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Northward density shift of bird species in boreal protected areas due to climate change

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Species ranges are expected to move latitudinally poleward because of the warming climate. We asked whether northward patterns are observable also in population densities of land birds in Finnish protected areas such that temporal population changes would be most pronounced toward species range boundaries. We compared population changes of northern species, southern species, and species distributed over the whole country from 1981–1999 to 2000–2009 in 96 protected areas. Northern species showed the greatest decrease in southern Finnish protected areas, and southern birds increased most in northern Finnish protected areas. Among species distributed over the whole country, there were population density shifts toward northern Finnish protected areas. Two thirds of the species that decreased most were northern, whereas many of the species showing the greatest increase were southern habitat generalists. The results show that there are already northward density shifts occurring that probably precede future species range shifts.

Introduction

Climate change is one of the most important threats to biodiversity (Parmesan and Yohe 2003, Root *et al*. 2003). Global climate change is increasingly affecting species populations and communities (Parmesan 2006), and future changes in climate are projected to cause considerable changes in the distribution of species representing several, quite different taxa (Beaumont and Hughes 2002, Thomas *et al*. 2004, Thuiller *et al*. 2005, Hickling *et al*. 2006). In Europe, bird species distributions have been forecast to change considerably in the 21st century as a consequence of climate change (Huntley *et al*. 2007, 2008). Species predicted to gain range in the 21st century in Europe were observed to increase, and those predicted to lose range were observed to decline in 1980–2005 (Gregory *et al*. 2009). Also in North America, ranges of bird species are moving northwards (Hitch and Leberg 2007, Zuckerberg *et al*. 2009).

Species ranges are expected to move latitudinally poleward because of climate change (Hickling *et al*. 2006, Parmesan 2006). This suggests major challenges for species adaptation. Species may rely on two means in their adaptation, dispersal (where possible) across fragmented landscape and adaptive persistence in protected areas. The protected area network facilitates adaptation to climate change, because many species are already threatened by intensive human land use causing habitat loss.

This paper examines bird population changes in a boreal protected area network in northern Europe. We compare population densities of species in protected areas as assessed through large-scale quantitative censuses performed in Finland in 1981–1999 and in 2000–2009. Protected areas are essential for such comparison, because direct habitat alteration, which otherwise would affect bird species' density, is minimized. Therefore, protected areas provide possibilities for studying the effects of climate change on biodiversity at northern latitudes.

In a previous study, we compared population changes among the 37 bird species most common in protected areas, considering species distribution pattern and migration strategy, and observed that among northern birds both migratory and resident species declined whereas among southern birds they both increased from 1981–1999 to 2000–2009 (Virkkala and Rajasärkkä 2011). Thus, population dynamics of birds were already changing in natural boreal habitats in association with changing climate.

In the present work, we extend our previous work and study population changes of all land bird species (152 species) in relation to protected area location. As species are expected to move latitudinally, we ask whether this can be observed already in species' population density patterns. Changes in population densities over time may be observable much earlier than range shifts, which are often based on coarse-scale presence/absence data (*see* Hagemeijer and Blair 1997, Huntley *et al*. 2007). Studies dealing with range shifts of species are frequent (e.g. Thomas *et al*. 2004, Lawler *et al*. 2006, Beaumont *et al*. 2007, Huntley *et al*. 2007, 2008, Zuckerberg *et al*. 2009), but studies of species density shifts due to climate change are much more rarely reported (*see*, however Shoo *et al*. 2005). Therefore in this work, we study — by dividing our data based on location of protected areas — whether population changes would be most pronounced toward the edges of species range such that northern species would decline more in protected areas in southern Finland and southern species would increase particularly in northern Finnish protected areas. Moreover, we compare the largest population changes (both decrease and increase) among all bird species in protected areas.

Material and methods

Protected areas

The total area of reserves (n = 96) in Finland (60–70°N, 21–31°E) in which bird counts were done was 22 493 km^2, with the protected areas studied ranging in size from three to 2524 km^2 (median = 51.6 km^2, *see* Fig. 1). The protected areas studied accounted for 62.5% of the land area of all Finnish protected areas. The largest areas (over 1000 km^2 in size) included four wilderness areas (Hammastunturi, Kaldoaivi, Käsivarsi, and Pöyrisjärvi) and two national parks (Lemmenjoki and Urho Kekkonen) in northernmost Finland. Most of the protected land is in northern Finland (Virkkala *et al*. 2000, Virkkala and Rajasärkkä 2007). Forests cover 56% of the land area in the reserves studied, with the rest being open mires and mountain areas. Two thirds of the protected forest stands are over 100 years old (Virkkala *et al*. 2000).

Protected areas were grouped by location. On the basis of latitude, Finland was divided from south to north into three regions (uniform grid, *see* Fig. 1). Uniform grid units 67–70 formed southern Finland, 71–74 the north-central region, and 75–77 the northernmost region in our analysis.

Bird censuses

Land birds in protected areas were counted by using the Finnish line transect census method, which is suitable for counting birds over large areas (Väisänen *et al*. 1998, Virkkala and Rajasärkkä 2007). The line transect method applies a one-visit census in which birds are counted during breeding season along a transect with an average length of 5–6 km. In the line transect method, a 50-metre-wide main belt along the walking line and a supplementary belt outside the main belt are separated. The latter covers all birds observed outside the main belt (e.g., Järvinen *et al*. 1991, Väisänen *et al*. 1998, Virkkala 2004).

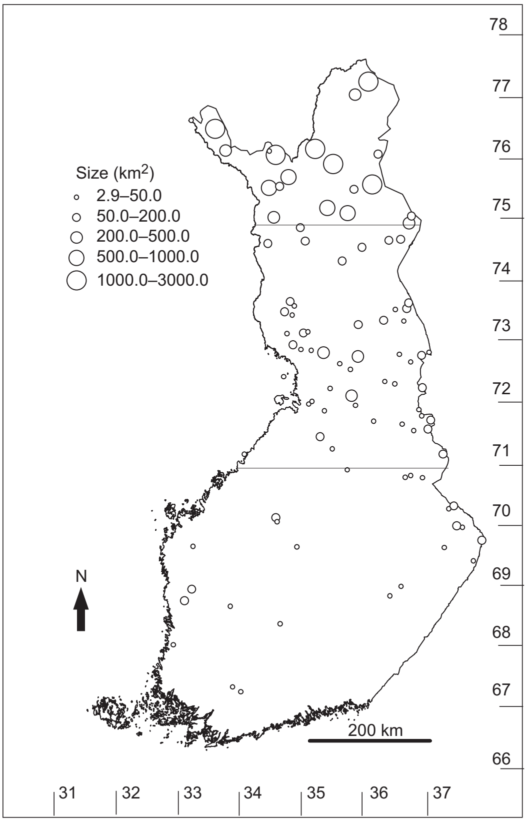

Fig. 1. Location of the protected areas studied: southern Finland (grids 67–70), north-central Finland (grids 71–74), northernmost Finland (grids 75–77). Grid numbers are from the Uniform Coordinate System (uniform grids) used in Finland.

Densities of bird species were calculated on the basis of observations in the whole survey belt, including both main and supplementary belts. Species-specific correction coefficients were used in the density calculation. These coefficients vary according to the proportion of main belt observations to all survey belt observations. Details on calculation of the species-specific coefficient and density are given in the work of Järvinen and Väisänen (1983) and Virkkala and Rajasärkkä (2007). All correction coefficients used in this study were calculated on the basis of line transect data collected from protected areas in Finland and neighbouring countries in the boreal and hemiboreal vegetation zones.

The total lengths of line-transect censuses in the 96 protected areas were 6587 and 5087 km in 1981–1999 and 2000–2009, respectively. In each period, the birds were counted in every protected area, where the total transect length was at least 10 km. The median census years were 1992 in the first and 2006 in the second period, so the average time span in the study was 14 years. The same transects were not repeated, but censuses in each protected area included the same proportion of habitats in the two periods.

Analyses

Bird species were categorized according to their distribution (*see* Appendix). Distribution pattern (southern or northern) was classified in terms of distribution and regional density variation in Finland (Väisänen *et al*. 1998). About two thirds of northern species (32 out of 49 species) also had their overall ranges' southern boundary in Finland, the rest of the northern species showing southward density decrease in Finland and/or having separate populations south of Finland. Species without any northward or southward pattern in their regional density or species with wide-ranging sporadic distribution were deemed a separate class ('whole country').

Densities of species between the two periods were compared pairwise in each protected area with either a paired *t*-test or a Wilcoxon signed rank test. When population changes of species groups were compared in relation to location or size of protected areas, a one-way analysis of variance (ANOVA), an analysis of covariance (ANCOVA), or a regression analysis was used.

Percentage changes above and below 100% are not strictly comparable; for example, a two-fold increase from 100 gives a value of 200, but a similar decrease to half that yields 50. To avoid this discrepancy, we used a logarithmic ratio (log-ratio) of per cent change in densities, where, for example, 100% increase in density from 1981–1999 to 2000–2009 would be log(200/100) = +0.301 and 50% decrease is log(50/100) = –0.301.

Climate change

The mean temperature of the coldest month (February) and that of April–June essential for bird species (*see* Heikkinen *et al*. 2006, Virkkala *et al*. 2008) were taken from the Finnish Meteorological Institute database. The mean temperature of the coldest month rose by 0.9 °C in southern Finland (for uniform grid units 66–70, from –7.24 °C in 1981–1999 to –6.32 °C in 2000–2009) and by 0.7 °C in northern Finland (for grid units 71–77, from –11.20 °C in 1981–1999 to –10.50 °C in 2000–2009) and that of April–June by 0.5 °C in S Finland (1981–1999: 8.36 °C, 2000–2009: 8.87 °C) and by 0.9 °C in N Finland (1981–1999: 5.42 °C, 2000–2009: 6.29 °C).

Results

There was no statistically significant differences in density of the whole bird community or densities of species distributed over the whole country between the periods (Table 1). However, the density of southern species had increased significantly, by 24%, and that of northern species decreased by 20% from 1981–99 to 2000–2009. When, based on their location, protected areas were divided into three categories from south to north, population changes between the periods varied considerably among the different distribution pattern groups (Table 2). For the northern birds, the decrease was largest in southern Finnish protected areas (one-way ANOVA: $F_{2,93} = 5.533$, $p = 0.005$; pairwise comparisons Tukey's test: southern < north-central**, southern < northernmost*), whereas for the southern birds the increase was the largest in north-central and northernmost Finnish protected areas (ANOVA: $F_{2,93} = 6.311$, $p = 0.003$; pairwise comparisons Tukey's test: southern < north-central**, southern < northernmost*). The density of northern birds decreased to almost half in southern Finnish protected areas but only 22% and 18% in north-central and in northernmost protected areas, respectively (Table 2). Southern birds increased in numbers by only 10% in protected areas of southern Finland but by 78% and 66% in protected areas of north-central and northernmost Finland, respectively. For species distributed over the whole country, there

Table 1. Mean densities (pairs km^{-2} ± SE) of different land-bird species groups in protected areas in 1981–1999 and 2000–2009, as shown by quantitative line transect censuses, with species categorized by distribution pattern (*see* Appendix); statistical testing was done using a paired *t*-test (df = 95) (species numbers in each group are in brackets).

Species group	1981–1999	2000–2009	*t*	*p*
Whole bird community (152 spp)	112.20 ± 5.10	109.04 ± 4.50	0.914	0.363
Distribution pattern				
Northern (49)	36.35 ± 2.52	29.01 ± 2.17	5.412	< 0.001
Southern (71)	29.70 ± 3.71	36.95 ± 3.91	4.837	< 0.001
Whole country (32)	46.16 ± 2.61	43.09 ± 2.13	1.555	0.123

Table 2. Mean (± SE) population changes of species groups in the different distribution patterns in the protected areas situated in different parts of Finland (southern: uniform grid units 67–70, north-central: 71–74, and northernmost: 75–77); log ratio = log (density in 2000–2009/density in 1981–1999), and the value of the log ratio (*x*) is transformed as per cent index by 10^x (per cent index of 1.00 = no change, while 0.53 indicates that the density in 2000–2009 is 53% of that in 1981–1999).

Location	Northern species		Southern species		Species distributed over the whole country		*n*
	Log ratio	Per cent index	Log ratio	Per cent index	Log ratio	Per cent index	
Southern	–0.276 ± 0.062	0.530	0.040 ± 0.030	1.097	–0.119 ± 0.044	0.760	24
North-central	–0.108 ± 0.028	0.780	0.249 ± 0.028	1.775	0.004 ± 0.026	1.009	51
Northernmost	–0.088 ± 0.034	0.817	0.220 ± 0.083	1.658	0.060 ± 0.044	1.149	21

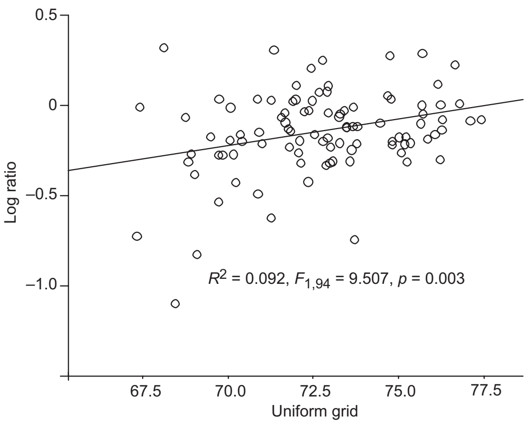

Fig. 2. Population density change (linear regression) for northern bird species from 1981–1999 to 2000–2009, based on log ratio [log ratio = log(density in 2000–2009/density in 1981–1999)] in each protected area according to location from south to north (for uniform grid details, *see* Fig. 1).

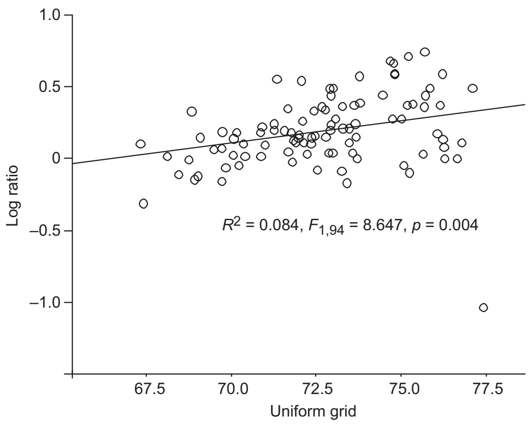

Fig. 3. Population density change (log ratio) for southern bird species in each protected area, according to location from south to north (uniform grid); linear regression presented.

was a decrease in density in protected areas situated in southern Finland and an increase in those in north-central and northernmost Finland (ANOVA: $F_{2,93} = 5.186$, $p = 0.007$; pairwise comparisons, Tukey's test: southern < north-central**, southern < northernmost*).

Regression analyses between location of each protected area and density change index (log ratio) showed significance for both the northern and southern species (Figs. 2 and 3). For northern species, the decrease was clearly the most pronounced in the southern protected areas but, all told, there were only two areas where the density more than doubled (log ratio > 0.301) and 17 areas where the density declined to less than half (log ratio < –0.301; *see* Fig. 2). Correspondingly, for southern species, the increase in proportion was most pronounced in the northern protected areas (*see* Fig. 3). In total, there were 29 areas where the density more than doubled and only two areas where the density declined to less than half (the northernmost protected area being a possible outlier in the data; *see* Fig. 3).

The size of protected areas was highly significantly correlated with location, with the smallest areas found in the south and the largest in the north (log-transformed area *vs*. northern latitude: $r_{\text{Pearson}} = 0.629$, $p < 0.001$, $n = 96$; *see* Fig. 1). However, when the size of a protected area was used as a covariate, all differences in the density change indices of bird groups between the three regions were still statistically significant (shown by ANCOVA): for northern birds, $F_{2,92} = 4.180$ and $p = 0.018$; for southern birds, $F_{2,92} = 5.678$ and $p = 0.005$; and for species distributed throughout the country, $F_{2,92} = 3.746$ and $p = 0.027$.

Overall, the mean population density of 12 species decreased to less than half of the previous levels and seven species at least doubled in their density (Table 3). Eight species showing a decline were northern and four southern, whereas of the species showing the greatest increase, four were southern, two northern, and one distributed throughout the country.

Discussion

Species density shifts vs range shifts

Southern bird species are expected to extend and northern species to reduce their ranges in northern Europe as a result of climate change (Huntley *et al*. 2007, Virkkala *et al*. 2008, 2010). Climate-change-driven range shifts are probably among the most dramatic at northern latitudes because of the greater temperature increase projected for these regions (Jetz *et al*. 2007). For example, in Finland, according to the worst-case climate-change scenario, mean annual temperature will increase by as much as 7 °C by 2080 in comparison with the baseline period, 1961–1990 (Jylhä *et al*. 2004).

Our present results showed that northern species decreased most in protected areas of southern Finland and southern species increased most in those in north-central and northernmost Finland. This means that population densities have changed most towards species range boundaries and there is, indeed, a pattern of strengthening density decrease or increase toward species' southern or northern range boundary, respectively, when the climate becomes warmer at northern latitudes.

The northward expansion of species ranges (leading edge) is usually more easily observed than the retraction of southern ranges (trailing edge) of species (Thomas and Lennon 1999, Brommer 2004, *see*, however, Zuckerberg *et al*. 2009). Leading range boundaries may be more accurately determined by strict climatic restrictions for southern species than are trailing range boundaries for northern species (Jump *et al*. 2009). Range shift studies are usually based on presence/absence data for species whereas the quantitative changes within species ranges can be considerable without any observable change in distribution. Moreover, presence/absence data are usually based on a coarse 10 × 10 km or 50 × 50 km grid scale, which may mask smaller-scale changes. Lack of latitudinal range retraction results may, therefore, be due to a lack of research effort (Thomas *et al*. 2006, Jump *et al*. 2009). Data quality may also affect these comparisons so that expanding species may be relatively common and thus easily observed, whereas retreating species are much rarer and, therefore, not included in low-quality data (Thomas 2010). For British butterflies, it has been shown that southern edges of species are as sensitive to climate change as are northern range margins (Franco *et al*. 2006).

For species distributed over the whole country, there seemed to be a density shift towards the north, although there was no density change in these species between the periods when all protected areas were compared. In many species in this group, the Finnish population is among

Table 3. Species whose mean density (pairs km^{-2} ± SE) decreased to at least half and species that at least doubled their density from 1981–1999 to 2000–2009 (species observed in at least 10 protected areas are included); statistical testing was done using a Wilcoxon signed rank test (ranks = negative/positive/tied; N = northern species, S = southern species, W = species distributed over the whole country); z = test statistic.

Species group	1981–1999	2000–2009	z	Ranks	p
Species showing decrease					
Hen harrier *Circus cyaneus* (N)	0.011 ± 0.003	0.004 ± 0.001	2.304	16/7/73	0.021
Rough-legged buzzard *Buteo lagopus* (N)	0.037 ± 0.009	0.011 ± 0.004	4.051	23/4/69	< 0.001
Temminck's stint *Calidris temminckii* (N)	0.044 ± 0.022	0.013 ± 0.009	1.886	8/2/86	0.059
Ruff *Philomachus pugnax* (N)	0.639 ± 0.156	0.181 ± 0.064	5.059	47/7/42	< 0.001
Red-necked phalarope *Phalaropus lobatus* (N)	0.260 ± 0.079	0.119 ± 0.057	2.147	16/10/70	0.032
Long-tailed skua *Stercorarius longicaudus* (N)	0.063 ± 0.028	0.029 ± 0.013	2.191	8/2/86	0.028
Wryneck *Jynx torquilla* (S)	0.054 ± 0.009	0.022 ± 0.004	3.692	45/18/33	< 0.001
Greenish warbler *Phylloscopus trochiloides* (S)	0.082 ± 0.026	0.039 ± 0.013	2.103	18/9/69	0.035
Wood warbler *Ph. sibilatrix* (S)	1.056 ± 0.279	0.337 ± 0.091	4.593	45/12/39	< 0.001
Two-barred crossbill *Loxia leucoptera* (N)	0.207 ± 0.059	0.065 ± 0.018	3.085	34/17/45	0.002
Scarlet rosefinch *Carpodacus erythrinus* (S)	0.129 ± 0.034	0.049 ± 0.012	2.913	31/13/52	0.004
Rustic bunting *E. rustica* (N)	2.043 ± 0.205	1.023 ± 0.146	6.025	69/16/11	< 0.001
Species showing increase					
Waxwing *Bombycilla garrulus* (N)	0.088 ± 0.022	0.503 ± 0.061	7.393	2/73/21	< 0.001
Red-flanked bluetail *Tarsiger cyanurus* (N)	0.009 ± 0.004	0.044 ± 0.015	2.722	4/15/77	0.006
Blackbird *Turdus merula* (S)	0.136 ± 0.052	0.358 ± 0.132	3.154	6/22/68	0.002
Fieldfare *T. pilaris* (W)	0.405 ± 0.067	0.907 ± 0.132	5.285	19/69/8	< 0.001
Blue tit *Parus caeruleus* (S)	0.032 ± 0.021	0.222 ± 0.741	3.294	1/14/81	0.001
Great tit *P. major* (S)	1.015 ± 0.198	2.267 ± 0.283	6.732	8/76/12	< 0.001
Greenfinch *Carduelis chloris* (S)	0.013 ± 0.007	0.070 ± 0.041	3.172	5/19/72	0.002

the largest in Europe and there is a northerly distribution on the European scale but not in Finland (e.g., for the capercaillie *Tetrao urogallus*, crane *Grus grus*, redstart *Phoenicurus phoenicurus*, fieldfare *Turdus pilaris*, redwing *T. iliacus*, willow warbler *Phylloscopus trochilus*, spotted flycatcher *Muscicapa striata*, willow tit *Parus montanus*, and parrot crossbill *Loxia pytyopsittacus*; *see* Hagemeijer and Blair 1997, Väisänen *et al*. 1998, Birdlife International 2004). Therefore, this density shift in species distributed over the whole country may reflect climate change effects. Also, for these species our study shows that atlas-based presence/absence data may capture only some of the changes in species distribution and abundance patterns, because density changes within species ranges can be considerable without any observable changes in species ranges.

Density changes among northern and southern species

Two northern species have increased considerably in the recent decades, the waxwing *Bombycilla garrulus*, and the red-flanked bluetail *Tarsiger cyanurus*. The waxwing has an irregular distribution pattern, with considerable temporal variation (Väisänen *et al*. 1998; *see* also Virkkala 1987, Virkkala and Rajasärkkä 2006). Berries of the rowan *Sorbus acuparia* are an important food source for the waxwing in winter, and good rowanberry yields are probably becoming more frequent, which benefits waxwing (Väisänen 2003). The red-flanked bluetail clearly increased in Finnish protected areas in the past years, but it may have been equally common also in the early 1970s (Rajasärkkä 2010).

The fieldfare, which has increased in protected areas, prefers cultivated landscapes in Finland and occurs often near human settlements, but it breeds also in small numbers in remote forest-mire habitats (Väisänen *et al*. 1998). Other species showing a strong increase are typical southern habitat generalists, most of them being abundant across large parts of Europe (the blackbird *Turdus merula*, blue tit *Parus caeruleus*, great tit *P. major*, and greenfinch *Carduelis chloris*; *see* Hagemeijer and Blair 1997). The rapid increase in density of these species, typical to large parts of Europe and several habitats including human settlements suggests homogenization of bird communities in natural boreal habitats (*see* Olden 2006, Olden and Rooney 2006).

On the basis of climate variables, Virkkala *et al*. (2008) predicted that 27 northern species having their southern range boundary in Finland would lose — depending on the climate scenario — on average 74%–84% of their range in Finland and nearby areas by 2051–2080. The proportion of these species' occurrences in protected areas was predicted to decline in northern Fennoscandia by 2051–2080, indicating that a smaller proportion of the populations of these species will be found in protected areas in the future (Virkkala *et al*. 2010). The densities of these northern species declined significantly, by 22%, from 1981–1999 to 2000–2009; this decline was about the same as the decrease in the density of all northern-bird species (20%). Six of these 27 species (the rough-legged buzzard *Buteo lagopus*, Temminck's stint *Calidris temminckii*, red-necked phalarope *Phalaropus lobatus*, long-tailed skua *Stercorarius longicaudus*, two-barred crossbill *Loxia leucoptera,* and rustic bunting *Emberiza rustica*) declined to less than half in protected areas, and the density of only one species, the waxwing (*see* above), increased in protected areas. Interestingly, the two-barred crossbill was the only species predicted to disappear by 2051–2080 under both of the climate scenarios studied (Virkkala *et al*. 2008) and its mean density declined by almost 70% in protected areas from 1981–1999 to 2000–2009. However, the two-barred crossbill exhibits very large year-to-year density variations, depending on the spruce seed crop (Virkkala 1989), so the results are susceptible to stochastic variation.

Among the species showing the greatest decline, there were also some southern species (four out of the 12 species). All of these southern species (the wryneck *Jynx torquilla*, greenish warbler *Phylloscopus trochiloides*, wood warbler *Ph. sibilatrix*, and scarlet rosefinch *Carpodacus erythrinus*) are long-distance migrants, many of which have been observed to have declined in the past few decades (Väisänen 2006). Dentities of many long-distance migrants wintering in Africa or South Asia have decreased in Europe (Sanderson *et al*. 2006). Based on climate variables, the winter ranges of trans-Saharan migrants were predicted to decline by 2100 for several species — by more than 50% for 16 out of the 37 species studied (Barbet-Massin *et al*. 2009).

Therefore, it seems that the average quantitative population changes observed in protected areas are in line with the predictions of range reductions of these species. Population decline of northern bird species is apparently in progress in natural habitats of protected areas.

Conclusions

Because of climate change, latitudinal poleward density shifts are taking place, and they are probably observable far in advance of the actual latitudinal poleward range shifts. This also means that quantitative census data sets are extremely valuable and important in verifying species' latitudinal poleward shifts. Studies in protected areas, where land use is minimized, are crucial in detection of these patterns in relation to climate change.

It should be emphasized that the protected area network itself should be large and connected, to minimize the negative effects of climate warming (Hannah *et al*. 2007). Among the protected areas of the world's 14 main biomes, the climate is expected to change most rapidly by 2100 in boreal protected areas (Loarie *et al*. 2009). Therefore, in conservation planning, future range and density shifts of species should also be taken into account, to ensure that protected areas preserve biodiversity in the future (*see* Araújo *et al*. 2004, 2011).

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Appendix. Number of observations of species on the transects in 1981–1999 and in 2000–2009. The distribution pattern of species (W = whole country, including sporadic distribution; S = southern, N = northern) is presented. Species breeding on buildings — the swallow *Hirundo rustica* and house martin *Delichon urbica* — and observed only occasionally were not included.

Species	1981–1999	2000–2009	Distribution pattern
Bittern *Botaurus stellaris*	0	3	S
Honey buzzard *Pernis apivorus*	9	13	S
White-tailed eagle *Haliaetus albicilla*	2	8	W
Marsh harrier *Circus aeruginosus*	1	1	S
Hen harrier *C. cyaneus*	51	22	N
Goshawk *Accipiter gentilis*	40	32	W
Sparrowhawk *A. nisus*	24	11	S
Buzzard *Buteo buteo*	38	12	S
Rough-legged buzzard *B. lagopus*	113	38	N
Golden eagle *Aquila chrysaetos*	17	17	N
Osprey *Pandion haliaetus*	36	26	W
Kestrel *Falco tinnunculus*	34	29	W
Merlin *F. columbarius*	33	28	N
Hobby *F. subbuteo*	36	37	S
Gyrfalcon *F. rusticolus*	1	0	N
Peregrine falcon *F. peregrinus*	18	24	N
Hazel grouse *Bonasa bonasia*	305	279	S
Willow grouse *Lagopus lagopus*	406	389	N
Ptarmigan *L. muta*	59	45	N
Black grouse *Tetrao tetrix*	766	862	S
Capercaillie *T. urogallus*	351	271	W
Pheasant *Phasianus colchicus*	3	1	S
Water rail *Rallus aquaticus*	1	0	S
Spotted crake *Porzana porzana*	6	1	S
Corncrake *Crex crex*	2	1	S
Crane *Grus grus*	827	1014	W
Oystercatcher *Haematopus ostralegus*	1	3	S
Little ringed plover *Charadrius dubius*	2	0	S
Ringed plover *C. hiaticula*	51	34	N
Dotterel *C. morinellus*	46	28	N
Golden plover *Pluvialis apricaria*	1477	1589	N
Lapwing *Vanellus vanellus*	430	280	S
Temminck's stint *Calidris temminckii*	35	10	N
Dunlin *C. alpina*	68	56	N
Broad-billed sandpiper *Limicola falcinellus*	234	245	N
Ruff *Philomachus pugnax*	667	224	N
Jack snipe *Lymnocryptes minimus*	360	270	N
Snipe *Gallinago gallinago*	2205	1921	W
Woodcock *Scolopax rusticola*	82	40	S
Black-tailed godwit *Limosa limosa*	1	2	S
Bar-tailed godwit *L. lapponica*	20	44	N
Whimbrel *Numenius phaeopus*	967	1036	N
Curlew *N. arquata*	582	829	S
Spotted redshank *Tringa erythropus*	300	252	N
Redshank *T. totanus*	49	68	W
Marsh sandpiper *T. stagnatilis*	1	0	S
Greenshank *T. nebularia*	1208	1254	N
Green sandpiper *T. ochropus*	650	556	S
Wood sandpiper *T. glareola*	5351	4572	N
Common sandpiper *Actitis hypoleucos*	257	170	W
Red-necked phalarope *Phalaropus lobatus*	191	148	N

continued

Appendix. Continued.

Species	1981–1999	2000–2009	Distribution pattern
Long-tailed skua *Stercorarius longicaudus*	126	127	N
Stock dove *Columba oenas*	2	3	S
Woodpigeon *C. palumbus*	250	310	S
Turtle dove *Streptopelia turtur*	1	0	S
Cuckoo *Cuculus canorus*	5392	4784	W
Eagle owl *Bubo bubo*	4	1	S
Snowy owl *Nyctea scandiaca*	0	9	N
Hawk owl *Surnia ulula*	38	19	N
Pygmy owl *Glaucidium passerinum*	4	7	S
Ural owl *Strix uralensis*	6	6	S
Great grey owl *S. nebulosa*	11	1	N
Short-eared owl *Asio flammeus*	51	63	N
Tengmalm's owl *Aegolius funereus*	5	2	W
Swift *Apus apus*	300	188	S
Wryneck *Jynx torquilla*	205	65	S
Grey-headed woodpecker *Picus canus*	1	2	S
Black woodpecker *Dryocopus martius*	273	239	S
Great spotted woodpecker *Dendrocopos major*	1337	1502	S
White-backed woodpecker *D. leucotos*	0	1	S
Lesser spotted woodpecker *D. minor*	10	9	W
Three-toed woodpecker *Picoides tridactylus*	258	298	N
Skylark *Alauda arvensis*	40	57	S
Sand martin *Riparia riparia*	43	12	W
Tree pipit *Anthus trivialis*	11777	7769	W
Meadow pipit *A. pratensis*	7424	5438	N
Red-throated pipit *A. cervinus*	22	13	N
Yellow wagtail *Motacilla flava*	4498	3059	N
Grey wagtail *M. cinerea*	1	5	W
White wagtail *M. alba*	520	326	W
Waxwing *Bombycilla garrulus*	152	712	N
Dipper *Cinclus cinclus*	7	14	N
Wren *Troglodytes troglodytes*	238	330	S
Dunnock *Prunella modularis*	686	597	S
Robin *Erithacus rubecula*	2711	2335	S
Thrush nightingale *Luscinia luscinia*	4	1	S
Bluethroat *L. svecica*	1092	710	N
Red-flanked bluetail *Tarsiger cyanurus*	34	95	N
Redstart *Phoenicurus phoenicurus*	7696	7881	W
Whinchat *Saxicola rubetra*	505	563	W
Wheatear *Oenanthe oenanthe*	737	319	W
Ring ouzel *Turdus torquatus*	38	16	N
Blackbird *T. merula*	83	244	S
Fieldfare *T. pilaris*	551	930	W
Song thrush *T. philomelos*	4550	4427	S
Redwing *T. iliacus*	5383	4629	W
Mistle thrush *T. viscivorus*	890	1050	S
Grasshopper warbler *Locustella naevia*	2	0	S
Sedge warbler *Acrocephalus schoenobaenus*	755	234	W
Blyth's reed warbler *A. dumetorum*	3	3	S
Reed warbler *A. scirpaceus*	1	0	S
Icterine warbler *Hippolais icterina*	24	4	S
Lesser whitethroat *Sylvia curruca*	261	231	S
Whitethroat *S. communis*	26	11	S
Garden warbler *S. borin*	769	314	S

continued

Appendix. Continued.

Species	1981–1999	2000–2009	Distribution pattern
Blackcap *S. atricapilla*	35	30	S
Greenish warbler *Phylloscopus trochiloides*	91	41	S
Arctic warbler *Ph. borealis*	22	6	N
Wood warbler *Ph. sibilatrix*	1220	264	S
Chiffchaff *Ph. collybita*	414	255	S
Willow warbler *Ph. trochilus*	44046	27568	W
Goldcrest *Regulus regulus*	1845	1318	S
Spotted flycatcher *Muscicapa striata*	4658	3717	W
Red-breasted flycatcher *Ficedula parva*	32	33	S
Pied flycatcher *F. hypoleuca*	3485	2202	W
Long-tailed tit *Aegithalos caudatus*	1	8	S
Willow tit *Parus montanus*	1297	1054	W
Siberian tit *P. cinctus*	254	146	N
Crested tit *P. cristatus*	515	438	S
Coal tit *P. ater*	27	21	S
Blue tit *P. caeruleus*	15	74	S
Great tit *P. major*	964	1651	S
Treecreeper *Certhia familiaris*	512	500	S
Golden oriole *Oriolus oriolus*	6	2	S
Red-backed shrike *Lanius collurio*	30	13	S
Great grey shrike *L. excubitor*	27	40	N
Jay *Garrulus glandarius*	71	75	S
Siberian jay *Perisoreus infaustus*	453	356	N
Magpie *Pica pica*	21	11	W
Nutcracker *Nugifraga caryocatactes*	1	0	S
Hooded crow *Corvus corone cornix*	757	468	W
Raven *C. corax*	622	465	W
Starling *Sturnus vulgaris*	10	0	S
Chaffinch *Fringilla coelebs*	16801	14892	S
Brambling *F. montifringilla*	29552	17517	N
Greenfinch *Carduelis chloris*	9	47	S
Siskin *C. spinus*	7474	7681	S
Twite *C. flavirostris*	17	0	N
Redpoll *C. flammea*	7464	4405	N
Two-barred crossbill *Loxia leucoptera*	359	108	N
Crossbill *L. curvirostra*	4445	2908	W
Parrot crossbill *L. pytyopsittacus*	247	237	W
Scarlet rosefinch *Carpodacus erythrinus*	221	65	S
Pine grosbeak *Pinicola enucleator*	147	84	N
Bullfinch *Pyrrhula pyrrhula*	1245	911	S
Lapland bunting *Calcarius lapponicus*	1138	1552	N
Snow bunting *Plectrophenax nivalis*	153	75	N
Yellowhammer *Emberiza citrinella*	87	125	S
Ortolan bunting *E. hortulana*	5	0	S
Rustic bunting *E. rustica*	1776	502	N
Little bunting *E. pusilla*	71	26	N
Reed bunting *E. schoeniclus*	1970	1402	W