by using residual examination and partial correlation.

Results Densities of resident birds were in general negatively correlated with both latitude and longitude and temperature and precipitation factors, but latitude and temperature proved to be the strongest individual factors along which resident densities varied. The higher the latitude or the lower the temperatures, the lower were the densities of most resident birds. Partial correlation analysis suggested that of those two factors, latitude was the dominant one. Both the density of resident and migrant birds decreased towards the north, but the decrease of residents was steeper, and in the north they comprised only a small fraction of breeding bird numbers, whereas further south they commonly comprise half of the breeding bird numbers.

Main conclusions The best explanatory factor for resident densities was latitude. For this reason, it was difficult to separate the relative effect of each individual factor, because latitude partly describes all the original variables (temperature and precipitation). The results suggested that precipitation was of less importance and that the interplay between latitude and ambient temperatures was not the sole factor behind the strong effect of latitude. We suggest that the coupled effect of harshening climate and decreasing amount of available energy with increasing latitude is limiting the population sizes of resident birds. We also propose that the effect of those factors is most apparent in northern Fennoscandia, where resident densities are suggested to be lower than would be expected on the basis of summer time carrying capacity.

Keywords
Biogeography, population limitation, population density, climate, abiotic factors, latitude, forest birds, Europe.

INTRODUCTION

The role of abiotic factors, such as climate, affecting the distribution and abundance of species is acknowledged to be potentially important but rarely affecting in isolation from biotic factors, such as competition and predation (Brown & Lomolino, 1998). However, the relative importance of abiotic and biotic factors may vary among environments. Dobzhansky (1950) and MacArthur (1972) suggested that abiotic stress is a major factor affecting abundance and distribution of animals at high latitudes, whereas biotic interactions are of more importance further south. Andrewartha & Birch (1954) also specified weather, together with food and other animals, to be one of the most important elements of environment affecting animal numbers. Later authors have emphasized that climate *per se* does not regulate populations, but together with density-dependent factors such as competition for territories or food resources, may affect population sizes and fluctuations (e.g. Lack, 1954; Begon & Mortimer, 1986; Cappuccino, 1995; Turchin, 1995). Nevertheless, climate has been shown to be important factor determining distributional ranges of a wide variety of organisms (Heino, 2001), and especially in some insect populations it may have substantial effect on population sizes and fluctuations (Kingsolver, 1989; Solbrek, 1995). Another puzzling question has been the most critical season of population regulation. Lack (1954, 1966) proposed that scarcity of food during late summer or winter is the bottle-neck season for temperate zone birds. Since then the importance of winter conditions for population limitation has remained a dominant view (see e.g. Fretwell, 1972; Newton, 1998; but see Martin, 1987).

The role of winter as a critical season for population limitation has sprung up a number of studies with somewhat contradictory results. Some studies have indeed found that winter temperatures are positively correlated with the population density of the following breeding season (Kluyver, 1951; Von Haartman *et al.*, 1967; Hildén, 1982; Nilsson, 1987), whereas in others there have been no apparent correlations (Lack, 1966; von Haartman *et al.*, 1967). Mortality of resident birds has also been found to correlate with winter temperatures (Gibb, 1960; Nilsson, 1987) whereas in some other studies the association has been relatively weak (Lahti *et al.*, 1998) or negligible (Perrins, 1965; Lack, 1966; Loery & Nicholls, 1985). On the other hand, almost every study with supplemental winter food provisioning has resulted in an enhanced survival or breeding density (Krebs, 1971; Yom-Tov, 1974; Van Balen, 1980; Jansson *et al.*, 1981; Källander, 1981; Brittingham & Temple, 1988; Desrochers *et al.*, 1988; Hogstad, 1988; Lahti *et al.*, 1998; but see Krebs, 1971; Yom-Tov, 1974) suggesting that the amount of available food coupled with winter climate is an important factor limiting population densities.

Studies conducted at the local scale are crucial in determining the mechanism and timing of the population regulation. However, their temporal scale is usually rather short and the extremity of conditions at the time of the study may have qualitative effects on the results. Consequently, the results of local studies do not lend themselves as such to make inferences about long-term effects of climate on populations and to the big picture of large-scale covariation between climate and abundance of species. More insight into the effects of climate on resident bird populations could perhaps be gained from a larger scale approach in which densities of birds are examined against climatic variables.

Existing indirect evidence suggests that the populations of resident birds are negatively correlated with the severity of winter. MacArthur (1959) was the first to note that in the north, migrants constitute a greater proportion of the total individuals than of the total number of species, whereas in the south the trend is reversed. Patterns in resident/migrant proportions are especially obvious in Europe where the proportion of the abundance of migrant species in breeding assemblages increases from low to high latitudes (Herrera, 1978; Helle & Fuller, 1988; see also MacArthur, 1959 and Willson, 1976 for North American patterns). MacArthur (1959) suggested that high annual turnover in bird assemblages is due to seasonality of food resources. Seasonality, and especially the conditions of the non-breeding season, has been suggested to limit resident bird populations, which in turn would explain the increasing proportion of migrants with increasing latitude (Herrera, 1978). However, so far resident populations have been studied only at the local scale (see refs. above) and the geographical population trends in relation to climate have gone uncovered.

In this study, we examined the densities of eight European resident forest bird species or species groups in relation to geographical location and climate. We included climate variables describing the conditions of both breeding and non-breeding season. Breeding season was also included because cool summer temperatures (Kluyver, 1951; Orell & Ojanen, 1983a,b) and high rainfall (Kluyver, 1951) have been observed to increase nestling mortality of resident birds and food limitation may also occur during summer, affecting the reproductive success of birds (Martin, 1987). The chosen resident forest birds include a wide variety of species with different body masses, nesting and feeding habits and their distribution covers Europe from Mediterranean to northern Lapland. Due to the overwhelming evidence suggesting the importance of winter as a bottle-neck season for resident birds, we expected that the density of residents would decrease with increasing harshness of winter and increasing latitude, which can be considered as a good surrogate for important factors, such as climate and food supplies (Newton & Dale, 1996). In summer, at the time of the reproductive output, both residents and migrants are affected by the same conditions. Therefore, we used the density of migrant birds as a control group to examine whether resident populations are lower than would be expected on the basis of summer-time productivity in some part of Europe. We also used the proportion of residents in breeding bird numbers to examine the inverse trend between proportion and latitude suggested by Herrera (1978) and Helle & Fuller

(1988). Geographical and climate variables are always strongly intercorrelated and we also made an attempt to discern the relative effects of climate from geographical co-ordinates.

DATA AND METHODS

Census data and geographical and climate variables

Bird census data was collected from published and one unpublished census results (see Appendix 1). To keep the data set as homogeneous as possible, we selected only censuses conducted in mature forests. Tree height (>20 m) and/or the age (>100 years) of the forest were used as criteria. In addition, we excluded censuses conducted in high-elevation areas (>500 m above sea-level) because of their peculiar climate conditions compared with the prevailing climate of the area and birds' possibility to move to lower altitudes for the winter. Bird assemblages of mature forests provide a consistent 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 the habitat, censuses were categorized into three broad forest types: coniferous, deciduous and mixed forests. If censuses were carried out over several years, average densities of species were calculated.

We extracted from the censuses, densities (pairs/10 ha) of eight resident species or species groups (see Table 1) and density of migrant birds. All other species not mentioned in Table 1 were considered as migrants, except the starling (*Sturnus vulgaris* Linnaeus), which was excluded from the data because of its habit of foraging in open areas and therefore not being a true forest bird. Density of migrants was used as a control group for residents in examining the impact of winter conditions on population density in relation to summer carrying capacity. We also used the pooled density of residents and migrants to describe the total density of forest birds to examine the proportion of resident bird numbers of the breeding community across Europe. We chose the resident birds from the Fennoscandian point of view, meaning that members of the eight groups occur,

and are residents across the whole Europe up to northern Lapland (except the nuthatch, *Sitta europaea* L.) and this therefore makes the comparison feasible. Many species that are migrants in Fennoscandia, such as many thrush species and finches, are partial migrants or residents in western or Central Europe. The focal species include practically all bird species that are mainly residents in Europe and for which commonly used census methods provide reliable density estimates. However, part of the populations in some species, such as in blue tit (*Parus caeruleus* L.) and nuthatch, migrate in the fall. Especially in the goldcrest (*Regulus regulus* L.) the proportion of migratory individuals is related to latitude (Hildén, 1982). Nevertheless, the main strategy for non-breeding season in those birds is residency, and migrations are not as regular and far ranging as true migratory birds. Thus, those species can be safely considered as residents in the context of the scale of this study. Resident groups provide a wide variety of body masses from the goldcrest, with body mass about 6 g, to the jay (*Garrulus glandarius* L.) weighing roughly 450 g. Titmice species (*Parus* spp.) were divided into two groups: hoarding and non-hoarding species, because differences in food caching behaviour may affect their response to winter climate.

Censuses were made using four different census methods: mapping (Enemar, 1959), line transect (Merikallio, 1946; Järvinen & Väisänen, 1983), point count (Blondel et al., 1970) and single visit study plot (Palmgren, 1930) methods. In order to test whether the density of species varied among census methods, Europe was divided into three subregions and comparison of densities was made within each subregion. The area north of 60° latitude formed northern Europe and western Europe consisted of Great Britain and western France (west of 2°E). The rest of Europe was regarded as Central Europe. Western European censuses were all mapping results. In northern and Central Europe, methods were more variable but the results of the Kruskal–Wallis tests suggested that density estimates did not vary among methods (all P-values <0.08). Therefore, we pooled the censuses over the census methods. The total number of the censuses was sixty-five. They covered Europe from southern France to Finnish Lapland and from Great Britain to western

Table 1 Resident species or species groups in the study and their general ecology

Family or subfamily	Species	Nest	Diet
Paridae, hoarding	*Parus palustris, P. montanus, P. cinctus, P. cristatus, P. ater*	Cavity	Insects, seeds
Paridae, nonhoard.	*P. caeruleus, P. major*	Cavity	Insects, seeds
Sittidae	*Sitta europaea*	Cavity	Insects, seeds
Certhiidae	*Certhia familiaris, C. brachydactyla*	Crevice on tree trunk	Insects, seeds
Sylviidae	*Regulus regulus, R. ignicapillus*	Open cup	Insects
Fringillidae	*Pyrrhyla pyrrhula*	Open cup	Seeds, buds
Corvidae	*Garrulus glandarius, Perisoreus infaustus*	Open cup	Omnivorous
Picinae	*Picus canus, P. viridis, Dryocopus martius, Dendrocopos major, D. medius, D. leucotos, D. minor, Picoides tridactylus*	Cavity	Insects, ants, seeds

Russia. The number of censuses varied among species groups because some studies had not taken into account Corvidae or Picinae. The analyses on *S. europaea* were restricted to censuses made below sixtieth latitude because of the more southern distribution range of this species.

We compiled from each census location geographical co-ordinates (latitude and longitude) and a set of climatic variables, which may potentially affect population sizes through mortality or breeding success. We kept the list of the factors as short as possible because they are usually intercorrelated and a large number of independent factors would complicate the interpretation of the results substantially. Mean temperature of the coldest month (January), the average temperature of the whole year and as well as the average temperature of the breeding season (April–June) describes the thermal conditions of both breeding and non-breeding period. Precipitation during the breeding season and the total annual precipitation were chosen to portray moisture conditions. Temperature and precipitation data were extracted from the Climatic Atlas of Europe (Anonymous, 1970), which shows climatic variation as contour maps. If the census location was between contours, its value was estimated by using the distance to the nearest contour.

Statistical analyses

The chosen geographical and climatic variables were strongly intercorrelated (all *P*-values of the Pearson correlation coefficients were <0.000). In addition, our variables included two rather different sets of factors. Geographical co-ordinates are surrogate factors along which a wide array of biotic and abiotic conditions changes. Temperature and precipitation, however, are variables, which describe the conditions of each census location and may directly or indirectly affect bird abundances. Therefore, we analysed the data in two parts. First, we separately analysed the association of resident birds with latitude and longitude. Secondly, we examined the distribution of resident densities in relation to climate factors. However, as the climatic variables were intercorrelated, we performed a factor analysis to condense the variation in the original temperature and precipitation variables into a few uncorrelated principal components. Factor analysis was performed on the correlation matrix because the scale, on which variables were measured, varied. We used unrotated principal component solution. Factor analysis results in principal component scores for each census location on each extracted principal component, which describe the temperature and precipitation conditions of the location. Principal component scores were further used in the analyses.

To describe the association of each resident group with each of the explaining factor (latitude, longitude and the principal components), we fitted both linear and second-degree polynomial (quadratic) regression model between resident densities [$\log_{10}$-transformed, $\log_{10}(x_i + 0.5)$] and the explaining factors. The statistically most significant model was chosen to depict the relationship between density of residents and the factor. To separate the relative effect of each factor and to find the strongest factor explaining density variation of each bird group, we used residual examination. Density variation was first explained by one of the factors and in the next step remaining residual variation was explained by the other factor. Then the order of the factors was changed and the same procedure was repeated. Geographical co-ordinates and principal components were examined separately. If there was a linear relationship between density variation and a factor, we used an ANOVA model to explain density variation and producing residuals. Forest type (coniferous, deciduous and mixed forest) was included in the model as a fixed factor. Latitude, longitude or principal component scores were included in the model as continuous covariates. We included, in every model, all main effects and an interaction term between the factor and the covariate. A statistically significant interaction term between a covariate and a factor would indicate that the effect of covariate is not parallel among forest types. The residuals produced by the ANOVA were then explained by the other factor in a linear or quadratic regression model. If there was a nonlinear relationship between resident density and a factor, residuals were produced by the quadratic regression model after which they were explained by the ANOVA model described above.

Climate, among other things, changes along latitude and longitude. Therefore it is difficult to distinguish what or which is/are the main factor(s) behind the patterns. We made an effort to discern the effect of separate factors by employing a partial correlation analysis. Latitude and the first principal component were the strongest factors explaining variation in density. Therefore, we correlated densities of residents against both factors while keeping one of the factors constant.

RESULTS

General climate and density patterns in Europe

Europe covers about 40° of latitude and longitude, which results in a substantial variation in climate conditions. In all respects, northern Europe has the most extreme conditions during breeding and non-breeding time. Winter and annual temperatures are lower and precipitation is smaller in northern Europe than in the rest of Europe (Table 2). For example, in northern Europe the average temperature in January is about −10 °C, whereas elsewhere it is close to 0 °C. Western Europe is characterized by mild and benign temperature conditions with rather high amount of precipitation. Differences in temperatures and precipitation between central and western Europe are not big, but conditions are clearly more continental (drier, cooler winters and hotter summers) in Central Europe (see Table 2).

There is substantial variation in the density of resident birds in Europe too. However, the amplitude of the range depends on the species group. The general trend was very clear: densities were considerably lower in northern Europe in all groups, except in the *Pyrrhyla pyrrhula* (L.) whose abundance is low everywhere (Table 3). Densities in central

Table 2 The average temperature (°C) and total precipitation (mm) variables in different subregions in Europe. The values in the brackets indicate the standard deviation of the mean

	Locality		
Variable	Northern Europe	Central Europe	Western Europe
Temperature, January	−9.60 (3.70)	−2.12 (3.04)	3.50 (0.50)
Temperature, breeding	5.90 (1.60)	11.70 (1.50)	11.40 (0.80)
Temperature, year	1.90 (2.20)	7.72 (1.92)	9.70 (0.50)
Precipitation, breeding	100 (20)	160 (50)	140 (60)
Precipitation, year	530 (120)	740 (220)	830 (340)

Table 3 The average densities (pairs/10 ha) of resident birds and total density of forest passerines in three regions in Europe

	Locality		
Residents	Northern Europe	Central Europe	Western Europe
Paridae, hoarding	1.18 (1.09)	3.92 (3.64)	3.85 (2.14)
Paridae, non-hoarding	0.73 (1.48)	8.00 (6.35)	10.10 (10.91)
S. europaea	–	1.87 (2.13)	1.17 (1.39)
Certhia spp.	0.32 (0.59)	2.30 (1.78)	1.65 (1.34)
Regulus spp.	0.96 (1.17)	3.44 (4.43)	0.98 (1.66)
P. pyrrhula	0.25 (0.41)	0.20 (0.33)	0.38 (0.58)
Corvidae	0.09 (0.17)	0.54 (0.57)	0.39 (0.28)
Picinae	0.12 (0.28)	1.90 (1.64)	0.68 (0.54)
Total density	22.84 (19.67)	65.00 (32.32)	48.06 (20.97)

The values in the brackets indicate the standard deviation of the mean. For further explanations see the text.

and western Europe were usually three- to sevenfold compared with northern Europe. Largest difference was observed in non-hoarding titmice where average densities were fourteen-fold in western Europe compared with the north (Table 3). Differences between central and western Europe were somewhat modest, densities being generally slightly higher in Central Europe (Table 3).

Geographical location and resident densities

Densities of resident birds varied inversely in relation to both latitude and longitude, and especially latitude explained a considerable amount of variation of resident bird densities in Europe (Fig. 1 and Table 4). Associations between density and latitude were clearly linear (except in *S. europaea*) and latitude explained close to 50% or more of the variation in every group except *S. europaea*, *Regulus* spp. and Corvidae. *Pyrrhyla pyrrhula* was the only species in which density was invariably low across the whole Europe, it had no variation, whatsoever, in relation to latitude (Fig. 1) and longitude and was excluded from further analyses. Patterns in the variance of density along latitude were also very similar in almost every group: density variance was low at high latitudes and burst suddenly below sixtieth latitude (Fig. 1). The explanatory power of longitude was smaller than that of latitude. Longitude explained about half of the variation of the non-hoarding titmice but clearly less in other groups (Table 4). Densities also varied more curvilinearly with longitude than with latitude. Densities of non-hoarding titmice, *S. europaea* and Picinae were low in western Europe,

reached their peak in Central Europe and decreased again towards east (Table 4).

Of the geographical co-ordinates, latitude was clearly the dominant factor. The ANOVA model in which latitude was a covariate and forest type a factor, explained significantly the density variation of every resident bird group (Table 5). Not surprisingly, latitude was the most important individual variable in the model, and forest type had some importance for hoarding titmice and Picinae only (Table 5). *S. europaea* was the only resident that had a nonlinear distribution with respect to latitude (regression equation: $y = -9.93 + 0.44x - 0.005x^2$, $F = 4.90$, $P = 0.013$, $R^2 = 0.22$) peak densities occurring in Central Europe. After removing the variation explained by the ANOVA model (see Table 5) (or for *S. europaea*, by the quadratic regression model), longitude only had a very modest explanatory power for the remaining residuals (range of the R^2 among residents 0.1–9.0%). Longitude explained best, although not statistically significantly, only the residual variation of the non-hoarding titmice ($y = -0.05 + 0.02x - 0.01x^2$, $P = 0.063$, $R^2 = 0.09$) and Picinae ($y = -0.13 + 0.02x - 0.001x^2$, $P = 0.086$, $R^2 = 0.08$), which showed unimodal distribution in relation to longitude. When first removing the effect of longitude, latitude was still able to explain significantly the residual variation in every bird group except *S. europaea* (range of the R^2 of latitude 6–32%, results are not shown). Thus, although resident bird densities correlated with both latitude and longitude, latitude was clearly the dominating factor along which resident bird populations linearly decreased towards higher latitudes. The relatively weak effect of longitude is explained
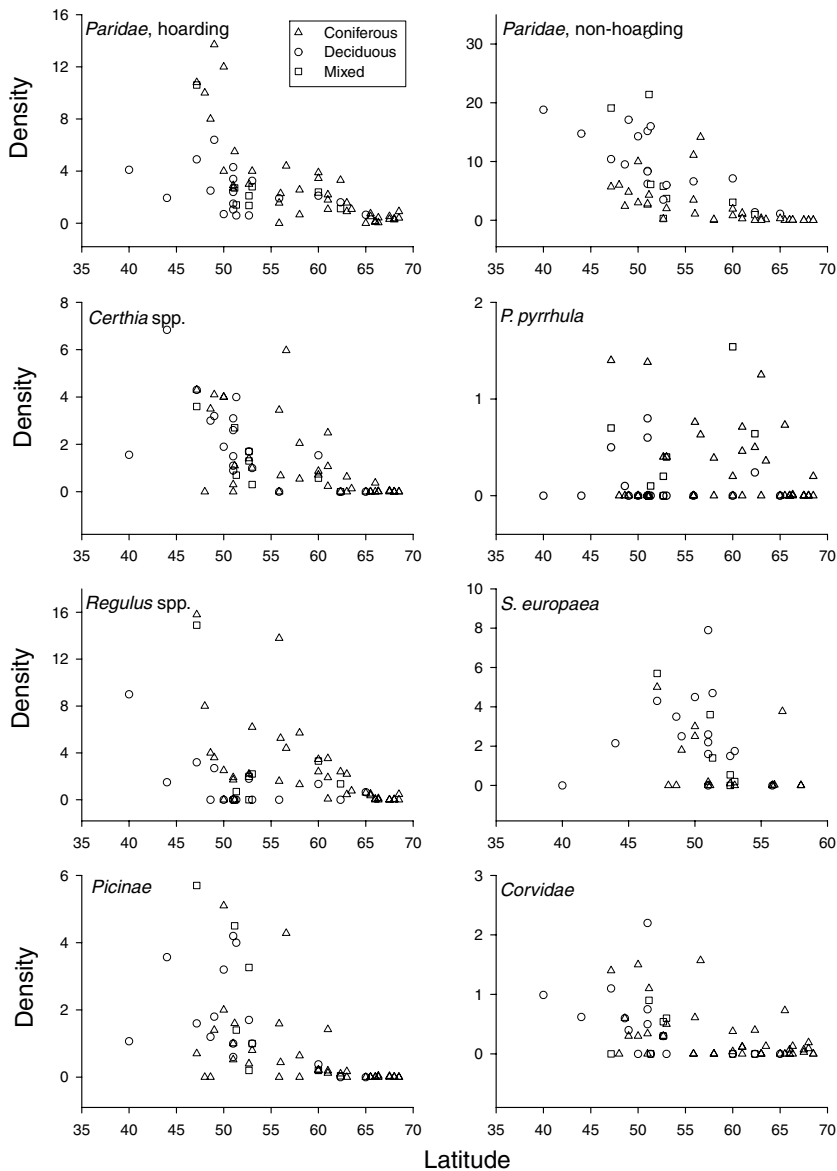
Figure 1 Densities of resident species or species groups in relation to latitude.

partly by the distribution of our census results (and the shape of Europe). Our data points were located on an SW–NE axis ranging from southern France to Finnish Lapland, which means that moving eastwards automatically increases latitude. However, regardless of that, longitude had some importance for the non-hoarding titmice and Picinae. To sum up, densities of most resident birds were inversely associated with latitude and longitude, but latitude was the most significant individual factor explaining density variation in Europe. Longitude and forest type has some importance for some groups but they were clearly of minor importance.

The distribution of sampling units in the geographical space may also have its own impact on results through spatial autocorrelation (see Haining, 1990; Legendre, 1993; Lennon, 2000). The effect of spatial autocorrelation on the interpretation of the results is strongest if the spatial structure of the data is a continuous lattice (Lennon, 2000). In our data, the distribution of census locations was widely and irregularly scattered across Europe and the temporal distribution of censuses ranged from 1950s to 1990s, which will minimize the impact of spatial autocorrelation on our conclusions. In addition, Badgley & Fox (2000) showed that after removing the effect of certain climate factors, as we did here, from the distribution of North American species' number, the remaining residuals did not show any spatial autocorrelation.

Climate and resident densities

Factor analysis extracted two principal components, which together explained 92.67% of the total variance, of which,

Table 4 The best either linear or second-degree polynomial regression model explaining density variation of resident birds along latitude and longitude

| Residents | Best fitting model | | | | | |
	Latitude	P	R^2	Longitude	P	R^2
Paridae, hoarding	$y = 2.04 - 0.03x$	<0.000	0.48	$y = 0.79 - 0.02x$	<0.000	0.34
Paridae, non-hoarding	$y = 3.51 - 0.05x$	<0.000	0.66	$y = 0.95 + 0.004x - 0.001x^2$	<0.000	0.51
S. europaea	$y = -9.94 + 0.44x - 0.005x^2$	0.013	0.22	$y = 0.30 + 0.02x - 0.001x^2$	0.271	0.07
Certhia spp.	$y = 1.81 - 0.03x$	<0.000	0.51	$y = 0.51 - 0.01x$	0.001	0.18
Regulus spp.	$y = 1.37 - 0.02x$	0.002	0.14	$y = 0.50 - 0.01x$	0.053	0.06
Corvidae	$y = 0.62 - 0.01x$	<0.000	0.27	$y = 0.21 - 0.006x$	0.001	0.17
Picinae	$y = 1.54 - 0.02x$	<0.000	0.46	$y = 0.30 + 0.01x - 0.001x^2$	<0.000	0.24

R^2 is the coefficient of determination of the model.

Table 5 ANOVA table showing resident bird densities explained by latitude (covariate) and forest type (factor)

Residents	Source of variation	d.f.	MS	F	P
Paridae, hoarding $n = 65$	Model, $R^2 = 0.62$	5	0.67	19.07	<0.000
	Forest type	2	0.21	5.97	0.004
	Latitude	1	0.87	24.85	<0.000
	Forest type × latitude	2	0.16	4.58	0.014
	Error	59	0.04		
Paridae, nonhoarding $n = 65$	Model, $R^2 = 0.76$	5	2.11	37.25	<0.000
	Forest type	2	0.03	0.51	0.606
	Latitude	1	2.33	41.01	<0.000
	Forest type × latitude	2	0.02	0.35	0.709
	Error	59	0.06		
Regulus spp. $n = 65$	Model, $R^2 = 0.37$	5	0.57	6.78	<0.000
	Forest type	2	0.11	1.27	0.289
	Latitude	1	0.59	7.03	0.010
	Forest type × latitude	2	0.05	0.64	0.531
	Error	59	0.08		
Certhia spp. $n = 65$	Model, $R^2 = 0.52$	5	0.50	12.67	<0.000
	Forest type	2	0.09	0.24	0.790
	Latitude	1	1.05	26.88	<0.000
	Forest type × latitude	2	0.01	0.28	0.756
	Error	59	0.04		
Corvidae $n = 62$	Model, $R^2 = 0.30$	5	0.06	4.74	0.001
	Forest type	2	0.06	0.46	0.636
	Latitude	1	0.11	8.68	0.005
	Forest type × latitude	2	0.01	0.48	0.619
	Error	56	0.01		
Picinae $n = 61$	Model, $R^2 = 0.54$	5	0.41	12.69	<0.000
	Forest type	2	0.10	3.26	0.046
	Latitude	1	1.01	31.62	<0.000
	Forest type × latitude	2	0.09	2.85	0.066
	Error	55	0.03		

Variables n and R^2 denote the number of census results and the coefficient of determination of each model, respectively.

the first principal component (PC 1) alone accounted for 71.36%. The PC 1 was interpreted to depict primarily temperature, but also precipitation in a lesser extent, whereas the second principal component (PC 2) clearly described precipitation across Europe. High negative loadings on the PC 1 described cold winters, relatively low mean annual and breeding time temperatures and small precipitation, whereas high positive loadings referred to mild winters, warm summers and relatively moist conditions (Table 6). High positive loadings on PC 2 indicate high annual and breeding time precipitation whereas negative loadings depict drier conditions (Table 6).

Table 6 Loadings of the original variables on the two principal components extracted by the factor analysis

	Principal component loadings	
Variables	PC 1	PC 2
January temperature	0.90	−0.34
Breeding period temperature	0.92	−0.28
Mean annual temperature	0.93	−0.35
Breeding period precipitation	0.73	0.61
Annual precipitation	0.72	0.61

Principal component 1 was clearly the major explaining factor. Densities of residents correlated linearly and positively with increasing temperatures, and the fitted regression model was able to explain relatively large proportion of the density variation among residents (Table 7). In other words, low densities were associated with cold winters, low average annual temperatures and cooler, drier summers. When moving along PC 1 towards milder winters and warmer, moister summers, the densities of residents increased simultaneously (Fig. 2). Patterns in the variance of density followed the same pattern as in latitude: variance was very low with harsh winter conditions and relatively cool summers and burst suddenly when conditions became more benign (Fig. 2). The only exception was again *P. pyrrhula*, in which densities did not vary along either principal components, and it was again excluded from further analyses. PC 2, describing precipitation, was able to explain significantly the variation of both titmice groups, *Certhia* spp. and *Regulus* spp. but the explanatory power of the regression models was relatively weak (Table 7). Distribution of many resident groups was curvilinear on PC 2; densities being higher at relatively moist and dry conditions whereas lowest densities were found at intermediate precipitation conditions (Table 7).

Fitted ANOVA model (forest type as a fixed factor and PC 1 scores as a covariate) explained over 40% of the variation of most resident densities and even over 70% of the variation of non-hoarding titmice (Table 8). Poorest fit was for *S. europaea* and Corvidae and even then, the model

explained 30% and 22% of variation, respectively (Table 8). PC 2 was of importance for some residents too and it was able to explain significantly the unexplained residual variation after PC 1 was accounted for in the non-hoarding titmice, *Certhia* spp. and Picinae, and to a lesser extent, in *Corvidae* (see Fig. 3) (range of the R^2 of PC 2 among groups 0.0–14%). Residuals of the non-hoarding titmice, *Certhia* spp. and Corvidae were negatively correlated with the precipitation whereas Picinae had a unimodal relationship with increasing precipitation (Fig. 3). When first removing the effect of the PC 2, PC 1 accounted for a significant proportion of the unexplained residuals in every resident group except *S. europaea* (range of the R^2 of PC was 1 17–53%, results are not shown).

To sum up, temperature was the primary factor along which densities of resident birds varied. The colder the climate (winter and summer), the lower densities were. Precipitation correlated negatively with some groups but its significance was clearly smaller than that of the temperature factor.

Relative importance of latitude and climate

As we emphasized earlier, climatic variables and geographical co-ordinates were highly correlated and therefore their relative importance is difficult to judge. For example, PC 1 was correlated with both latitude ($r_{Pearson} = -0.95$, d.f. = 65, $P < 0.0000$) and longitude ($r_{Pearson} = -0.80$, d.f. = 65, $P < 0.0000$). We used partial correlation between the two strongest factors (latitude and the PC 1) to examine the relative importance of those factors. Longitude and the PC 2 were not considered because their explanatory power was marginal and because of their several nonlinear associations with resident densities. *Sitta europaea* was also excluded from the analyses because of its nonlinear association with latitude. The results of the partial correlation analysis suggested that latitude was clearly the dominant factor. While holding latitude constant, PC 1 did not correlate with densities of any of the seven resident bird groups, whereas latitude had a negative correlation with every bird group except hoarding titmice and *Regulus* spp. (Table 9).

The importance of latitude on density of resident birds was again emphasized when we compared the relationship

Table 7 The best either linear or second-degree polynomial regression model explaining density variation of resident birds along PC 1 and PC 2

Residents	Best fitting model					
	PC 1	P	R^2	PC 2	P	R^2
Paridae, hoarding	$y = 0.47 + 0.20x$	<0.000	0.48	$y = 0.38 - 0.06x + 0.09x^2$	0.003	0.17
Paridae, non-hoarding	$y = 0.55 + 0.37x$	<0.000	0.62	$y = 0.41 - 0.22x + 0.14x^2$	0.001	0.22
S. europaea	$y = 0.18 + 0.20x$	0.047	0.11	$y = 0.39 + 0.11x - 0.04x^2$	0.147	0.10
Certhia spp.	$y = 0.29 + 0.18x$	<0.000	0.41	$y = 0.24 - 0.09x + 0.05x^2$	0.045	0.10
Regulus spp.	$y = 0.34 + 0.14x$	0.002	0.19	$y = 0.24 - 0.07 + 0.10x^2$	0.006	0.15
Corvidae	$y = 0.11 + 0.06x$	<0.000	0.21	$y = 0.11 - 0.02x$	0.164	0.03
Picinae	$y = 0.24 + 0.16x$	<0.000	0.41	$y = 0.23 - 0.04x$	0.282	0.02

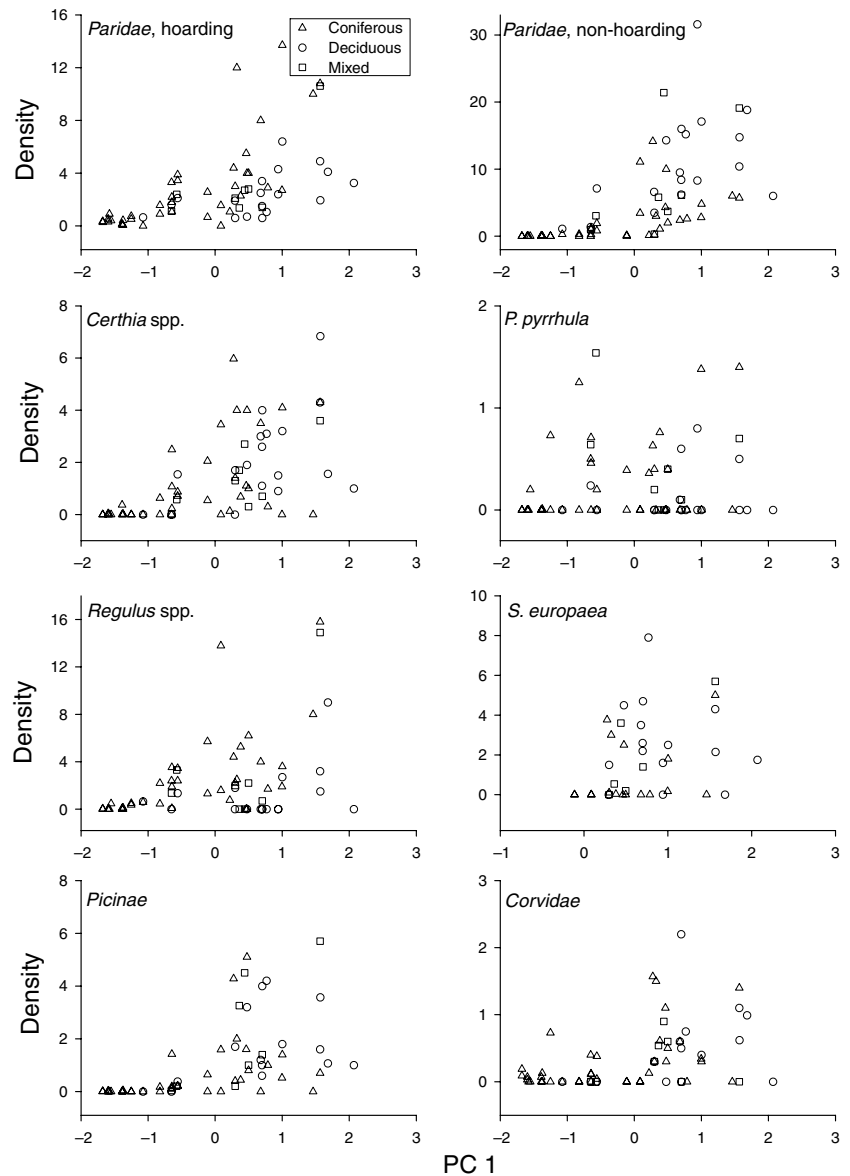R^2 is the coefficient of determination of the model.

Figure 2 Densities of resident species or species groups in relation to the first principal component (PC 1) that describes primarily temperature, and secondarily precipitation conditions, in Europe.

between the total density of both resident and migrant birds and latitude. Both the pooled density of residents (regression equation: $y = 4.40 - 0.06x$, $P < 0.000$) and migrants ($y = 3.26 - 0.03x$, $P < 0.000$) decreased with increasing latitude (Fig. 4a). The decline of migrants towards higher latitudes, however, was not as steep as in resident birds (difference between coefficients: $t_{126} = 42.96$, $P < 0.000$). In central and western Europe the average density difference between residents and migrants was rather small but it increased steadily with increasing latitude, and at high latitudes those two groups were clearly separated. This results in a decreasing proportion of resident numbers in breeding bird communities with increasing latitude, and in northern Fennoscandia residents comprised only a small fraction of the breeding bird numbers, whereas further south, their proportion is commonly 40–50% (Fig. 4b).

DISCUSSION

To briefly summarize the main results of the study, densities of resident birds were correlated with both geographical co-ordinates and temperature and precipitation factors, but latitude and temperature proved to be the strongest individual factors along which resident densities varied. Latitude and temperature, however, are strongly intercorrelated and partial correlation analysis suggested that of those two factors, latitude was the dominant one. This suggests that latitudinal temperature variation alone cannot explain the observed latitudinal patterns. Some residents were also negatively correlated with precipitation but its impact was relatively weak.

Resident densities decreased towards high latitudes and with decreasing temperatures irrespective of body size, breeding habits or diet, thus supporting the suggestion by

Table 8 ANOVA table showing resident bird densities explained by the first principal component describing primarily temperature (covariate) and forest type (factor)

Residents	Source of variation	d.f.	MS	F	P
Paridae, hoarding $n = 65$	Model, $R^2 = 0.60$	5	0.65	17.39	<0.000
	Forest type	2	0.11	3.03	0.056
	PC 1	1	1.06	28.47	<0.000
	Forest type × PC 1	2	0.09	2.54	0.087
	Error	59	0.04		
Paridae, nonhoarding $n = 65$	Model, $R^2 = 0.73$	5	2.02	31.32	<0.000
	Forest type	2	0.68	10.50	<0.000
	PC 1	1	2.14	33.15	<0.000
	Forest type × PC 1	2	0.03	0.47	0.627
	Error	59	0.06		
Regulus spp. $n = 65$	Model, $R^2 = 0.40$	5	0.62	7.81	<0.000
	Forest type	2	0.50	6.30	0.003
	PC 1	1	0.78	9.76	0.003
	Forest type × PC 1	2	0.12	1.49	0.234
	Error	59	0.08		
Certhia spp. $n = 65$	Model, $R^2 = 0.42$	5	0.4	8.49	<0.000
	Forest type	2	0.01	0.19	0.828
	PC 1	1	0.82	17.41	<0.000
	Forest type × PC 1	2	0.01	0.15	0.860
	Error	59	0.05		
S. europaea $n = 34$	Model, $R^2 = 0.30$	5	0.22	2.74	0.036
	Forest type	2	0.25	3.11	0.058
	PC 1	1	0.30	3.62	0.066
	Forest type × PC 1	2	0.16	1.90	0.166
	Error	32	0.08		
Corvidae $n = 62$	Model, $R^2 = 0.22$	5	0.04	3.20	0.013
	Forest type	2	0.00	0.11	0.894
	PC 1	1	0.06	4.20	0.045
	Forest type × PC 1	2	0.00	0.31	0.735
	Error	56	0.01		
Picinae $n = 61$	Model, $R^2 = 0.49$	5	0.37	10.60	<0.000
	Forest type	2	0.04	1.09	0.342
	PC 1	1	0.90	25.67	<0.000
	Forest type × PC 1	2	0.09	2.49	0.092
	Error	55	0.03		

Variables n and R^2 denote the number of census results and the coefficient of determination of each model, respectively.

Herrera (1978) that the conditions of the non-breeding season may limit resident populations. Further support for this conclusion provided the result that densities of both resident and migrant birds decreased towards higher latitudes but not in parallel. The decline of resident birds was steeper, and in northern Europe, the density of residents was lower than that of migrants. This may suggest that in Fennoscandia the density of residents is lower than would be expected on the basis of breeding time carrying capacity.

Mechanism between climate and population density

The result that density of most resident groups was correlated with all or most independent factors (latitude, longitude, PC 1 and PC 2) made it difficult to determine the relative contribution of each factor on density variation.

We were, however, able to exclude the secondary factors. First, residual examination suggested that latitude and the first principal component (PC 1) describing primarily the temperature conditions, seemed to be of more importance than longitude and precipitation (PC 2). Secondly, the results of the partial correlation analysis suggested that latitude was clearly a more dominant factor than temperature. The only result suggesting that both latitude and temperature may contribute to population density was that neither of them correlated with the density of hoarding titmice and *Regulus* spp. in the partial correlation analysis. This is, if both factors roughly equally explained the density distribution, keeping either of them constant may result in a non-significant correlation. The overwhelming strength of latitude, however, was not very helpful in determining the impact of climate on population densities because latitude
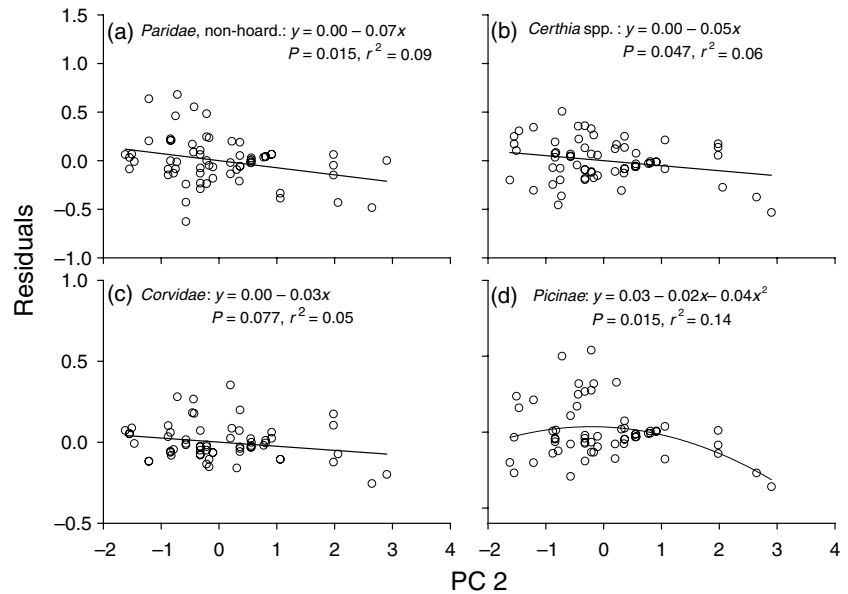
Figure 3 Residual distribution of densities of (a) non-hoarding titmice, (b) *Certhia* spp., (c) *Corvidae* and (d) *Picinae* in relation to the second principal component (PC 2). Residuals were obtained after removing the effect of the PC 1 and forest type.

Table 9 Partial correlations and their significance levels between resident bird densities and latitude (after controlling for PC 1) and PC 1 (after controlling for latitude)

Residents	d.f.	Latitude	P	PC 1	P
Paridae, hoarding	62	−0.16	0.216	0.15	0.230
Paridae, non-hoarding	62	−0.34	0.006	0.08	0.511
Regulus spp.	62	−0.04	0.772	0.10	0.447
Certhia spp.	62	−0.43	<0.000	−0.16	0.221
Corvidae	59	−0.32	0.011	−0.15	0.244
Picinae	58	−0.29	0.025	−0.01	0.918

partly describes all those factors that were excluded. As Newton & Dale (1996) emphasized, latitude is a mere surrogate, but a good one, in depicting those factors that have biological importance to organisms. However, some suggestions can be made. The result that temperature was overplayed by latitude suggests that the covariation of ambient temperature with latitude is not the sole factor affecting population sizes of resident birds. One potential additional agent could be the interaction between ambient temperatures and food resources.

Latitude is strongly correlated with potential evapotranspiration, which describes the amount of available net atmospheric energy (solar radiation) (see Currie, 1991; Begon *et al.*, 1996). Taking into account that increasing latitude is associated with decreasing temperatures and a decreasing amount of available energy suggests an apparent mechanism between ambient temperatures, latitude and variation in resident densities. As endothermic animals, birds are not directly dependent on ambient temperature, but rather on the relationship between temperature and food resources up to a certain point. As temperature falls, birds have to replace heat loss by increasing standard metabolic rate (Calder & King, 1974; Weathers, 1979), which augments energy demands

(King & Farner, 1961). It has been observed that at high latitudes, standard metabolic rates of birds are higher than further south (Lasiewski & Dawson, 1967; Kendeigh & Blem, 1974; Weathers, 1979). In winter, increasing latitude coupled with decreasing temperatures, diminishing length of day available for feeding and decreasing amount of available food would together act in limiting the densities of resident birds in a density-dependent way. The results of the feeding experiments carried out at the local scale also emphasize the importance of food resources during winter (Krebs, 1971; Yom-Tov, 1974; van Balen, 1980; Jansson *et al.*, 1981; Källander, 1981; Brittingham & Temple, 1988; Desrochers *et al.*, 1988; Hogstad, 1988; Lahti *et al.*, 1998).

If the interaction between available energy and ambient temperatures has significant impact on populations, densities should have been negatively correlated with longitude because temperatures decrease towards east while potential evapotranspiration remains relatively constant at the same latitudes. Most residents indeed had a negative, either linear or unimodal, distribution with longitude. However, after removing the effect of latitude, only non-hoarding titmice and *Picinae* showed a weak unimodal pattern with decreasing density trend towards east. Geographic
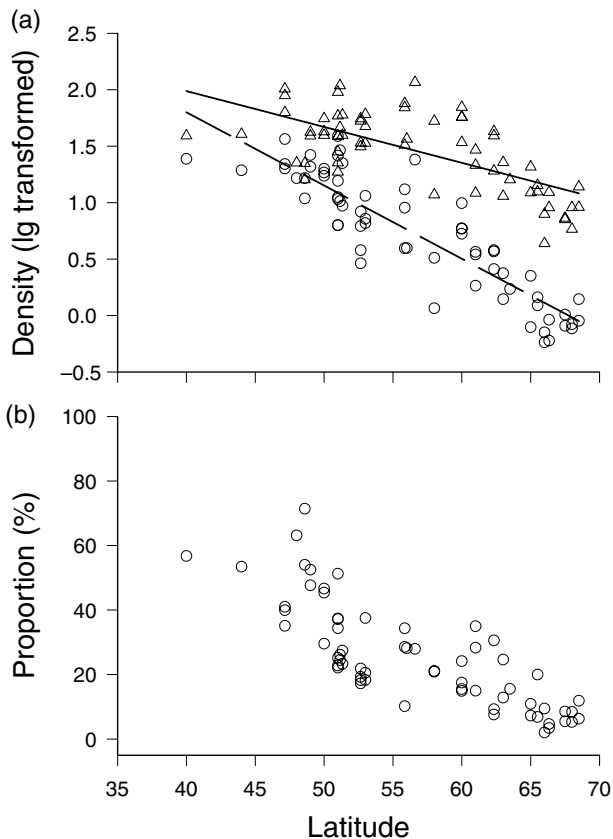
Figure 4 Densities (a) of both resident (squares, broken line) and migrant (triangles, solid line) birds in their breeding assemblages and (b) proportion of residents of breeding bird numbers in relation to latitude. Lines refer to regression equations.

comparisons may, however, be complicated by anthropogenic changes in environment, their effects being more pervasive and long lasting in the west and south (Mönkkönen & Welsh, 1994; Tomialojć, 2000). Another potential alternative factor that can produce patterns resembling the observed relationships between the latitude and density is the decrease in abundance from the centre of distribution range towards the range edges (Brown & Lomolino, 1998). In Europe, the northern edge of boreal forest and the southern edge of temperate deciduous forest set the limit for the distribution of many forest birds. However, in our data there was no indication of a decrease in densities from Central Europe towards south. Untransformed densities suggested that the distribution was in fact exponential; densities were invariably low at high latitudes and increased rapidly towards south. Therefore, the observed patterns were not artifact resulting from the relationship between species range position and abundance.

Relative importance of abiotic conditions

All patterns are dependent on scale and factors operating on a given scale cannot be generalized as such to other

spatial levels (Wiens, 1989; Böhning-Gaese, 1997). The result that densities of resident birds declined somewhat linearly with increasing latitude does not mean that all European resident bird populations are controlled, for example, by the interaction between latitude and climate as suggested. In fact, large variation in densities in central and western Europe suggests that abiotic factors may not play such an important role there. In a model by Newton (1998), the density of residents is not limited by winter mortality until all non-territorial and part of the territorial birds have disappeared. In other words, we can ask, where the breeding density of residents is lower than would be expected on the basis of the breeding time carrying capacity of the environment (*sensu* Ashmole, 1963; see also Ricklefs, 1980)?

Our results suggest that northern Fennoscandia might be such an environment. First, the variation in density of almost every group was reduced substantially north from sixtieth latitude compared with more southern areas. It was remarkable that even density differences among forest types were negligible in the north, given that there quite likely is variation in the amount of food resources among forest types (Von Haartman, 1971). Secondly, if Dobzhansky's (1950) and MacArthur's (1972) suggestions about more dominating role of biotic interactions in the south is correct, one could hypothesize greater density variation in the south compared with the north. This is because climate patterns occur on a larger scale than variation in biotic interactions. Small-scale variation in factors affecting biotic interactions, such as predation or competition, would result in large variance in density among different locations whereas large-scale climatic conditions would tend to equalize densities and variances over large areas. These patterns were indeed observed when comparing northern and southern Europe. Thirdly, assuming that carrying capacity of the environment decreases with increasing latitude one would expect both resident and migrant bird densities to decrease parallel towards the north. However, densities of residents decreased more steeply with latitude and densities of the two groups were clearly separated in the north as residents comprised only a fraction of the breeding bird numbers in northern Fennoscandia. These results suggest that in northern Fennoscandia resident densities might be lower than would be expected on the basis of breeding time carrying capacity and resident populations are limited by winter mortality.

The importance of species-specific physiological tolerance limits for abiotic conditions may also be emphasized in the north. This means that species' internal physiological capabilities to cope with external abiotic conditions would determine its range and abundance. Such a mechanism has actually been proposed by Root (1988a,b). She found that the northern winter range limits of many North American birds were associated with some crucial features describing the harshness of the winter, such as the mean temperature of January and the average duration of the frost-free period (1988a, see also Chesser, 1998). Also the winter ranges of fourteen studied birds were restricted to areas where the

energy needed to compensate for a colder environment was not greater than *c.* 2.5 times their basal metabolic rate (Root, 1988b; but see Castro, 1989; Repasky, 1991). Some other studies have also found support for the idea that species physiological capacities can determine distributional ranges (Weathers & von Riper, 1982; Hayworth & Weathers, 1984). However, mechanisms rarely operate alone, and such a deterministic view has raised criticism (see Repasky, 1991). The ultimate reason for increased winter mortality may be individualistic tolerance limits for the amount of food and abiotic conditions, but proximate reasons bring about a wide array of biological interactions in terms of whether mortality is caused by intra- or inter-specific competition, predation, etc. For example, younger individuals have usually higher mortality because of their lower position in social hierarchy (Ekman, 1984; Koivula & Orell, 1988). Interspecific interactions are involved when individuals of different species are making trade-offs between food and predation risk (Suhonen, 1993) or when climate-associated shifts in nest-site selection bring about costs in terms of increased nest predation (Martin, 2001).

Climate change

The relative importance of biotic and abiotic factors on the mechanism of population limitation probably varies among geographical locations. Our results suggested that at high latitudes the role of climate might be more important than further south. In this light, the ongoing change in global climate may have profound consequences on populations and the community structure in birds. It has been estimated that the average temperatures will rise from 1.5 °C up to 4.5 °C during the next century, and that the change would be most distinct at high latitudes in winter (see Schneider, 1993). This means that northern Lapland would roughly have winter conditions of southern Fennoscandia in the future. While there of course is uncertainty in these models and predictions, many birds have already adjusted their onset of breeding to the increased spring temperatures (e.g. Crick *et al.*, 1997; Both & Visser, 2001). The predicted changes would bring about substantial changes and transitions in resident bird populations and the structure of breeding bird communities in Europe, especially in Fennoscandia. Extrapolating from our results, we may predict that resident birds will show higher abundance and a higher level of variation among sites. This may then negatively affect migrant populations, because competition between resident and migrant birds quite likely becomes important only at high-resident densities (Forsman *et al.*, 2002). Unwillingly, we are in the midst of a large-scale experiment where the effect of temperature on population limitation and species interactions may partly be resolved in the future.

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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

Locality and co-ordinates	Forest type	Census method	Reference
Northern Europe			
68°N, 27°E	C	S	Inkeröinen (1995)
68°N, 27°E	C	L	Virkkala (1989)
67°N, 29°E	C	L	Virkkala (1987)
66°N, 28°E	C	L	Virkkala (1987)
66°N, 29°E	C	L	Helle (1985)
66°N, 28°E	C	L	Virkkala (1987)
65°N, 25°E	C, D	M	Forsman *et al.* (1998)
65°N, 17°E	C	L, M	Enemar (1964)
63°N, 28°E	C	L	Mönkkönen (1984)
63°N, 10°E	C	M	Hogstad (1993)
62°N, 21°E	C, M, D	M	Nordström (1953)
61°N, 24°E	C	L	Haapanen (1965)
60°N, 20°E	C, M, D	L	Haila (1980)
Central Europe			
58°N, 33°E	C	M	Morozov (1992)
56°N, 22°E	C	M	Matiukas (1992)
56°N, 14°E	C	M	Nilsson (1980)
56°N, 13°E	D	M	Enemar (1966)
55°N, 13°E	C	M	Svensson (1975)
53°N, 9°E	C, M	M	von Dierschke 1973
52°N, 24°E	C, M, D	M	Tomialojć *et al.* (1984)
52°N, 13°E	M	M	Witt (1974)
51°N, 9°E	D	M	Jedicke (1996)
51°N, 23°E	C,M	M	Cieslak (1984)
51°N, 17°E	D	M	Tomialojć & Profus (1977)
51°N, 16°E	M, D	M	Tomialojć (1974)
51°N, 12°E	C	M	Socher (1983)
50°N, 20°E	C	M	Glowaciñski & Weiner (1980)
50°N, 20°E	D	M	Glowaciñski (1979)
50°N, 15°E	C	M	A. Exnerova, unpubl.
49°N, 7°E	C, D	P	Muller (1981)
48°N, 8°E	C	M	von Vidal 1975
47°N, 8°E	C, M, D	M	Christen (1983)
44°N, 4°E	D	P	Blondel (1981)
40°N, 9°E	D	P	Blondel (1981)
Western Europe			
53°N, 4°W	D	M	Jones (1972)
51°N, 1°W	C	M	Williamson (1973)
51°N, 1°E	D	M	Fuller & Steel (1990); Fuller & Henderson (1992)
49°N, 2°E	C, D	M	Le Louarn (1970)