# “Influence of habitat and climate change on European bird communities”

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## 1 ABSTRACT OF THE THESIS

Forest fragmentation, habitat loss, the invasion of exotic species, and climate change are important environmental factors influencing ecological communities. Birds seem to be qualified as pioneer indicators for environmental changes and, in particular, for changes related to global warming. For my thesis, I used a macroecological approach. First, I reviewed the effects of global climate change on the size and position of geographic ranges and the richness and composition of bird communities from the literature. Plenty of evidence exists demonstrating that range boundaries of birds are correlated with climatic factors. Range shifts in northern direction have been observed for several temperate bird species. For bird communities, increases in species richness are predicted for northern latitude and high-elevation sites and declines of species richness in arid regions. With increasing winter temperature, declines in the proportion of migratory species in bird communities have been predicted and observed. Secondly, I investigated the impact of climate change on the structure of bird communities on a European scale. To test whether changes in the composition of bird communities have been influenced by recent climate change, I focused on the proportion of migratory and resident bird species because migratory birds are expected to respond differently to climatic change than resident birds. I used the spatial dependence of bird community structure on climatic factors (temperature of the coldest month, spring temperature, spring precipitation) in Europe to predict changes in 21 European bird communities under recent climate change. I used bird atlas data for observed changes in the bird communities and compared them with expected changes calculated from a spatial regression model. Observed changes corresponded significantly to predicted changes and could not be explained by effects of spatial autocorrelation or alternative factors such as changes in land-use. Thirdly, I analyzed changes in species abundance and range size in a central European bird community to quantify the impact of habitat degradation, the introduction of exotic species, and climate change. I demonstrated that changes in regional abundances from 1980-1981 to 2000-2003 were influenced by their breeding habitat, latitudinal distribution, and migratory behaviour. Significant declines were found in populations of farmland species, in long-distance migrants, and in species with more northern distributions. Persisting declines in long-distance migrants and declines especially in northern species indicate that climate change might be currently the most important threat for birds in Europe.

# 2 GENERAL INTRODUCTION

Changes in the environment as a result of anthropogenic impacts are increasingly influencing animal and plant communities during the last decades (Soulé 1990, Sekercioglu et al. 2004). Changes in vegetation, land-use, and climate are the main factors thought to be responsible for changes in biodiversity (Sala et al. 2000, Donald et al. 2001, Walther et al. 2002). In several ecoregions biodiversity and ecological function are at great risk because of extensive habitat conversion. Among these regions are some of the most biologically distinctive, species-rich ecosystems on Earth, as well as the last home of many threatened and endangered species (Hoekstra et al. 2005). Beside habitat conversion, the invasion of new species increasingly affects the composition of ecological communities (Drake et al. 1989, Williamson 1996). In addition to habitat conversion and biological invasions, global climate change has been shown to strongly affect the Earth's flora and fauna (Parmesan 1996, Forchhammer et al. 1998, Lemoine & Böhning-Gaese 2003). Global warming is observable influencing the phenology, reproductive success, abundance, range size and range position of several plant and animal species (Peñuelas & Filella 2001, Walther et al. 2002, Root et al. 2003).

## 2.1 BIRD AS INDICATORS FOR ENVIRONMENTAL CHANGES

Birds are a very well-studied group of organisms and respond rapidly to environmental changes. They are very mobile and have an active metabolism. Therefore, they can react immediately to environmental changes. Birds seem to be highly influenced by the current changes in vegetation, land-use, and climate (Gaston et al. 2003, Böhning-Gaese & Lemoine 2004, Watkinson et al. 2004), and by invasive species (Blackburn & Duncan 2001, Duncan et al. 2003). As a result, birds seem to be eminently qualified as a pioneer indicator group for environmental changes (Juutinen & Mönkkönen 2004, Schulze et al. 2004, Tankersley 2004, Venier & Pearce 2004). Consequently, bird communities have already been used as indicators for changes in land-use, forest management, and for changes in other taxonomic groups in several studies (e.g. Gregory et al. 2004, Schulze et al. 2004, Tankersley 2004, Müller et al. 2005).

## 2.2 IMPACT OF ENVIRONMENTAL CHANGES ON BIRDS

One important factor influencing bird communities might be the increasing intensity of land-use. The general agricultural intensification has been identified as a major cause of declines in farmland bird populations, although species respond differently according to their ecology (Fuller et al. 1995, Chamberlain et al. 2000). Another factor influencing the indigenous avifauna might be the introduction of species to areas beyond the limits of their natural distribution. A growing number of species have been transported and introduced by humans to new locations and have established self-sustaining wild populations. Despite the fact that only a proportion of these introductions have resulted in the establishment of new populations (Long 1981, Drake et al. 1989, Duncan et al. 2003), many of these species may cause significant environmental damage (Williamson 1996, Mack et al. 2000). In addition to habitat conversion and invasive species, global climate change has been shown to strongly affect bird communities (Lemoine & Böhning-Gaese 2003, Crick 2004, Møller et al. 2004). Range expansions of bird species have already been documented in several studies (e.g. Johnson 1994, Thomas & Lennon 1999, Peterson 2003a, Böhning-Gaese & Lemoine 2004), and as climate continues to change further alteration of many species' ranges can beexpect. In France, for example, northerly distributed bird species were observed to be more negative growth rates than species with a southern distribution. These results seem to reflect the impact of global climate warming (Julliard et al. 2003).

## 2.3 MIGRATORY BEHAVIOUR

Bird migration is one of the most interesting phenomena in ornithology. Migratory birds are birds of two worlds, breeding in the temperate zone, then living as tropical birds for most of the year. Several long-distance migratory bird species breed in northern Europe and migrate to Africa or Asia to overwinter in tropical areas. Short-distance migratory bird species overwinter in the Mediterranean region. Long-distance migrants solve the problem of severe winter conditions in the temperate zone and escape from the highly competitive breeding situation in the tropics. Contrary to the tropics, resident birds in temperate regions are probably limited by food resources during the winter (Martin 1987). A high proportion of the resident avifauna does not survive severe winter conditions in temperate regions (Newton 1998). Consequently, resident birds in spring can consume only a small part of the abundant springtime food resources. Incoming migrants, arriving on their breeding ground, can use the food abundance and share the existing resources with overwintering residents. After the breeding season, migratory birds leave their breeding area and, with it, the impending lack of food during the winter, to spend the non-breeding season in tropical areas.

### 2.4 EFFECT OF CLIMATE CHANGE ON MIGRATING BIRDS

For many bird species the influence of climate change could be interpreted as a rather positive effect. If winter temperature for example increases, more resident birds might survive, with increasing mean annual temperature, birds can probably start breeding earlier and migratory birds might stay longer and have more broods. However, in some regions declines especially in long-distance migrants have been detected. In the Lake Constance region, Central Europe, for example, a significant decline in the abundance of long-distance migratory birds between 1980-1981 and 1990-1992 could be observed, while short-distance migrants and resident birds did not change (Böhning-Gaese & Bauer 1996). These declines in the proportion of long-distance migrants were in line with isochronic temperature and precipitation changes (Lemoine & Böhning-Gaese 2003).

### 2.5 A MACROECOLOGICAL APPROACH

In the last two decades macroecology has become a respectable discipline within the biological sciences. Macroecology is the study of abundance and distribution of species at large spatial and temporal scales (Brown & Maurer 1989, Brown 1995, Blackburn & Gaston 1998, Maurer 1999). Using a macroecological approach instead of studying separate components in the relationship of organisms and their environment may allow the understanding of ecological systems and reveal patterns in the whole that are not evident in the separate parts ("top-down" approach). This is contrary to the traditional "bottom-up" approach which tries to clarify questions by investigating the component parts (Gaston & Blackburn 2000). The most important advantage of the large-scale approach is the distant view a scientist has on ecological systems where the idiosyncratic details disappear and only the important generalities remain (Brown 1995).

## 2.6 AIMS OF THE THESIS

In this thesis I investigated the influence of environmental changes on European bird communities using a macroecological approach. One aim was to review the literature to evaluate the importance of climate change for the ranges, communities and conservation of birds. Range changes and, therefore, changes in the composition of bird communities are some of the expected responses of birds to global warming. A second aim was to test whether temporal changes in European bird communities could be explained by global climate change. Therefore, I used the spatial relationship between bird community structure and climatic conditions in Europe to calculate changes in the composition of European bird communities which can be expected when climate changed. As a third aim I investigated temporal changes in a single bird community in the Lake Constance region to analyse the main factors influencing the bird community and to quantify the degree to which climate change is affecting the composition of bird communities.

This thesis consists of three major chapters (chapter 3-5) which can be read independently. The first of these three chapters is a review of the literature, the following two chapters are organized like journal publications containing an introduction, followed by a methods, results and discussion section and by a brief summary. The thesis closes with general conclusions including the deliverables of all three chapters.

In chapter 3, I focused on the effects of global climate change on the size and position of geographic ranges and the richness and composition of bird communities. First I gave an overview to what extent climate changed until now, why these changes in climate can influence the birds’ ranges and communities and how effects of climate change on birds can be analysed. Second, I reviewed the impact of climate change on the ranges of birds and on avian communities according to the literature. A basic understanding of the impact that climate change has on the birds’ ranges and on bird communities, was important to understand the consequences of climate change on the bird community structure which can be expected from several modelling approaches and allowed a comparison of modelled and observed consequences.

In chapter 4, I investigated the impact of climatic changes on the composition of bird communities on a large spatial scale (100 x 100 km) in Europe. I analysed temporal changes in 21 bird communities in Europe in the last decades. My aim was to detect changes in the proportion of migratory and resident bird species and to compare these observed changes with changes I would expect from the spatial relationship between bird community composition and climate (Lemoine & Böhning-Gaese 2003). I, furthermore, tested whether temporal changes in bird communities could be explained by spatial autocorrelation effects or by alternative factors such as changes in forest area and the intensity of agricultural land-use. In the case that observed and expected changes in bird community composition showed a good congruence and spatial autocorrelation or alternative factors were of minor importance, the spatial relationship between bird community composition and climate can be used to make future predictions for changes in European bird communities using climate change scenarios.

To identify the main factors influencing changes in a regional bird community I analysed in chapter 5 the impact of environmental changes like habitat conversion, the invasion of exotic bird species, and climate change on population trends in a bird community in Central Europe. The analysis included temporal changes in abundance and range size of 159 bird species in the bird community of the Lake Constance region. These investigations were made on a small spatial scale (2 x 2 km). I examined the impact changes in land-use, climate and the impact of invasive species by contrasting the population trends of birds differing in breeding habitat, latitudinal distribution, origin (exotic versus native), and migratory behaviour.

# 3 IMPORTANCE OF CLIMATE CHANGE FOR THE RANGES, COMMUNITIES AND CONSERVATION OF BIRDS

## 3.1 INTRODUCTION

Recent climate change has been shown to have significant influence on numerous plant and animal species in North America and Europe (Grabherr et al. 1994, Parmesan 1996, Hill et al. 1999, Parmesan et al. 1999, Kirschbaum 2000, Parmesan et al. 2000, Cameron & Scheel 2001, Walther et al. 2001, Warren et al. 2001, Bale et al. 2002, Hill et al. 2002, Shine et al. 2002, Konvicka et al. 2003, Parmesan & Yohe 2003, Root et al. 2003). Especially compelling evidence has been found for the impact of global climate change on the phenology, breeding biology and population dynamics of birds. One important open question is if global climatic change has consequences for the geographic ranges of birds and bird communities. Range contractions, local extinctions and declines in species richness are three of the most frequently used indicators of changing environments that often initiate conservation action. Thus, it is of special interest to search for potential effects of global climate change on ranges and communities. If such effects are found, this might lead to modifications in conservation policy and practice to anticipate and to deal with the most pressing effects of global climate change on birds.

Changes in climate should lead to changes in the geographic ranges of birds. In a changing climate species can respond by (1) evolutionary adaptation, i.e. true evolutionary change, (2) phenotypic adaptation, i.e. phenotypic plasticity, (3) movement, and (4) extinction (Peterson et al. 2001). The result can be changes in geographic ranges, with possible differences between changes in breeding and non-breeding ranges. For example, if a population of short-distance migratory birds gradually evolves lower levels of migratory restlessness this would lead to increasing numbers of individuals staying on the wintering grounds and, simultaneously, a possible extension of the wintering range (Berthold 2000).

Through changes in species' geographic ranges, changes in climate can also lead to changes in species richness of bird communities. Changes in species richness have to be studied explicitly because effects of climate change on the ranges of individual bird species do not necessarily lead to changes in species richness (Lennon et al. 2000). For example, if temperature increases at a site, the area might loose species whose southern range boundaries move north, but one might gain southern species. It could be possible to predict the range changes of the individual species using for example the Genetic Algorithm for Rule-set Prediction (GARP, Stockwell & Noble 1992, Stockwell & Peters 1999). However, the interactions of a species with its habitat, resources, competitors, predators and parasites might change as well and make predictions unreliable (Schwartz 1992, Davis et al. 1998). Thus, species richness might decline, remain stable or even increase depending on the net effect of local extinctions and colonisations.

Furthermore, climate can be expected to lead to changes in the composition of bird communities. For example, increases in winter temperature but not in temperature during the breeding season should lead to colonisation of resident species and local extinctions of migratory species with a corresponding decline in the proportion of migratory species within the community (Lemoine & Böhning-Gaese 2003). In this chapter I, therefore, focus on the effects of global climate change on the size and position of geographic ranges and the richness and composition of bird communities. I then use these results to evaluate consequences for the conservation of birds.

## 3.2 CHANGES IN CLIMATE

Changes in climate that influence birds' ranges and communities are, first, increases in mean annual temperature. Warming occurred most rapidly during the periods 1925-1944 and 1978-1997 (Jones et al. 1999). In all probability, warming did not stop 1997, but newer data were not included in the cited reference. Ranges of species, however, are potentially influenced more by minimum than by average temperatures. Recent analyses of the changes in minimum and maximum temperature demonstrated that annual minimum temperatures increase more strongly than annual maximum temperatures (Easterling et al. 1997, Currie 2001). This leads to a decrease in intra-annual seasonality. Furthermore, temperature changes are spatially heterogeneous with higher temperature increases expected at higher latitudes. In addition, temperature changes seem to differ between continents. While Eurasia has shown an overall warming trend since the early 1970s, North America exhibits warming at a lower rate and even a slight cooling trend during the last 50 years in the eastern United States (Bogaert et al. 2002).

Land surface precipitation is another important factor influencing birds' ranges and communities. Precipitation increased about 0.5-1% per decade since the late 1960' in mid- to high latitudes, but showed a decadal decrease of 0.3% in the tropics and subtropics (IPCC 2001). Further, extreme weather events like extremely cold winters or long droughts are known to influence species' ranges and have been demonstrated to increase in frequency and intensity (Easterling et al. 2000). Finally, pronounced effects on birds' ranges and communities are expected through indirect effects of global climate change, in particular changes in fire regimes, vegetation, and land use. As one of the most severe threats one can consider rising sea levels which might lead to severe habitat loss in coastal areas, with the heaviest impact on intertidal habitat, salt marshes and sandy beaches (Galbraith et al. 2002, Kont et al. 2003). Theoretically it appears possible that rising sea levels also generate new habitats. However, in most coastal regions, e.g. the Wadden Sea, the coastline is "fixed" by artificial dikes.

## 3.3 HOW TO ANALYSE THE EFFECT OF CLIMATE CHANGE

While it is not difficult to delineate theoretically the consequences climate change has on birds' ranges and communities, it is a great challenge to actually demonstrate a causal relationship between changes in climatic factors and e.g. northward extension of a species' range. A number of different approaches have been taken:

1. A traditional approach has been to correlate the range of a species, particularly the range boundary, with a climatic variable over a latitudinal or an elevational gradient (Root 1988). Similarly, species richness or community composition has been correlated with climatic factors (Mac Arthur 1972, Currie 2001). This approach demonstrates only that climatic

factors are directly, or indirectly, involved in influencing ranges and communities. The approach does not show that climate change *causes* changes in ranges and communities.

2. In a second approach the correlation between climatic factors on the one hand and species' ranges and communities on the other hand has been used to predict changes in the face of expected climatic change. In most studies investigators established the relationship between e.g. the presence of a species or between species richness in a grid cell and the climatic factors of this grid cell, then used global circulation models (GCM) to calculate expected changes in the climatic factors in the respective grid cell and, finally, predicted the change in the presence of the species or in species richness (Currie 2001, Peterson et al. 2001, 2002, Peterson 2003b). This is the only method to gain an understanding about the magnitude that potential effects of climate change have on ranges and communities. The method, however, has a number of limitations: (a) It depends on the accuracy and resolution of the GCMs (Currie 2001, Peterson et al. 2001). (b) In a number of studies, predicted changes in climate lead to temperature or precipitation levels that were outside the range of variables in the contemporary data set. Predicted values for presence of a species or species richness in the respective areas may therefore be suspect (Currie 2001). (c) The studies about range changes, conducted so far, were limited to a politically defined region, e.g. Mexico. Species that are predicted to move their ranges outside this region will be noted as going locally extinct. It is, however, not possible to predict which species might expand the ranges into Mexico and colonise the region. This leads to a bias towards losses when predicting changes in species richness (Peterson et al. 2002). 4. The range models assume that present range boundaries are controlled only by climatic factors. Changes in biotic interactions might make predictions unreliable (Davis et al. 1998, Hulme 2003, Pearson & Dawson 2003).

3. In a third approach, observed changes in the ranges of species or in communities have been attributed to global climate change. For example, in the presence of a warming climate British birds showed a mean northward shift of the northern range boundary with no systematic shift of the southern range boundary (Thomas & Lennon 1999). In these studies, the authors have accumulated evidence that the observed changes are caused by climate change. For example, the changes conformed to a model that predicts how strong the change should be (given e.g. the spatial relationship between climatic factors and species richness and given the observed

climatic change; Lemoine & Böhning-Gaese 2003). Other authors used as evidence that the site under study has experienced climatic change, that the range boundary of the species under study correlates with a climatic factor, or that the species under study shows a fitting physiological temperature tolerance towards high or low temperatures (Thomas & Lennon 1999). Furthermore, some authors tested explicitly alternative factors. For example, Thomas and Lennon (1999) showed that the northward extension of a species' range is not correlated with a general increase in the abundance and range size of the species.

## 3.4 INFLUENCE OF CLIMATE CHANGE ON THE RANGES OF BIRDS

In this and the following section I present evidence that birds' ranges and communities are influenced by climate change. The structure of the two sections follows, in general, the three approaches described above. First, I assess evidence that the current ranges of species and the current richness and composition of bird communities are correlated with climatic factors. I use these correlations to make predictions that changes should occur under climate change. Second, I present the results of modelling approaches that analyse the potential impact of climate change on ranges and communities. Third, I review the literature about actually observed influences of global climate change on ranges and communities. Finally, I evaluate whether the changes I predicted were confirmed by the modelling and observational studies.

### 3.4.1 CORRELATIONS OF CLIMATIC FACTORS AND RANGE BOUNDARIES

For birds plenty of evidence exists demonstrating that range boundaries are correlated with climatic factors (for reviews see Brown & Lomolino 1998, Gaston 2003, Newton 2003). In a classic study, for example, Root (1988) demonstrated that 62 species of North American passerines and non-passerines have a northern range boundary that was associated with a particular January isotherm, with different species associated with different isotherms. Root (1988) suggested that the northern range limit is influenced by physiological constraints. This is supported by the fact that the metabolic rate of the species at the January temperature prevailing at the northern boundary was calculated at about 2.5 times the basal metabolic rate (but see Repasky 1991, Root & Schneider 1993). Other factors that are correlated with climatic factors and that might indirectly determine the northern range boundary are day length (influencing the time period available for foraging), and the presence of abundant, energy-rich food resources. In addition, northern range limits of breeding distributions might be influenced by high wetness as in Britain for example. There, the Capercaillie (*Tetrao urogallus*) may be limited in distribution by high rainfall, which leads to poor chick survival (Moss 1986).

In contrast, evidence exists that the southern range boundary of birds can be associated with heat or lack of water. The Black-billed Magpie (*Pica pica*) in North America, for example, has a heat limit of 40°C, while the related Yellow-billed Magpie (*Pica nuttali*) is more heat tolerant. Correspondingly, the Black-billed Magpie is confined to cooler areas, while the Yellow-billed Magpie can live in hotter areas (Hayworth and Weathers, 1984). The fact that lack of drinking water can limit bird distribution is shown by the failure of most species to penetrate far into deserts. When water is made available by humans, e.g. by providing drinking sites for cattle and sheep as in Australia, this can lead to range expansions of birds (Saunders & Curry 1990). Again, rainfall can act on birds also indirectly via the food supply of insects, flowers, and seeds (Newton 2003).

In general, the northern range limit of species seems to be influenced largely by abiotic factors such as cold temperatures or high wetness (MacArthur 1972, Newton 2003). The southern range limit of species might be influenced, on the one hand, by climatic factors such as heat or lack of water in regions in which they are limiting factors, e.g. in arid regions (Newton 2003). On the other hand, in more humid regions, biotic factors such as interspecific competition, predation, and parasitism might play a more pronounced role (Dobzhansky 1950, MacArthur 1972, Brown & Lomolino 1998, Hofer et al. 1999, Gross & Price 2000).

Given the observed changes in climate and my current knowledge about factors influencing range boundaries I can make predictions about the consequences of global climate change. With increasing annual temperatures, especially increasing minimum temperatures and increasing temperatures especially at high latitudes I would expect northward range expansions of birds at high altitudes and in temperate, boreal, and arctic regions. In contrast, with increasing temperatures and decreasing precipitation in subtropical and tropical regions, I would expect range contractions in the respective areas. Certainly, these predictions have to be treated with great care because indirect interactions between abiotic and biotic factors can lead to unexpected patterns, especially when trying to make forecasts for individual species. Particularly difficult to anticipate are changes in southern range boundaries in cases in which abiotic factors are not limiting and in which range boundaries are determined by a complex interplay of biotic factors or by certain vegetation types which might themselves be influenced by climate change (Thomas & Lennon 1999).

### 3.4.2 MODELLED CONSEQUENCES OF CLIMATE CHANGE FOR RANGE BOUNDARIES

A pivotal study that analysed the potential effects of global climate change on birds' range, using modelling approaches, was conducted by Peterson et al. (2001, Tab. 3.1, Fig. 3.1).

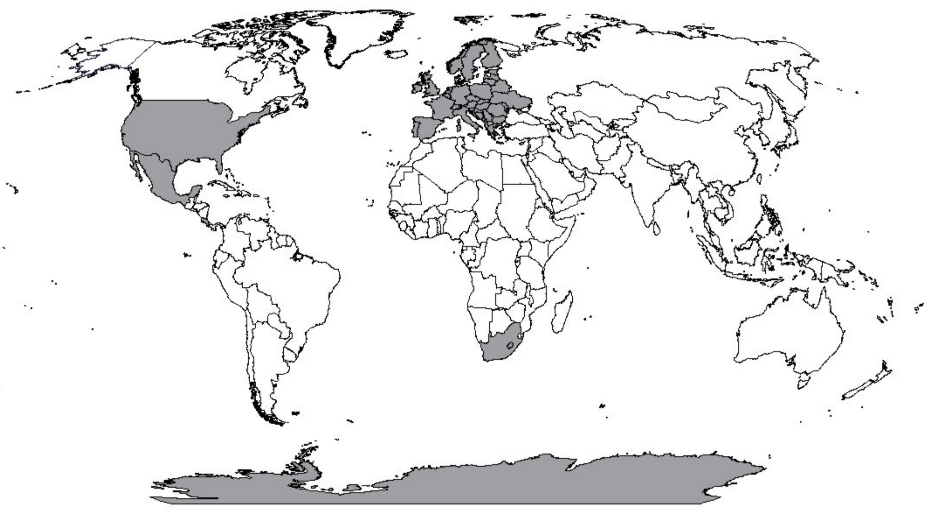


Fig. 3.1: Countries in which recent studies about the consequences of climate change for range boundaries or community composition of birds were conducted.

They described the current distribution of eight Mexican Cracidae species with an ecological niche model relating the presence of each species at a concurrent site to the environmental variables. They then used two GCMs, one conservative and one less conservative model, to calculate the climatic change during the next 50 years. For each climate scenario they evaluated the expected change in species' distributions under three assumptions regarding different dispersal abilities of the species (no dispersal, dispersal to contiguous areas and universal dispersal) and compared them with the current distribution of each species. Based on the two different scenarios of climate change and the three assumptions concerning species' dispersal abilities, the effects on species distributions show a great variety of patterns from radical reduction to moderate increases. These idiosyncratic changes of range boundaries for the different species indicate that the effects of climatic change can differ very much, depending on species, GCM, and dispersal scenario.

To find more general patterns in predicted range changes, Peterson (2003a, Tab. 3.1, Fig. 3.1) compared predicted changes of montane and lowland species. He expected to find that high-altitude species are especially threatened by climate change because increasing temperatures can reduce high-altitude habitat areas with associated range contractions and potential loss of high-altitude species (McDonald & Brown 1992). He compared expected range changes of 26 species restricted to the Rocky Mountains and 19 species restricted to the Great Plains using the same general approach as in Peterson et al. (2001). The results, however, did not fit the expectations. The predicted range reductions and range shifts of montane species were smaller than for the lowland species.

These results were attributed to the fact that much more dramatic horizontal shifts would be expected in lowland systems simply because of the geometry of the landscape, given the same intensity of temperature shifts. However, predictions might be different for highest-montane species that were not included in the data set (Peterson 2003b).

In contrast to these marginal effects on high-altitude species, more negative consequences were predicted for high-latitude, arctic species. Zöckler and Lysenko (1994, Tab. 3.1, Fig. 3.1) correlated the current distribution of 23 Arctic water bird species with the current vegetation, and then modelled the likely changes in the vegetation to investigate the impacts that this would have on species' distributions. For mapping vegetation changes, the Mapped Plant Soil System (MAPSS) equilibrium biogeography model was used, which links vegetation to climate. Two GCMs were then used to project the climate conditions with $CO_2$ doubling, which predicts a temperature increase of 4 to 7°C for Arctic latitudes. The majority of Arctic water birds spend their breeding season in areas of tundra vegetation. Changes in vegetation patterns will be most extreme for tundra areas. With climate warming it is expected that taiga and boreal forests expand their distribution towards the north. Overall losses of current tundra distribution are estimated between 40 and 57%, with most being replaced by forest. New tundra areas amount to only 5%. Assuming that habitat area is a limiting factor, and that birds are evenly distributed within their ranges, the predicted change in vegetation could mean, e.g., a loss of almost half of the total goose population.

Tab. 3.1: Modelled changes in the ranges and communities of birds attributed to future climate change.

| Reference | Variable modelled | Species modelled | Change | Method | Region |
|---|---|---|---|---|---|
| Zöckler & Lysenko 1994 | Breeding area | 23 Arctic bird species | Loss of breeding habitat, decrease of almost 50% of total goosese population | MAPSS model,<br>HadCM2GSa1 model,<br>UKMO model, $CO_2$ x 2,<br>4°-7° temperature increase | Tundra of northern hemisphere |
| Peterson et al. 2001 | Geographic distribution | 8 cracid species | Radical reductions to moderate increases | GARP model,<br>2 GCMs,<br>3 dispersal abilities,<br>$CO_2$ x 2 | Mexico |
| Benning et al. 2002 | Elevational range of disease vector | 10 forest birds | Range contractions of 10 endangered forests bird species | 30-m U.S. Geological Survey digital elevation model, 2°C temperature increase | Hawaiian Islands |
| Peterson 2003b | Geographic range | 26 Rocky Mountain birds,<br>19 Great Plain birds | Range shifts of montane birds smaller than for flatland species | GARP model,<br>2 GCMs,<br>3 dispersal abilities,<br>$CO_2$ x 2 | Central and western North America |
| Erasmus et al. 2002 | Geographic range | 34 bird,<br>19 mammal,<br>50 reptile,<br>19 butterfly,<br>57 “other invertebrate” species | Some range expansions,<br>most range contractions,<br>western movement towards eastern highlands | GCM,<br>$CO_2$ x 2,<br>2°C temperature increase | South Africa |
| Currie 2001 | Species richness | Birds,<br>mammals,<br>reptiles,<br>Amphibians,<br>Trees | Decrease in bird richness,<br>increase in cooler high-elevation areas, positive effects for reptiles and amphibians | Polynomal regression model of species richness,<br>mean January and July temperature and precipitation,<br>5 GCM,<br>$CO_2$ x 2 | conterminous USA |
| Peterson et al. 2002 | Geographic distribution, species richness | 1179 birds,<br>416 mammals,<br>175 butterflies | Colonizations and increase for major sierras,<br>extinctions and loss for Chihuahuan desert and costal plain | GARP model,<br>2 GCMs,<br>3 dispersal abilities,<br>$CO_2$ x 2 | Mexico |

While the previous studies analysed the impact of climate change on the upper, altitudinal and northern range boundary of birds, only one study described potential effects on the lower, altitudinal range boundary. In this study, Benning et al. (2002, Tab. 3.1, Fig. 3.1) used a modelling approach to predict the consequences global warming has on the distribution of a disease vector and connected changes in the distribution of birds. On the Hawaii islands, the distribution of many endemic Hawaiian bird species is limited by the distribution of the introduced mosquito, *Culex quinquefasciatus*, and the avian malaria that it transmits. The native species are restricted to high elevation forests because they are sensitive to avian malaria, and because the disease vector occurs only at lower elevations. With climate change, the elevational range of *Plasmodium* is expected to increase. Assuming a 2°C increase in temperature, which should occur by some time late in the current century, the forest area with intermediate and low risk of malaria infection is expected to decrease dramatically. This should lead to threatening range contractions of the 10 species of endangered forests birds that are now restricted to these high-elevation forests.

### 3.4.3 OBSERVED CONSEQUENCES OF CLIMATE CHANGE FOR RANGE BOUNDARIES

Actual range changes of birds are documented in many studies (for a summary, see Newton 2003, p. 425). However, in only the following cases have these range changes been explained by climate change. In two first studies, Kalela (1949, 1952, Tab. 3.2, Fig. 3.1) found changes in the distribution for a few mammal and several bird species in Germany and Finland since the 1850's, which he could connect with corresponding changes in winter, spring and/or summer temperature or the desiccation of a species' breeding area. But, as Kalela (1949, 1952) himself pointed out, range expansions, especially in southern Finland, can also be caused by cultural factors. Forest clearings, for example, have created huge areas of new habitat for open country species.

Similar shifts were observed by Burton (1995) in a European-wide study. He found spectacular changes in the breeding ranges of birds since 1900 with differences in the direction in which distributions shifted. He recorded a northwards advance of 195 and a westwards advance of 64 temperate bird species due to climatic warming mostly between 1900 and 1950. At the same time 32 species showed a retreat towards the southern parts and 7 species a retreat towards the eastern parts of their ranges.

Tab. 3.2: Observed changes in the ranges and communities of birds attributed to recent climate change.

| Reference | Variable observed | Species observed | Change | Cause | Time span | Region |
|---|---|---|---|---|---|---|
| Kalela 1949 | Northern range expansions | 37 species | northwards expansion of 17 species | Present climatic changes, increased atmospheric circulation, activities of man | 1850-1950 | Southern Finland and Germany |
| Kalela 1952 | Geographic distribution | 3 mammal, 38 bird species | Northwards expansion | increasing temperature or drying-up of lakes | 1850-1950 | Finland |
| Johnson 1994 | Nesting distribution | 24 bird species | Shift of nesting range mainly in northern direction | increased summer moisture, perhaps higher mean temperature | 1957-1992 | Western United States |
| Burton 1995 | Range expansions | 424 bird species | 195 advancing to north<br>64 advancing to west<br>56 retreating to south<br>7 retreating to east | Climate warming or cooling | 1900-1995 | Europe |
| Thomas & Lennon 1999 | Geographic range | 59 southern bird species, 42 northern bird species | 18.9 km northwards shift of northern boundary | Increasing temperatures | 1968-72 – 1988-91 | UK |
| Peterson 2003a | Geographic distribution | 5 bird species | 3 species northward shifts,<br>1 species southward shift | Global warming | Last 50 years | Great Plains of North America |
| Pounds et al. 1999 | Upper range boundary along elevational gradient | abundance of birds | increases in abundance and colonisation events of premontane species | increase in sea surface temperatures in the equatorial Pacific, altitudinal rise of orographic clouds | 1979-1998 | Monteverde Costa Rica |
| Lemoine & Böhning-Gaese 2003 | % long-distance migratory species | 151 landbird species | 1.76% decline in proportion of long-distance migrants | Warmer winter temperature | 1980-81 – 1990-92 | Lake Constance, central Europe |

Since 1950, 24 temperate bird species retreated to the southern parts of their ranges because of climate cooling. For northern breeding bird species the pattern was quite different. For 52 species, Burton (1995) found a retreat towards the northern parts of their breeding range and for 9 species a southward advance of ranges in response to climate warming. A southward advance of 55 northern breeding birds could be attributed to climatic cooling.

In the most recent European study, Thomas and Lennon (1999, Tab. 3.2, Fig. 3.1) analysed the northern and southern edge of the range of birds in Great Britain. They were the first to use a rigorous statistical, community-wide approach. They used atlas data of 1968-1972 and 1988-1991 and controlled for general range expansions and contractions of the species. They found that the northern range boundaries of 59 southern British bird species moved on average 18.9 km towards the north. Southern range boundaries of 42 northern bird species did not change systematically over the same time period. The authors claim that the most parsimonious explanation for these results was climatic change because recent changes in timing and breeding success of birds were correlated with spring temperatures (Crick et al. 1997, Visser et al. 1998), the spatial distribution of British bird diversity was connected with temperature (Turner et al. 1988), summer temperature was a significant predictor of breeding distribution of 45% of terrestrial and freshwater bird species (Lennon et al. 2000), and the observed shifts in range boundaries were concordant with a period of climate warming.

Range shift were observed not only for European but also for North American bird species. In the western United States Johnson (1994, Tab. 3.2, Fig. 3.1) observed changes for 24 bird species that expanded their breeding distribution over the last 30 years. 14 of them shifted northwards, four moved in the opposite direction, five species shifted in western direction and one species showed radial expansion. He attributed these range expansions to increased summer moisture, perhaps coupled with a higher mean temperature in the region.

In a recent study, Peterson (2003b, Tab. 3.2, Fig. 3.1) found changes in the geographic distributions of five bird species endemic to the Great Plains of North America. Three species showed significant or near-significant northward shifts, and one a significant shift southward. Over all five species examined, colonization events were focused in the northern half of the distributions of the species (5 of 5 species), whereas extinctions tended to be in the southern half of distribution of the species (3 of 5 species). Peterson (2003b) concludes that the changes in distribution have been subtle and might be associated with global climate change.

In addition, it is expected that the, in some regions dramatic, changes in the abundance of southern temperate and Arctic seabird species (chapter 12) also lead to changes in their ranges. For example, at least eight species formed new breeding locations well to the south of their historical range and/or have seen marked population increases at their more southerly colonies since the 19th century on a number of islands off the coast of Western Australia (Dunlop 2001). Similarily, Ainley et al. (1994) observed that colonies of the Adelie Penguin (*Pygoscelis adeliae*) declined and disappeared in the northern and increased in the southernmost part of the species' range during the last 50 years. However, for these species it is difficult to connect range changes with climate change because the populations are heavily influenced by El Niño Southern Oscillation activity which might itself change in frequency and intensity by climate change (chapter 5).

There were some anecdotal evidences for range expansions towards higher altitudes in middle Europe, but I found only one study that described recent changes in the upper range boundary along an altitudinal gradient. Pounds et al. (1999, Tab. 3.2, Fig. 3.1) studied changes in climatic factors and bird communities in highland forests at Monteverde, Costa Rica. They found, connected with an increase in sea surface temperatures in the equatorial Pacific, a rise of the average altitude at the base of the orographic cloud bank which leads to a decrease in dry-season mist frequency. Studying the abundances of bird species at 1540 m height between 1979 and 1998, they found significant increases in abundance and colonisation events of premontane, cloud-forest intolerant species. In contrast, there was no consistent trend for lower montane, cloud forest species. As one result of these changes, Keel-billed Toucans (*Ramphastos sulfuratus*), typical for lowlands and foothills, now nested alongside Resplendent Quetzals (*Pharomachrus moccino*) which symbolise Middle American cloud forests. The changes could not be explained by recent deforestation in the lowlands (Pounds et al. 1999).

Comparing my predictions about the effect of global climate change on ranges with the modelled and actually observed changes presents many consistencies. Despite the fact, that predicted and observed changes in range boundaries show great variation among different bird species, general patterns can be found. I expected northward range expansions of birds at high altitudes and in temperate, boreal, and Arctic regions. These range expansions have been predicted for many bird species in modelling approaches (Zöckler & Lysenko 1994, Peterson et al. 2001, Peterson 2003b) and in observational studies (Kalela 1949, 1952, Ainley et al.

1994, Johnson 1994, Thomas & Lennon 1999, Pounds et al. 1999, Dunlop 2001, Peterson 2003a). In arid subtropical and tropical regions, I expected range contractions with increasing temperatures and decreasing precipitation. This pattern has not been found in the literature reviewed above but evidence exists from the community-wide studies (see section 3.5 below, Erasmus et al. 2002, Peterson et al. 2002). For the southern, latitudinal and the lower, elevational range boundary in humid regions I had refrained from predictions because it is usually assumed that these boundaries are more strongly influenced by more complex, biotic interactions. Correspondingly, the southern range boundaries of British birds (Thomas & Lennon 1999) and the lower, elevational range limits of cloud-forest species on Monteverde (Pounds et al. 1999) did not shift under changing climate. The study on Hawaiian birds (Benning et al. 2002) demonstrated that the lower, elevational range limit of these birds was indeed controlled by a biotic factor, i.e. a disease vector. The disease vector, however, was itself controlled by temperature and was expected to shift its range boundary upwards leading to upward shifts of the lower, elevational range boundary of the birds.

## 3.5 INFLUENCE OF CLIMATE CHANGE ON AVIAN COMMUNITIES

### 3.5.1 CORRELATIONS OF CLIMATIC FACTORS AND AVIAN COMMUNITIES

With respect to avian communities, I will focus on species richness and the composition of bird communities. Also for species richness, plenty of evidence exists for a tight correlation between climatic factors and species richness (reviewed in Begon et al. 1996, Gaston 1996, Brown & Lomolino 1998). Among the climatic factors, measures of ambient energy (mean annual temperature, potential evapotranspiration (PET), solar radiation) either have a primary role or are an important modulating factor (Turner et al. 1988, Currie 1991, Lennon et al. 2000, van Rensburg et al. 2002, Hawkins et al. 2003). For example, Currie (1991) calculating bird species richness on the basis of 2.5 x 2.5° grid cells in northern North America found that PET, but not actual evapotranspiration (AET), was the best predictor of species richness. However, these results might be influenced by the spatial gradient of the analysis.

Other studies that included also more arid regions demonstrated that also water-related variables (AET, annual rainfall) might play a role. For example, van Rensburg et al. (2002) calculated bird species richness at 0.25, 0.5, and 1° grid cells over South Africa and Lesotho. They found that, in this region, the relationship between species richness and PET was unimodal because low rainfall constrained productivity in high-PET areas. In a global analysis of bird species richness at the scale of 220 x 220 km grid cells, Hawkins et al. (2003) demonstrated a latitudinal shift in constraints on diversity. Measures of ambient temperature, e.g. PET, best predicted the diversity gradient at high latitudes, whereas water-related variables, e.g. AET, best predicted richness in low-latitude, high-energy regions.

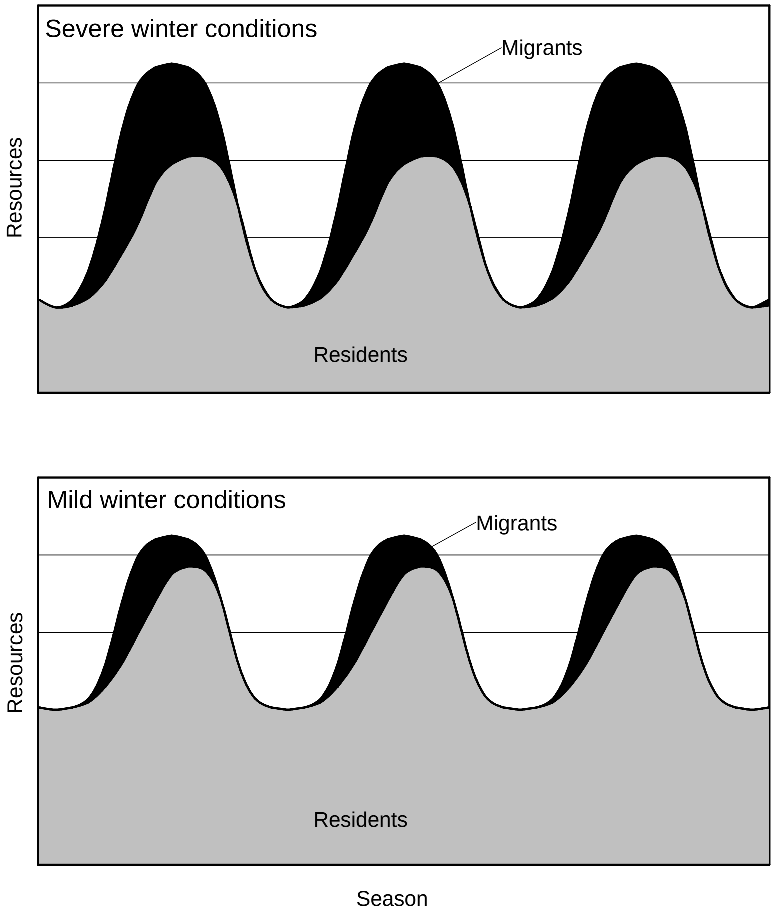


Fig. 3.2: Hypothetical fluctuations in resources in the course of the year under seasonal conditions, with severe and mild winters. Grey: resources potentionally used by resident birds, black: resources potentionally available to migrants.

With respect to the composition of avian communities most studies looking for large-scale patterns that are correlated with environmental factors have analysed the proportion of migrants in the communities. In an early study Herrera (1978) demonstrated that the proportion of migratory individuals in forest bird communities increases along an latitudinal gradient in Europe. He showed that the proportion of migrants is correlated with temperature of the coldest month and argued that the proportion of migrants was determined by the difference in carrying capacity between summer and winter, i.e. intra-annual seasonality (Fig. 3.2). Similar patterns were found by Rabenold (1979, 1993), Newton and Dale (1996a, 1996b), Hurlbert and Haskell (2003) and Lemoine and Böhning-Gaese (2003). For example, Lemoine and Böhning-Gaese (2003) correlated the proportion of long-distance migratory bird species in bird communities at the scale of 100 x 100 km grid cells within Europe (Fig. 3.3) with environmental factors.

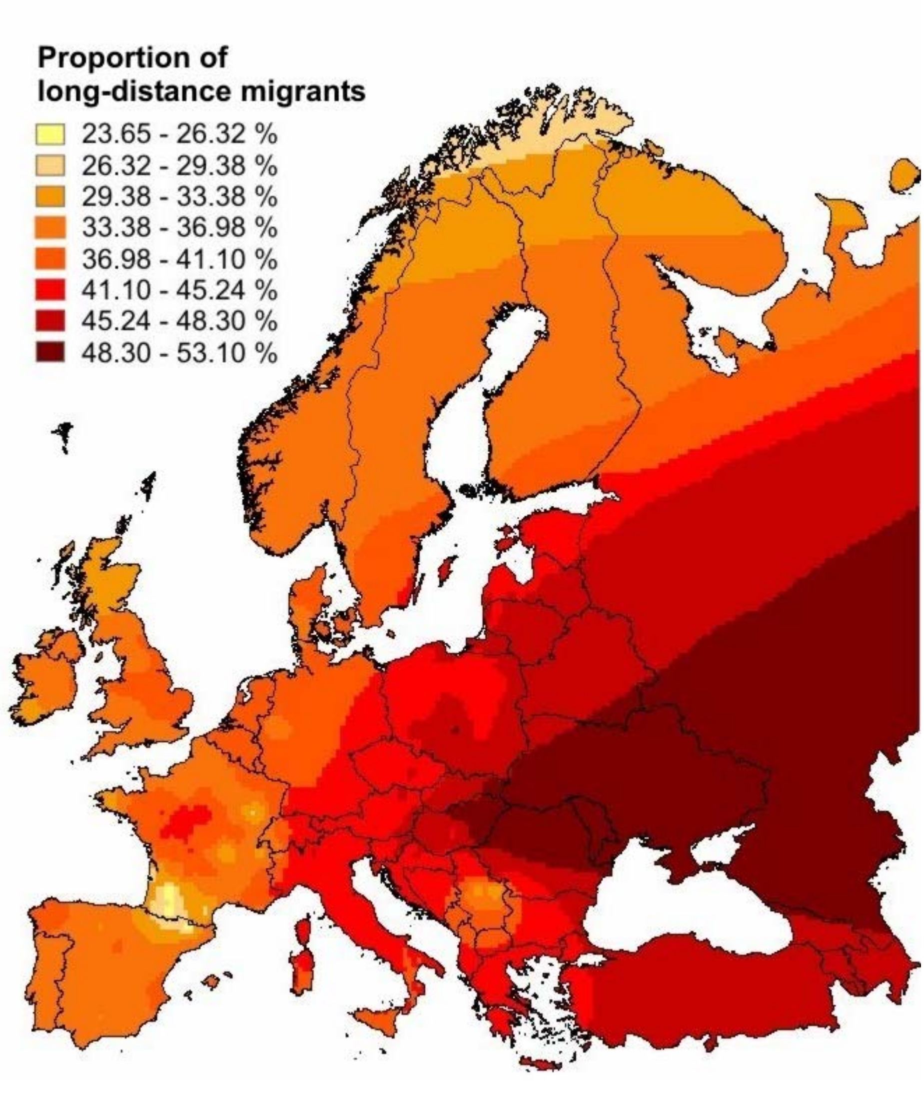


Fig. 3.3: Current proportion of long-distance migratory bird species in European bird communities. The map is based on an interpolation of data from 595 grid cells of 100 x 100 km. (data published in Lemoine and Böhning-Gaese, 2003).

They found that the proportion of long-distance migratory species increased with increasing spring temperature and decreasing temperature of the coldest month, i.e. with increasing seasonality (Fig. 3.4). Given the observed changes in climate and our current knowledge about factors influencing bird species richness and community composition I can, again, make predictions about the consequences of global climate change. With increasing annual temperatures especially at high latitudes I would expect increases in species richness in temperate, boreal, and Arctic regions. In contrast, with increasing temperatures and decreasing precipitation in arid subtropical and tropical regions, I would expect decreases in species richness in the respective areas. Furthermore, with the expected increases especially in minimum temperatures, and decreasing seasonality, I expect declines in the proportion of migratory individuals and species within communities.

### 3.5.2 MODELLED CONSEQUENCES OF CLIMATE CHANGE FOR AVIAN COMMUNITIES

Changes in species richness with climate change have, so far, only been studied using modelling approaches. One type of modelling approach is an extension of the modelling methods used to predict range changes. If range changes for all species in a community can be predicted, it is then possible to add up the number of species per grid cell and to calculate predicted changes in species richness. Using this approach, Peterson et al. (2002, Tab. 3.1, Fig. 3.1) extended the methods used in Peterson et al. (2001) (see *3.4. Influence on climate change on birds' ranges*) to all bird taxa, all mammal taxa and all butterflies in the families Papilionidae and Pieridae in Mexico. The three taxonomic groups showed similar results. Species showed idiosyncratic changes in ranges with 0.0-2.4% of the species predicted to lose ≥ 90% of the present distributional area, depending on the dispersal assumption. Colonizations and increases in species richness were predicted for the major sierras of Mexico. Extinctions and loss of species richness occurred in the broad, open Chihuahuan desert and the north-western coastal plain. Foci of species turnover were northern Mexico in the Chihuahuan desert and the interior valleys in the Baja California peninsula.

Erasmus et al. (2002, Tab. 3.1, Fig. 3.1) used a similar approach in South Africa working with 34 bird, 19 mammal, 50 reptile, 19 butterfly, and 57 "other invertebrate" species. They applied a multivariate climate envelope approach to describe the current distribution of the species. They then used a GCM simulating a doubling $CO_2$ concentration that is expected to cause a mean temperature increase of 2°C, and predicted the new distributions of the species. Again, a similar pattern was found for the five different taxonomic groups. The species showed idiosyncratic changes in ranges with some species predicted to experience range expansions but most species to suffer range contractions.

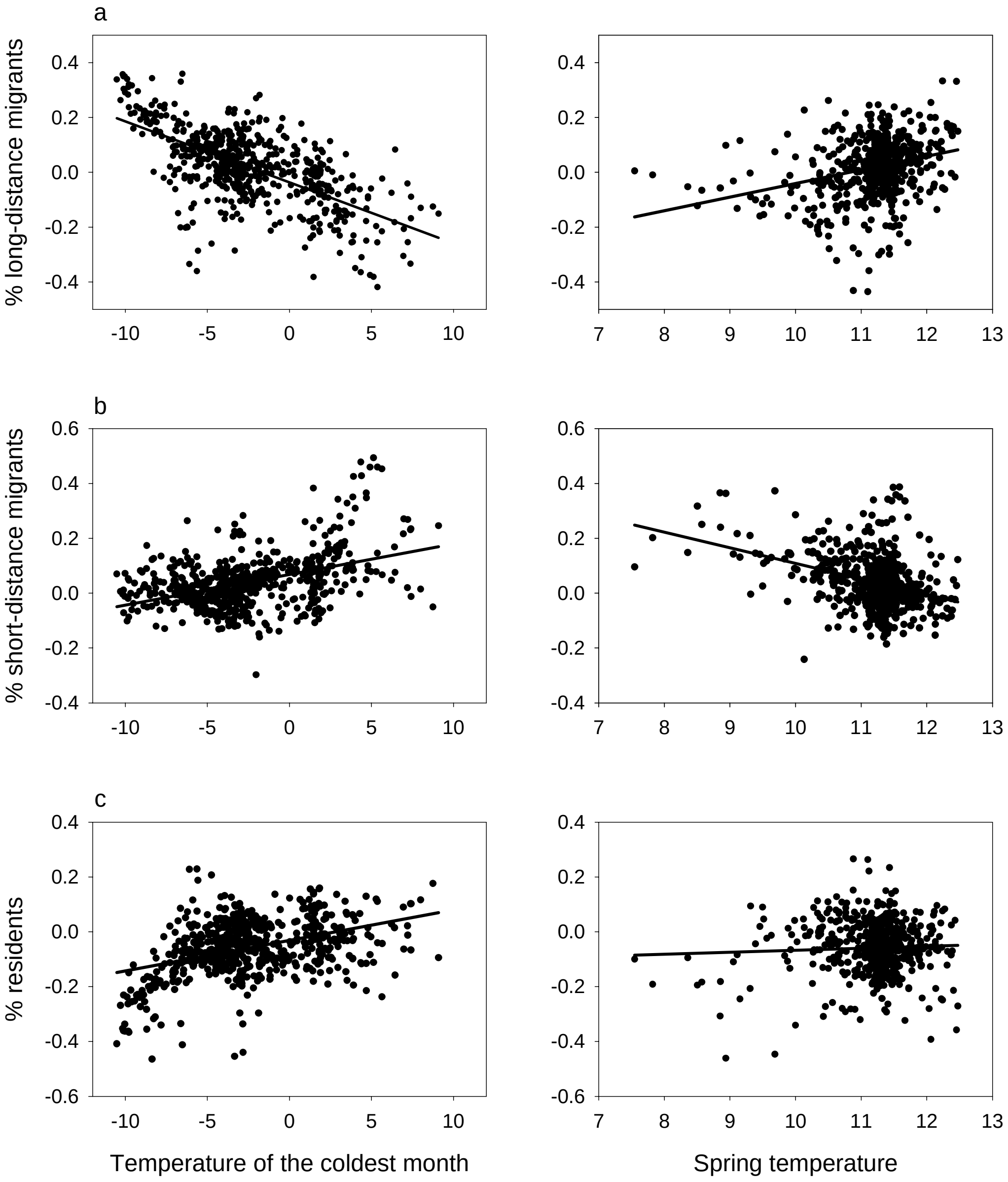


Fig. 3.4: Influence of temperature of the coldest month and temperature in spring on the proportion of (a) long-distance migrants, (b) short-distance migrants and (c) resident bird species in Europe, after spring precipitation and their squared values were controlled. Lines are regression lines (data published in Lemoine and Böhning-Gaese, 2003).

Four species (2.2%) were predicted to go locally extinct. Most species showed a western movement and also movement up altitudinal gradients towards the eastern and southeastern highlands. This leads to a predicted concentration of the most species-rich areas on the eastern escarpment, with significant species losses occurring in the western arid regions. In general, the size of species-rich areas was predicted to decline.

A second type of modelling approach was used by Currie (2001, Tab. 3.1, Fig. 3.1). He correlated species richness of birds, mammals, reptiles, amphibians, and trees directly with a number of environmental variables in grid cells of 2.5 x 2.5° over the conterminous United States. He then used five different GCMs and predicted, for a doubling $CO_2$ scenario, changes in environmental variables and, thus, species richness of the different taxonomic groups. Bird species richness was predicted to be severely affected by climate change because bird richness, more than that of any other group, tended to be lower in hot areas. Predicted higher temperatures over most of the central and southern US should be accompanied by decreases in bird richness, except at higher elevations. Increases in richness are likely to occur in cooler, high-elevation areas, particularly in the western US. The same pattern was found for mammals. Positive effects of predicted climate change were found for reptiles and amphibians, and variable effects for trees.

Various changes in the ranges and community composition of birds have been predicted in the miscellaneous modelling approaches but one has to keep in mind that birds have also the option of evolutionary changes, which does not automatically leads to range changes. Those evolutionary changes were not included in any of the above mentioned modelling approaches.

### 3.5.3 OBSERVED CONSEQUENCES OF CLIMATE CHANGE FOR AVIAN COMMUNITIES

Only little evidence exists that climate change can lead to changes in the composition of bird communities. In their study of European bird communities, Lemoine and Böhning-Gaese (2003, Tab. 3.2, Fig. 3.1) showed a relationship of the proportion of long-distance migrants, short-distance migrants and resident bird species with spring temperature and temperature of the coldest month (see above, Fig. 3.2). They predicted that the proportion of long-distance migrants should decrease if winter temperature increases and spring temperature does not change (Fig. 3.4). They then used the spatial relationship between bird community structure and climate in Europe to make predictions for changes in the bird communities in the Lake Constance region, Central Europe, between two census periods (1980-1981 and 1990-1992). Winter temperature in this region increased significantly between the two censuses, whereas spring temperature did not change. As predicted from the models the proportion of long-distance migrants decreased and the proportion of short-distance migrants and residents increased between the two censuses. The significant declines of the long-distance migrants in the Lake Constance region were of a magnitude that can be explained by the observed climate change.

Comparing my predictions about the effect of global climate change on communities with the modelled and actually observed changes presents, again, many consistencies. With increasing annual temperatures especially at high latitudes I predicted increases in species richness in temperate, boreal, and Arctic regions. These predictions were confirmed by three independent, and in their approach very different models for the United States (Currie 2001), Mexico (Peterson et al. 2002) and South Africa (Erasmus et al. 2002). However, so far, no corresponding studies based on field data have been published. In arid subtropical and tropical regions I predicted a decrease in species richness with increasing temperatures and decreasing precipitation. Again, these predicted changes were supported in the three modelling studies but, up to now, not in the field. Furthermore, I expected declines in the proportion of migratory species within communities with increasing minimum temperatures and decreasing seasonality. Corresponding shifts in community composition were found in the Lake Constance region (Lemoine & Böhning-Gaese 2003).

### 3.6 CONSERVATION CONSEQUENCES OF CLIMATE CHANGE

No data demonstrating that climate change led to severe population declines or even extinctions of bird species have, to my knowledge, as yet been published. Thus, I have to rely on the predictions derived from the modelling approaches and the observed changes reported so far. In general, I predict and observe range expansions of birds that lead to increases in species richness in many temperate, boreal, and Arctic regions and at high altitudes. The question arises if high Arctic and Alpine species are threatened by these processes because their life-zones might contract. However, models developed by Peterson et al. (2003a) suggest that montane species suffer less range contractions and shifts than flatland species. A problem might pose the highest-arctic and –alpine species (Zöckler & Lysenko 1994). In contrast, I predict range contractions and loss of species richness with increasing temperatures and decreasing precipitation in arid subtropical and tropical regions. This demonstrates that the more threatening changes for species and communities are expected in arid subtropical and tropical regions. Thus, conservation efforts have to focus more on the high-temperature, low-precipitation part than on the low-temperature part of the latitudinal gradient.

The most frightening result of all approaches to model range changes are the large movements of ranges expected to occur within the next 50 to 100 years (Peterson et al. 2002, Erasmus et al. 2002). These range changes differ among species with range contractions being more frequent than range expansions. These changes can lead to a re-shuffling of bird communities with old interactions disappearing and new interactions being created. Climate change might also facilitate colonisation and range expansions of exotic, introduced bird species. For example, recent range expansions of birds formerly restricted to Africa and tropical Asia such as the Egyptian Goose (*Alopochen aegyptiacus*) and the Rose-ringed Parakeet (*Psittacula krameri*) in Central Europe have been aided by, among other factors, warmer winter temperatures (Bauer & Bezzel 2001).

Furthermore, centres of species richness are expected to shift or even to contract (Erasmus et al. 2002). This has severe consequences for conservation efforts. Currently, international conservation efforts focus on areas with many endemic bird species (Endemic Bird Areas, EBAs) or otherwise threatened species (Important Bird Areas, IBAs). With the predicted changes in ranges it can be expected that many threatened species move out of the areas that receive highest conservation efforts. The new ranges might then be placed in areas with high human population density or areas with conflicting land use (Erasmus et al. 2002).

For example, in their study on Hawaiian birds, Benning et al. (2002) demonstrate that not only the disease vector *Culex quinquefasciatus* is expected to shift in elevation. Rather it can be expected that global warming also leads to an increase in the lifting condensation level and height of orographic clouds. These changes would increase both the lower and upper altitudinal limits of montane cloud forests. Thus, if forests expanded to higher elevations, birds should be able to expand their ranges as well and to escape the areas with high risk of malaria infection. However, in one of the studied forest reserves, Hakalau Wildlife Refuge on the island of Hawaii, the predominant land use above Hakalau Refuge is pasture land which constrains the amount of forest available at higher elevations and could prevent migration of forests upslope. This demonstrates that under climate change the potential for land-use conflict increases (Erasmus et al. 2002). Thus, in the face of global climate change conservation policy and practice will need to be revised considerably (Berry et al. 2002, Midgley et al. 2002, Hannah et al. 2002).

### 3.7 CONCLUSIONS AND FUTURE DIRECTIONS

The most interesting conclusion of this review is that, so far, only few effects of climate change on ranges and communities have actually been reported using field data. This is surprising because strong effects of climate change on the phenology, reproductive success and population dynamics of birds are documented very well (Lehikoinen et al. 2004, Dunn 2004). This is also surprising because climate has already changed significantly and because expected changes, especially in ranges, are dramatic (Peterson et al. 2002, Erasmus et al. 2002). This result is, furthermore, surprising because birds are one of the few groups of organisms for which good, long-term data exist.

The reasons for this lack of effects are difficult to tell. One possibility is that only very few scientists have looked for effects of climate change on ranges and communities. A second factor might be that changes in ranges and communities are not as strong as one would predict and these ("negative") results have not been published. Finally, it is possible that the regions in which the best data sets exist are not the regions in which climate had changed so far (Fig. 3.1). For example, one of the best data sets with which it should be possible to document changes in the ranges of birds over the last 30 years is the North American Breeding Bird Survey (see Böhning-Gaese et al. 1993, Brown et al. 1995, Villard & Maurer 1996, Mehlmann 1997, Husak & Maxwell 2000, Rodriguez 2002). However, in contrast to Eurasia, North America exhibits warming at a lower rate and even a slight cooling trend during the last 50 years in the eastern United States (Bogaert et al. 2002).

Contrary to birds, reported changes in ranges and communities are numerous for plants and butterflies in North America and Europe (Grabherr et al. 1994, Parmesan 1996, Hill et al. 1999, Parmesan et al. 1999, Kirschbaum 2000, Parmesan et al. 2000, Cameron & Scheel 2001, Walther et al. 2001, Warren et al. 2001, Bale et al. 2002, Hill et al. 2002, Shine et al. 2002, Konvicka et al. 2003, Parmesan & Yohe 2003, Root et al. 2003). Birds are known to react very fast to environmental changes. Thus, no reason exists why birds should respond to climate change less rapidly than plants and butterflies. This suggests that only few scientists have actually looked for effects on birds' ranges and communities. Given the good data sets about birds and the importance of changes in ranges and communities to initiate conservation efforts, this field urgently needs more attention.

Studying range and community changes in birds, it is important to establish as well as possible the relationship between climate and range or community change. One prerequisite is to study not only single species, but groups of organisms or entire communities (Thomas & Lennon 1999, McCarty 2001). Second, it is useful to combine modelling and observational approaches (Lemoine & Böhning-Gaese 2003). This combination would aid in developing more realistic models, and it would demonstrate in which direction and how strongly individual bird species should shift their ranges. Further, it would be important to collect as much evidence as possible that the ranges of the studied species are limited by climatic factors, e.g. by correlating range boundaries with climatic factors or by studies of physiological temperature tolerance. Finally, it is necessary to explicitly test alternative hypotheses, especially confounding changes in habitat availability and other anthropogenic impacts (Thomas & Lennon 1999).

In addition, studying bird communities, so far no study has looked beyond bird communities and considered the consequences that changes in bird abundance and diversity have for the ecosystems within which birds live. Cases where birds have been shown to influence ecosystems are bottom-up and top-down control of food webs. Birds are important disease vectors, flower pollinators, and seed dispersers. For example, seabirds can transport considerable amounts of energy and nutrients from the sea onto islands and shape whole island food webs (e.g. Moreira 1997, Stapp et al. 1999). Top-down control of food webs can act through grazing or predation in terrestrial, freshwater or marine systems (Wotton 1992, Murakami & Nakano 2000, Strong et al. 2000, Sanz 2001). Birds play a crucial role for successful pollination as demonstrated by Robertson et al. (1999) in New Zealand. Similarly, birds are important seed dispersers and can have profound effects on forest regeneration (Bleher & Böhning-Gaese 2001). Climate-related changes in the abundance of birds might, therefore, have cascading, far-reaching effects as, vice versa, changes in the ecosystem are expected to cause changes in bird community composition.

Finally, current climate change can, somewhat cynically, be seen as a vast natural experiment. Current ecological theory has advanced to the point where a number of patterns and processes are well understood. With current climate change researchers are now able to put these theories on test. For example, many studies have shown that the number of migratory bird individuals and species in bird communities is related to the seasonality of their environment. With increasing minimum temperatures and decreasing seasonality it is possible to make clear predictions about the expected changes in bird communities. Within the next years, it will be possible to actually test if our understanding of birds' ranges and communities has predictive power.

## 3.8 SUMMARY

In this review I focus on the effects of global climate change on the size and position of geographic ranges and the richness and composition of bird communities. Plenty of evidence exists demonstrating that range boundaries of birds are correlated with climatic factors. In general, the northern range limit of species seems to be influenced rather by abiotic factors such as cold temperatures. The southern range limit of species appears to be determined by climatic factors such as heat or lack of water in arid regions and by biotic factors in more humid regions. For communities, species richness is best predicted by measures of ambient temperature at high latitudes and by water-related variables in low-latitude, high-temperature regions. Models predicting range changes under climate change show idiosyncratic responses of different species with range contractions being more frequent than range expansions. Range shifts have been observed in temperate regions with northward shifts of northern range boundaries and no consistent trend of southern range boundaries. Further, upslope movements have been observed on a tropical mountain. For communities, increases in species richness are predicted for northern latitude and high-elevation sites and declines of species richness in arid regions. With increasing winter temperature, declines in the proportion of migratory species in bird communities have been predicted and observed. Conservation consequences of global climate change are especially high threats to species in arid environments, expected movements of species out of protected areas and increasing land use conflicts. In general, surprisingly few studies document effects of climate change on birds' ranges and communities. Given that range contractions and declines of species richness often initiate conservation efforts, further studies are urgently needed.

# 4 SPECIES RICHNESS OF MIGRATORY BIRDS IS INFLUENCED BY GLOBAL CLIMATE CHANGE

## 4.1 INTRODUCTION

Global warming is increasingly influencing the phenology, reproductive success, abundance, range size and range position of plant and animal species, resulting in observable changes from the level of individuals to whole communities (Peñuelas & Filella 2001, McLaughlin et al. 2002, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003). Many plant species, for example, have extended their growing season (Menzel & Fabian 1999), some hibernating species abbreviated their winter sleep (Humphries et al. 2004). Birds start breeding earlier (Forchhammer et al. 1998, Dunn 2004), and migratory birds arrive earlier on their breeding grounds and leave later in autumn (Lehikoinen et al. 2004). Changes in climate also resulted in range shifts of a number of species (Thomas & Lennon 1999, Van der Veken et al. 2004, Walther 2004).

To evaluate the impact of climate change on the species richness and on the structure of ecological communities most studies have used modelling approaches. These modelling approaches predicted, for example, that forest composition, including species richness, should be strongly affected by climate change (Scheller & Mladenoff 2005). Several forest plant species in France, Belgium and The Netherlands can be expected to move several hundreds of kilometres northward and thereby change present-day community structures (Van der Veken et al. 2004). For 26 European forest herbs, expected consequences in terms of lost and gained range size and shifts in distribution were estimated (Skov & Svenning 2004), and loss of diversity for Mediterranean butterfly assemblages over the coming years can be predicted under the most plausible scenarios of climate change (Stefanescu et al. 2004).

However, only few studies have actually demonstrated empirically that climate change has already caused observable changes within species communities. Global warming should influence especially the species richness and structure of ecological communities. Climatic changes seemed to have altered, for example, the communities of specialised phytophagous beetles (Andrew & Hughes 2004) and bat populations of northern Costa Rica (LaVal 2004). Also changes in the proportion of long-distance migratory bird species in the bird communities of the Lake Constance region, Central Europe, between 1980-81 and 1990-92 were in line with isochronic temperature and precipitation changes (Lemoine & Böhning-Gaese 2003).

Birds are a very well-studied group of organisms and can probably respond rapidly to environmental changes. They have a very active metabolism and are, therefore, highly sensitive to climatic changes. Furthermore, they are very mobile and can react immediately to environmental changes. As a result, birds seem to be qualified as pioneer indicators for changes related to global warming and many bird species have already responded to climatic changes (Møller et al. 2004). Nevertheless, only little evidence exists showing that climate change results in systematic changes in the species richness and in the structure of bird communities (Böhning-Gaese & Lemoine 2004).

The proportion of migratory and resident birds in a temperate bird community is expected to be influenced by seasonal variation in temperature (Herrera 1978). The population density of resident birds might be limited by low resource levels related to low temperature in winter. High levels of resources in spring can then be shared between residents and incoming migrants. Changes in winter and spring temperature may change the proportion of migratory birds within the communities (O’Connor 1990, Lemoine & Böhning-Gaese 2003, Böhning-Gaese & Lemoine 2004). These changes can manifest themselves as evolutionary effects with changing proportions of migratory individuals within a species or as ecological effects with changing proportions of migratory species within bird communities. In the present study, I focus on ecological effects of global climate change and shifts in the composition of bird communities.

Global warming will probably be reflected in increasing winter- and spring temperature (McCarthy et al. 2001). As one consequence of those temperature changes for bird communities I expect changes in the proportion of long- and short-distance migratory bird species. Therefore, I analysed temporal changes in temperature and in the composition of bird communities in Europe over the last decades. One intrinsic problem when analysing temporal changes in bird communities is to verify that global climate change was actually the causal factor behind these changes. To evaluate the impact of climatic changes on bird communities it is necessary to analyse temporal changes in bird community composition in areas where isochronic climatic changes were observed. Those temporal changes in bird communities can then be compared with changes in bird communities, which I would expect under the observed climate change. The expected changes in bird community composition can be calculated by using the spatial variation in bird communities and climatic conditions in Europe (Lemoine & Böhning-Gaese 2003). Given that observed changes in bird community structure are similar to expected changes, the spatial relationship between bird communities and climatic factors can then be used to make predictions also for future changes in bird community composition.

In an earlier study, Lemoine and Böhning-Gaese (2003) analysed the spatial variation in the composition of bird communities and climatic factors in Europe. They developed spatial regression models and quantified the relationship between the proportion of migratory and resident bird species and climatic conditions. Lemoine and Böhning-Gaese (2003) used the mean temperature of the coldest month (TCM), mean spring temperature (TSPR, average of April, May and June), and spring precipitation (PSPR, sum of April, May and June) as measures of climatic conditions in winter and during the breeding period. The proportion of long-distance migrants increased with decreasing winter temperature, increasing spring temperature, and decreasing spring precipitation (Lemoine & Böhning-Gaese 2003). These spatial regression models can now be used to calculate expected changes in bird community composition under observed changes in winter and spring temperature and precipitation.

An additional problem when analysing temporal changes in bird communities is spatial autocorrelation of adjacent sites. Bird communities in neighbouring sites might show more similar changes than in more distant sites because for most bird species their ranges extent over more than one site. Climatic conditions in adjacent sites are also more similar than in more distant sites and can, therefore, be spatially autocorrelated. Finally, changes in bird community composition can also by caused by alternative factors besides global climate change. Migrants and residents have preferences for different habitat types (Mønkkønen et al. 1992, Böhning-Gaese & Oberrath 2003). Therefore, changes in species richness of migratory and resident bird species might have been caused by changes in land cover in Europe or by changes in the intensity of agricultural land use. Thus, it is necessary to test these alternative hypotheses.

In the present study, I analysed temporal changes in bird communities in Europe in the last decades using bird atlas data of 21 sites. My objectives were first to calculate changes in the proportion of migratory and resident bird species and to compare these observed changes with changes I would expect from the spatial relationship between bird community composition and climate (Lemoine & Böhning-Gaese 2003). Second, I tested whether temporal changes in bird communities could be explained by spatial autocorrelation effects or by alternative factors such as changes in forest area and fertiliser consumption. In the case that observed and expected changes in bird community composition showed a good congruence and spatial autocorrelation or alternative factors were of minor importance, I could then use the spatial relationship between bird community composition and climate to make predictions for future changes in bird community composition using a general circulation model for future climate change.

## 4.2 METHODS

### 4.2.1 BIRD DATA

To analyse the temporal changes in the bird communities, I compared observed changes and changes I would expect from the spatial relationship between bird community composition and climate (Lemoine & Böhning-Gaese 2003) for 21 sites in Europe (Fig. 4.1). The objectives for selecting the bird data and sites was first, the availability of species lists collected at a spatial scale of 100 x 100 km squares, because the spatial regression models of Lemoine and Böhning-Gaese (2003) were developed at that scale. The second objective for selecting the bird data and sites was the availability species lists for two separate time periods. These objectives could be met by using bird atlas data from areas where two separate censuses had been conducted. Of the available sites in Europe that met these conditions, I chose 21 sites with the additional objectives, first, to cover as much of Europe as possible and, second, to space the sites as uniformly over Europe as possible (Fig. 4.1).

At the 21 sites, the first bird census was conducted on average 1972-1976, the second census on average 1988-1991, with at least 7 years between the two census periods at each site, respectively. The sites and census periods included in the study were Czecheslowakia 1973–1977 (3 sites: CZ1-CZ3, Stastny et al. 1987) and 1985–1989 (Stastny et al. 1995), Denmark 1971–1974 and 1993–1996 (1 site: DK, Grell 1999), Finland 1974–1979 (3 sites: FN1-FN3, Bergmann et al. 1983) and 1986–1989 (Väisänen et al. 1998), France 1970–1975 (5 sites: F1-F5, Yeatman 1976) and 1985-1989 (Yeatman-Berthelot & Jarry 1994), Germany 1 (Saxony): 1978–1982 (1 site: D1, Nicolai 1993) and 1993–1996 (Steffens et al. 1998), Germany 2 (Hamburg): 1985 (1 site: D2, Rheinwald 1993) and 1997–2000 (Mitschke & Baumung 2001), Germany 3 (Lake Constance): 1980–1981 and 1990–1992 (1 site: D3, Bauer & Heine 1992), Great Britain 1968–1972 (3 sites: GB1-GB3, Sharrock 1977) and 1988–1991 (Gibbons et al. 1997), Ireland 1968–1972 (1 site: IRL, Sharrock 1977) and 1988–1991 (Gibbons et al. 1997), Switzerland 1972–1976 and 1993–1996 (1 site: CH, Schmid et al. 1998) and The Netherlands 1973–1977 (1 site: NL, Teixeira 1979) and 1998–2000 (Hustings & Vergeer 2002). The exact positions of the sites are shown in figure 4.1.

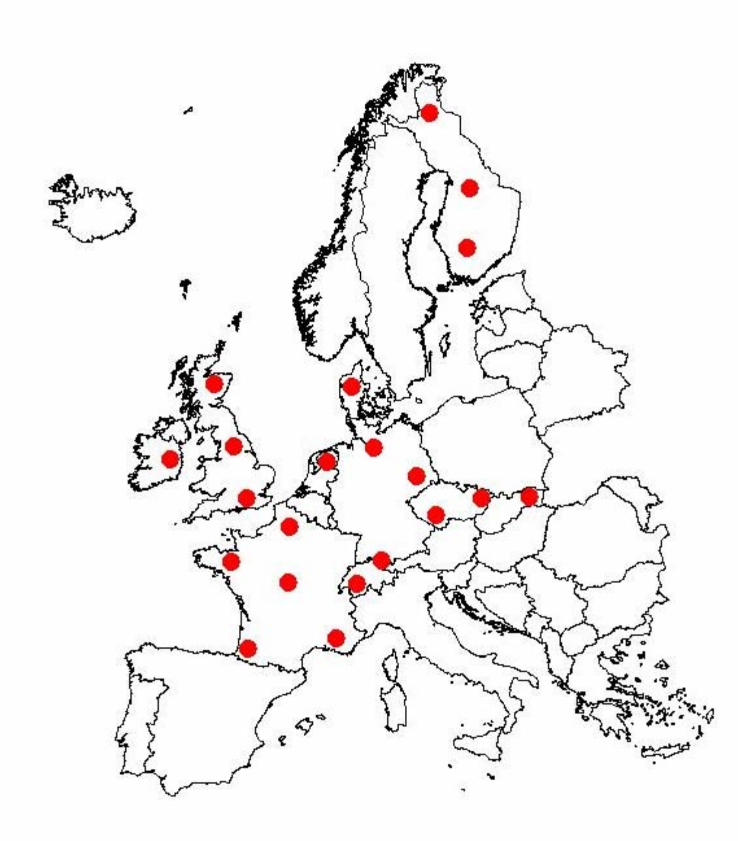


Fig. 4.1: The 21 sites in Europe for which changes in bird communities were compared among two census periods, respectively.

Unfortunately, the quality of the European bird atlas data and the methods of data collection were inconsistent among the different European countries and usually also between the two census periods within one site. Inconsistent data quality should have a strong influence on measures of absolute species numbers. We, therefore, calculated the proportion of long-distance migratory, short-distance migratory and resident bird species and used these values for further analyses. For each site and census period I compiled a species list for a 100 km x 100 km square and calculated the proportion of long-distance migratory, short-distance migratory and resident bird species. I excluded all species that use marine, coastal, freshwater, and wetland habitats because they have distinctly different ecological needs. Therefore, they might be influenced by climatic change in a different way. The migratory behaviour of a species was defined as a fixed trait according to the biogeographic distribution of the breeding and wintering range (Lemoine & Böhning-Gaese 2003). I defined long-distance migrants as birds regularly wintering south of the breeding range with the centre of the wintering range south of the Sahara or east of the Pakistan/India border, short-distance migrants as species regularly wintering south of the breeding range with the centre of the wintering range north of the Sahara or west of the Pakistan/India border, and residents as species not regularly leaving the breeding ground in winter (Lemoine & Böhning-Gaese 2003). For each of the 21 sites I calculated the change in the proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods.

### 4.2.2 CLIMATE DATA

For each site and census period I compiled climatic data for TCM, TSPR and PSPR (Lemoine & Böhning-Gaese 2003) from the Tyndall Centre for climate change research (Mitchell et al. 2004). I used the mean TCM as a measure of resources available for resident birds in winter, mean TSPR and PSPR to characterize the climatic conditions during the breeding period. Spring temperature and precipitation is thought to be a good measure of resource availability in the breeding period (e.g. Perrin & Boyer 2000). When compiling the climatic data, I also included the climatic values for the year before the census period started because the population size of migrants in one year appears to be influenced by the winter conditions of the previous year (O’Connor 1990). For example, the data of the "Atlas of Breeding Birds in Britain and Ireland" (Sharrock 1977) were collected from 1968 to 1972. As climatic data I then used the mean of 1967-1972.

### 4.2.3 COMPARISON OF OBSERVED AND EXPECTED CHANGES IN BIRD COMMUNITIES

For each site I calculated the observed changes in the proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods (see *Bird data*). To test if observed and expected changes in bird community composition showed a good congruence, I calculated expected changes for the proportion of long-distance migrants, short-distance migrants and resident bird species at the same sites. Expected changes were calculated from the spatial relationship between bird community composition and climatic conditions (Lemoine & Böhning-Gaese 2003) and the observed changes in TCM, TSPR and PSPR at the 21 sites between the two census periods.

The spatial relationship between bird communities and climatic conditions was derived from spatial regression models that quantified the proportion of long-distance migratory, short-distance migratory and resident bird species in 595 squares in Europe as a function of TCM, TSPR and PSPR from the long-term average of 1961-1990, both at the scale of 100 x 100 km squares (Lemoine & Böhning-Gaese 2003). The proportion of long- and short-distance migratory species were well described by TCM, TSPR and PSPR ($R^2_{long} = 68.7\%$, $R^2_{short} = 59.8\%$). For the proportion of resident species, the relationship with the climatic variables was weak ($R^2_{resid} = 26.3\%$, Lemoine & Böhning-Gaese 2003). To calculate the expected changes in the proportion of long-distance migrants, short-distance migrants and resident bird species I inserted the values for TCM, TSPR and PSPR for each of the 21 sites and each census period into the formulas of the spatial regression models (Lemoine & Böhning-Gaese 2003). I then calculated the change in the expected proportion of long-distance migrants, short-distance migrants and resident bird species between the two census periods. These expected changes are changes in the bird community composition I would expect if only climatic factors influenced the bird communities.

The observed changes between the two census periods were compared with the expected changes in bird community composition for each of the 21 sites in Europe. After testing for normality, I analysed the relationship between the observed and expected changes using Spearman Rank Correlations. Only a significant positive correlation between the observed and expected changes demonstrates that the temporal changes in bird community composition can be quantitatively predicted by the spatial regression models of Lemoine and Böhning-Gaese (2003).

### 4.2.4 AUTOCORRELATION EFFECTS AND ALTERNATIVE FACTORS

To control for possible effects of spatial autocorrelation I repeated the analyses using Mantel Tests and included the spatial distance of the 21 sites as a co-variable (Oberrath & Böhning-Gaese 2001). With this method, for each pair of grid cells their dissimilarity in the dependent variable is compared with their spatial distance and with their dissimilarity in the other independent variables. As dependent variable I used the observed changes in the proportion of long-distance migrants (short-distance migrants and resident bird species, respectively) and as independent variables the spatial distance between the 21 sites and the predicted changes in the proportion of long-distance migrants (short-distance migrants and resident bird species, respectively) .

Finally, I tested whether changes in the proportion of long-distance migrants, short-distance migrants and resident species between the two census periods might have been caused by changes in land cover or by changes in the intensity of agricultural land use in Europe. As indicators for changes in land cover and intensity of agricultural land use I used forest area and fertiliser consumption. Forest area was calculated as percentage of land area, and fertiliser consumption as sum of nitrogenous, potash and phosphate consumption. Both data sets were available only at the spatial scale of the country, but at the temporal scale of years (FAOSTAT data 2004). Thus, I calculated for each site and census period, the mean value for forest area and fertiliser consumption. I then calculated the changes in forest area and fertiliser consumption for each site between the two census periods. To analyse the influence of forest area and fertiliser consumption on the observed changes in the proportion of long-distance migrants, short-distance migrants and resident bird species I used Spearman Rank Correlations similar to the comparison of the observed and expected changes in bird community composition.

### 4.2.5 FUTURE PREDICTIONS

In the case that observed and expected changes in bird community composition showed a good congruence and that spatial autocorrelation or alternative factors were of minor importance, I can use the spatial regression models (Lemoine & Böhning-Gaese 2003) to make predictions for future changes in bird community composition under future climate change. Future surface temperatures and precipitation in Europe were predicted from the Hadley General Circulation Model (GCM) HadCM3 (Gordon et al. 2000). HadCM3 (Gordon et al. 2000) is the first of a new generation of coupled atmospheric GCMs that do not require flux corrections to be made. The atmospheric model used is the HadCM3 version of the UK Met. Office's unified forecast and climate model with a horizontal resolution of 2.5 x 3.75 degrees. For the predicted temperature and precipitation data I used HadCM3A2, an ensemble of integrations forced with the SRES A2 emissions scenario. With this GCM, I calculated the average of TCM, TSPR and PSPR for the time period 1961-1990 and 2040-2069 and inserted the values into the spatial regression models (Lemoine & Böhning-Gaese 2003). I then calculated the changes in the proportion of long-and short-distance migrants for about 2050 in Europe as predicted under future climate change. For resident species, predictions were not reliable because neither the spatial regression models nor the temporal changes in species richness (Fig. 4.2C) showed a strong relationship between the proportion of resident species and climatic factors.

## 4.3 RESULTS

First, I calculated the mean changes in bird community composition and in climatic conditions between the two census periods at the 21 sites in Europe. The mean proportion of long-distance migratory species increased only slightly (Paired t-test: $t = 1.09$, $p = 0.29$, $n = 21$, Tab. 4.1), the proportion of short-distance migratory species decreased significantly (Paired t-test: $t = -2.29$, $p = 0.033$, $n = 21$, Tab. 4.1) and the proportion of resident bird species showed hardly any change (Paired t-test: $t = 0.48$, $p = 0.64$, $n = 21$, Tab. 4.1). For the climatic conditions I found that TSPR increased significantly by 0.47°C between the two census periods (Paired t-test: $t = 5.66$, $p < 0.0001$, $n = 21$), TCM and PSPR decreased non-significantly (Paired t-test: $t = -1.39$, $p = 0.18$, and $t = -0.12$, $p = 0.91$, respectively).

Analysing the relationship between observed and expected changes in bird community composition, I found significant correlations for the proportion of migratory bird species but not for residents (Spearman Rank Correlation: long-distance migrants: $rho = 0.45$, $p = 0.038$, Fig. 4.2A, short-distance migrants: $rho = 0.46$, $p = 0.037$, Fig. 4.2B, residents: $rho = 0.23$, $p = 0.32$, Fig. 4.2C, $n = 21$). Observed changes in the proportion of long-distance migratory species were significantly more negative than expected (Wilcoxon Signed Rank test: d.f. = 20, $S = -66.5$, $p = 0.017$, Fig. 4.2A), observed changes in the proportion of short-distance migratory species were significantly more positive than expected ($S = -79.5$, $p = 0.003$, Fig.

4.2B) and observed changes for resident bird species were marginally more positive than expected with the spatial regression models (S = -49.5, p = 0.085, Fig. 4.2C).

Tab. 4.1: Geographic position of the 21 sites in Europe and the proportion of long-distance migratory (% long), short-distance migratory (% short) and resident bird species (% resid) for each site and census period.

| | | | 1. census period | | | 2. census period | | |
|---|---|---|---|---|---|---|---|---|
| | Lonitude | Latitude | % long | % short | % resid | % long | % short | % resid |
| CH | 7.50 | 46.51 | 30.61 | 32.65 | 36.73 | 32.41 | 32.41 | 35.17 |
| CZ 1 | 14.27 | 49.29 | 33.58 | 35.04 | 31.39 | 33.58 | 34.31 | 32.12 |
| CZ 2 | 17.88 | 49.57 | 34.04 | 34.75 | 31.21 | 34.51 | 33.81 | 31.69 |
| CZ 3 | 21.40 | 48.93 | 35.17 | 33.79 | 31.03 | 34.53 | 33.81 | 31.65 |
| D 1 | 13.41 | 51.40 | 35.34 | 36.09 | 28.57 | 33.06 | 35.48 | 31.45 |
| D 2 | 10.36 | 53.21 | 32.32 | 36.36 | 31.31 | 33.02 | 36.79 | 30.19 |
| D 3 | 9.73 | 47.84 | 31.25 | 36.61 | 32.14 | 30.70 | 36.84 | 32.46 |
| DK | 9.34 | 56.47 | 35.34 | 39.10 | 25.56 | 32.43 | 38.74 | 28.83 |
| F 1 | 2.76 | 49.72 | 33.94 | 37.61 | 28.44 | 33.93 | 37.50 | 28.57 |
| F 2 | -1.82 | 48.00 | 30.84 | 37.38 | 31.78 | 33.04 | 36.61 | 30.36 |
| F 3 | 2.45 | 46.84 | 35.34 | 36.21 | 28.45 | 35.65 | 35.65 | 28.70 |
| F 4 | -0.68 | 43.56 | 31.25 | 36.72 | 32.03 | 32.82 | 35.11 | 32.06 |
| F 5 | 5.58 | 43.87 | 33.56 | 34.25 | 32.19 | 35.86 | 31.03 | 33.10 |
| FN 1 | 24.08 | 61.59 | 33.33 | 33.33 | 33.33 | 33.88 | 33.88 | 32.23 |
| FN 2 | 27.05 | 64.24 | 29.52 | 37.14 | 33.33 | 31.30 | 35.65 | 33.04 |
| FN 3 | 26.74 | 68.49 | 25.56 | 42.22 | 32.22 | 28.28 | 41.41 | 30.30 |
| GB 1 | -3.31 | 57.08 | 24.76 | 44.76 | 30.48 | 25.74 | 45.54 | 28.71 |
| GB 2 | -1.54 | 53.93 | 25.77 | 41.24 | 32.99 | 25.74 | 42.57 | 31.68 |
| GB 3 | -0.57 | 51.28 | 31.37 | 40.20 | 28.43 | 30.48 | 40.00 | 29.52 |
| IRL | -6.96 | 53.16 | 21.74 | 52.17 | 26.09 | 20.83 | 51.39 | 27.78 |
| NL | 6.34 | 52.84 | 32.48 | 38.46 | 29.06 | 32.50 | 37.50 | 30.00 |
| Mean | | | 31.29 | 37.91 | 30.80 | 31.63 | 37.43 | 30.93 |

Possible effects of spatial autocorrelation between the 21 sites did not influence the results (Multivariate Signed Mantel test: effect of spatial distance: long-distance migrants: t = 2.76, p = 0.16, short-distance migrants: t = 0.80, p = 0.53, residents: t = -0.26, p = 0.99, n = 210, 10 000 permutations). Changes in bird community composition were correlated neither with changes in forest area nor in fertiliser consumption between the two census periods (Spearman Rank Correlation: forest area: long-distance migrants: rho = -0.20, p = 0.41, short-distance migrants: rho = -0.40, p = 0.094, residents: rho = -0.06, p = 0.82, fertiliser consumption: long-distance migrants: rho = 0.04, p = 0.86, short-distance migrants: rho =

0.04, p = 0.85, residents: rho = -0.11, p = 0.65, n = 21 respectively). Changes in the proportion of long-distance and short-distance migratory species could be predicted by the spatial relationship between bird community composition and climatic conditions. No influence of spatial autocorrelation effects or of alternative factors could be detected. Thus, the spatial regression models can be used to make predictions for changes in bird community composition the future.

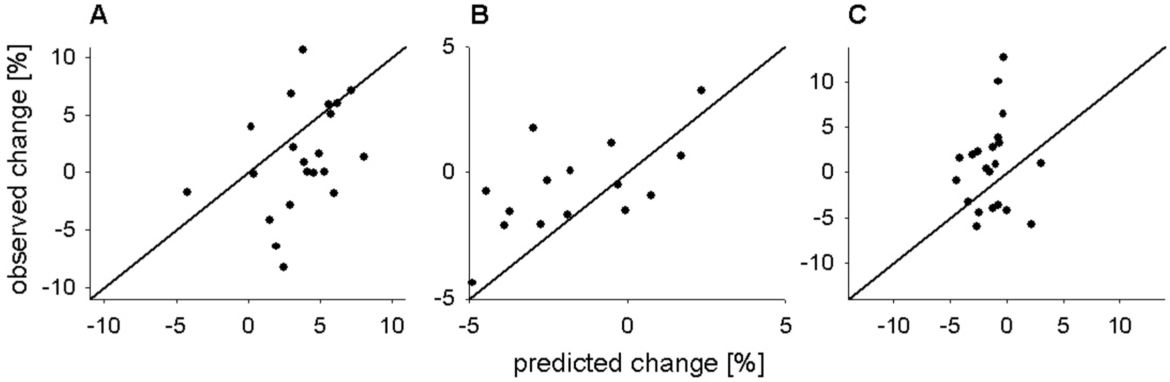
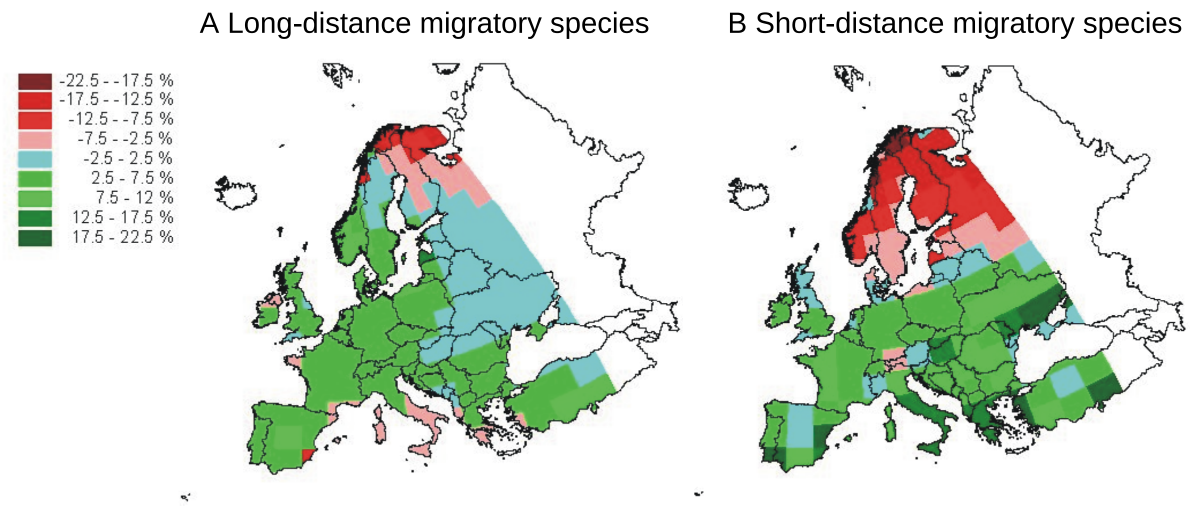


Fig. 4.2: Observed and predicted changes in the proportion of long-distance migratory (A), short-distance migratory (B) and resident bird species (C) in Europe. The line is the bisecting line of the angle.

The General Circulation Model HadCM3A2 estimated an increase in mean TCM in Europe by 3.95°C, in TSPR by 2.68°C and a decrease in PSPR by 0.02 mm between 1961-1990 and 2040-2069. Inserting the estimated values of the HadCM3A2 for TCM, TSPR and PSPR into the spatial regression models (Lemoine & Böhning-Gaese 2003) I calculated the predicted changes in the proportion of long- and short-distance-migratory species between 1961-1990 and 2040-2069 (Fig. 4.3). The results suggested increases in the proportion of long- and short-distance migratory species in western, central and eastern Europe, and decreases in northern Europe with more severe changes in short- than in long-distance migrants (Fig. 4.3).

## 4.4 DISCUSSION

My analyses indicated that observed changes in bird community composition could be predicted from climate change (Fig. 4.2). I did not find any significant influence of spatial autocorrelation or of alternative factors on the changes in bird community composition. Predictions for future changes in the composition of bird communities in Europe indicated no changes or even increases in the proportion of migratory bird species for most regions of Europe. Only in the northern part of Europe declines can probably be expected (Fig. 4.3).


A Long-distance migratory species

B Short-distance migratory species

Fig. 4.3: Predicted changes in the proportion of long– (A) and short-distance migratory species (B) in bird communities for the time period 2040–2069 in relation to 1961-1990 in percent.

Observed changes in bird community composition between the two census periods were rather small (Tab. 4.1, Fig. 4.2). Nevertheless, observed changes in species richness of migratory birds corresponded significantly to the expected changes if only climate change had influenced the birds. The correlation of observed and expected changes in bird community composition was statistically significant although sample size was small (n = 21) and expected values were calculated with a rather large error. The spatial regression models, on which the expected values were based, were able to explain only 68.7% of the variance in the proportion of long-distance migratory species and 59.8% of the variance in the proportion of short-distance migratory species by climatic factors (Lemoine & Böhning-Gaese 2003). I found a good congruence of observed and expected changes for the proportion of long- and short-distance migrants. In contrast, I did not find any significant correlation between observed and expected changes in the proportion of resident bird species. This might be explained by a poor relationship between species richness of resident birds and climatic factors. Correspondingly, the spatial regression models explained only 26.3% of the variance in the proportion of resident bird species by climatic factors (Lemoine & Böhning-Gaese 2003).

Observed changes in the proportion of long-distance migratory species were significantly more negative than predicted (Fig. 4.2A), and significantly more positive than predicted in short-distance migratory species (Fig. 4.2B). These results indicate that factors apart from climate influenced the changes in the proportion of migratory birds. Therefore, I also analysed alternative factors like changes in forest area and fertiliser consumption on the breeding grounds. However, I did not find any significant influence of these factors on the changes in bird community composition. Unfortunately, the data for forest area and fertiliser consumption were not very detailed. I could only use data at the scale of the country, and not for the specific sites, where the bird data had been collected. A more detailed investigation of alternative factors might probably lead to different results. Nevertheless, this is one of the first studies on climate change that analysed alternative factors at all. Only Thomas and Lennon (1999), who analysed the breeding distributions of British birds, controlled for alternative factors, in their study overall population expansions and retractions.

Alternatively, the decreases of long-distance migratory species and the increases of short-distance migratory species might be caused by factors acting on the wintering grounds. For example, long-distance migrants might face, in addition to the change in climatic factors on the breeding grounds, deteriorating conditions on the wintering grounds in tropical Africa or Asia. It would be very interesting to test for such alternative factors. However, a prerequisite for testing these factors is to know where the different migratory species at the 21 sites spend their winter. Presently, such knowledge is unavailable. Thus, factors on the wintering grounds cannot easily be tested.

Moreover, it is not known which factors might influence migratory birds on their wintering grounds. In addition to climatic factors, changes in food resources, interspecific competition or predation pressure might be important. In general, long-distance migrants might be influenced by other factors on their breeding than on their wintering grounds. Short-distance migrants, in contrast, mainly overwinter in the Mediterranean region. Thus, in contrast to long-distance migrants, they might benefit from increases in winter temperature in Europe. Furthermore, the migratory behaviour of short-distance migrants might be controlled more by environmental factors like temperature, while the migratory behaviour of long-distance migrants seems to be more genetically controlled. Thus, short-distance migrants can probably adapt faster to climatic changes and arrive earlier on their breeding grounds than long-distance migrants (Møller et al. 2004). In the case, that short-distance migrants and resident bird species are able to adapt to warmer spring conditions faster and start breeding earlier (Møller et al. 2004), for incoming long-distance migrants then fewer nest sites are available and competition pressure will probably increase.

In addition to the ecological effects of global climate change on the composition of bird communities, analysed in this study, I expect evolutionary changes in the migratory behaviour of these birds. Migratory birds can change their migratory behaviour rapidly in only a few generations (Berthold 1999, 2000). As a consequence of global climate change, several species of partial and short-distance migrants already show trends to become residents (Berthold 1999, 2000). Thus, the phenomenon of migration is influenced on the one hand by changes in the number and proportion of migratory species, i.e. by ecological sorting, and on the other hand by evolutionary changes in the behaviour of these birds. In this study I made the assumption, that migratory behaviour was a fixed trait within a bird species and was the same over the whole range of the species within Europe. I did not include intraspecific variation in the migratory behaviour of migrants nor evolutionary changes of migratory behaviour into the analyses. Provided that the migratory behaviour of the species also evolves, I would expect that migratory restlessness will probably decrease and, therefore, changes in the proportion of migratory birds will be less than predicted. In case that evolutionary changes in the migratory behaviour of the species are more important than ecological sorting, migrants will become less migratory and therefore no change in the proportion of migratory birds and in bird community composition should be expected. In the present study such evolutionary changes could not be tested. Nevertheless, even with this conservative approach, I found changes in bird community structure caused by climate change demonstrating that there are ecological sorting effects on the proportion of migratory birds, which seem to change bird community composition.

My predictions of future changes in bird community composition suggest increases for the proportion of migratory birds for the most part of Europe. Only in high northern and far eastern regions migratory birds and especially short-distance migrants seem to be threatened by global warming. It would be interesting to evaluate if these changes in the proportion of migratory species can be related to changes in the absolute numbers of species. Unfortunately, earlier analyses including not only the proportion but the absolute number of species did not reach a satisfactory congruence between expected and observed changes in bird community composition. Therefore, it was not reasonable to predict changes in the number of migratory and resident bird species for the future. But, to my knowledge, so far no data demonstrating that climate change led to severe population declines or even extinctions of bird species have as yet been published (Böhning-Gaese & Lemoine 2004).

This study demonstrates for the first time that climate change has already changed the composition of European bird communities. The changes in bird community composition could be predicted quantitatively from spatial variation in bird communities and climatic factors across Europe. Furthermore, changes could not be explained by alternative factors. Changes in species richness of migratory birds over the past 40 years have been small and, in the future, declines are predicted to be balanced by increases (Fig. 4.3). It is important to note, however, that environmental changes on the wintering grounds are not included in my analyses and might lead to more negative trends than anticipated.

## 4.5 SUMMARY

Global climate change is increasingly influencing ecosystems. Long-term effects on the species richness and composition of ecological communities have been predicted using modelling approaches, but, so far, hardly demonstrated in the field. Here, I test whether changes in the composition of bird communities have been influenced by recent climate change. I focus on the proportion of migratory and resident bird species because these groups are expected to respond differently to climatic change. I used the spatial relationship between climatic factors and bird communities in Europe to predict changes in 21 European bird communities under recent climate change. Observed changes corresponded significantly to predicted changes and could not be explained by effects of spatial autocorrelation or alternative factors such as changes in land use. This demonstrates that global climate change has already influenced species richness and composition of European bird communities.

# 5 RECENT POPULATION TRENDS OF CENTRAL EUROPEAN BIRDS ARE CAUSED MORE BY CLIMATE THAN LAND-USE CHANGE

## 5.1 INTRODUCTION

Changes in vegetation, land-use and climate are the main factors which are suspected to cause current changes in biodiversity (Sala et al. 2000, Donald et al. 2001, Walther et al. 2002). Extensive habitat conversion leads to declines in biodiversity and ecological function (Whitmore 1992, Ehrlich 1994, Aebischer et al. 2000, Gaston et al. 2003, Daily 1997, Fahrig 2003). Furthermore, global climate change is expected to lead to profound changes in the composition of most biota (Parmesan et al. 2000, Walther et al. 2002, Root et al. 2003, Root et al. 2005). Finally, the invasion of exotic organisms is currently of great interest because of the damage caused by many invasive species (Drake et al. 1989, Williamson 1996, Leppäkoski, et al. 2002, Duncan et al. 2003).

Birds are a very well-studied group of organisms and respond rapidly to environmental changes. They seem to be greatly influenced by current changes in vegetation, land-use, and climate (Owens & Bennett 2000, Gaston et al. 2003, Møller et al. 2004), and by invasive species (Blackburn & Duncan 2001, Duncan et al. 2003). Consequently, a number of studies used bird communities as indicators for environmental change, for example in relation to land-use, forest management, and climatic change (Gregory et al. 2003, Gregory et al. 2004, Schulze et al. 2004, Tankersley 2004, Venier & Pearce 2004). Furthermore, birds have been used successfully as indicators for population changes in other taxonomic groups (Louette & Bijnens 1995, Lawton et al. 1998, Gregory et al. 2004, Schulze et al. 2004, Thomson et al. 2005).

One of the three most important factors influencing bird communities is, besides habitat loss and fragmentation, the increasing intensity of land-use practices. The general agricultural intensification has been identified as a major cause for declines in farmland bird populations in many temperate regions, especially in Europe (Fuller et al. 1995, Chamberlain et al. 2000). In addition, global climate change has been shown to strongly affect bird communities (Crick 2004, Møller et al. 2004). Compelling evidence has been found for the impact of global climate change on the phenology, breeding biology and population dynamics of birds (e.g. Forchhammer et al. 1998, Dunn 2004, Lehikoinen et al. 2004). Also range expansions have already been documented in several taxa (e.g. Johnson 1994, Pounds et al. 1999, Thomas & Lennon 1999, Peterson 2003a, Böhning-Gaese & Lemoine 2004). Accordingly, in France, bird species with geographic distributions at more northern latitudes were observed to show populations declines, while species with more southern distributions were relatively stable (Julliard et al. 2003).

As a third factor, the introduction of species to areas beyond the limits of their natural distribution has a major influence on the indigenous avifauna. A growing number of species have been transported and introduced by humans to new locations and have established self-sustaining populations. Despite the fact that only a proportion of these introductions have resulted in the establishment of new populations (Long 1981, Drake et al. 1989, Williamson 1996, Duncan et al. 2003), many of these species may cause significant environmental damage (Van Riper et al. 1986, Williamson 1996, Mack et al. 2000, Benning et al. 2002, Jarvi et al. 2003, Woodworth et al. 2005).

Finally, evidence for declines in long-distance migratory birds has caused considerable concern among conservationists (Berthold et al. 1986, Terborgh 1989, Askins et al. 1990, Bauer & Heine 1992, Berthold 2000). The analysis of the bird atlas data of the Lake Constance region in Central Europe between 1980-1981 and 1990-1992, for example, showed significant declines especially in long-distance migrants, whereas short-distance migrants and residents slightly increased (Böhning-Gaese & Bauer 1996). The reasons for these declines are not known for certain, but they have been attributed to habitat deterioration on the wintering grounds (Hjort & Lindholm 1978; Svensson 1985; Dallinga & Schoenmakers 1987, Baillie & Peach 1992), hunting (Schultz 1988, Magnin 1991, Rosen et al. 1999) and global climate changes acting on the breeding grounds, shifting the competitive relationship between resident and migratory birds (Lemoine & Böhning-Gaese 2003).

While it is known, that land use, climate change and exotic species have an impact on bird communities, it is unclear, which of these factors is currently most important. The aim of this study was, therefore, to determine which of these factors has currently the strongest influence on population trends of European birds. I examined the impact of these factors by contrasting the population trends of groups of birds, based on *a priori* hypotheses (Robbins et al. 1986, Böhning-Gaese & Bauer 1996, Julliard et al. 2003, Schmidt 2003). I tested the impact of land-use change by comparing the population trends of birds breeding in different habitat types. If, for example, changes in agricultural practices had a negative impact on birds, one should observe declines in farmland species. I tested the impact of global climate change by contrasting the population trends of birds breeding at different latitudes. If climate change influenced population trends of birds, one should observe declines in species with northern, and increases in species with southern geographic distributions. The potential influence of exotic species was tested by comparing the population trends of exotic and indigenous bird species. If exotic species pose a threat to indigenous bird communities I expect increases in exotic, and relative declines in indigenous species. Finally, to test whether migratory birds are still threatened, I compared the population trends of long-distance migratory, short-distance migratory and resident bird species.

For analysis, I used data of Central Europe from the breeding bird atlas Lake Constance. This bird atlas is one of the few European data sets which offers standardized abundance and range data for all regionally coexisting bird species both with a relatively high spatial resolution (4 km$^2$) and still on a relatively large spatial scale (1212 km$^2$, Schuster et al. 1983, Bauer & Heine 1992, Bauer et al. in press). Furthermore, it is the only bird atlas in Europe that contains standardized abundance and range size data collected with the same methodology for three different census periods, 1980-1981, 1990-1992 and 2000-2002, respectively (Schuster et al. 1983, Bauer & Heine 1992, Bauer et al. in press). In an earlier analysis of the Lake Constance data set, Böhning-Gaese & Bauer (1996) found significant declines in farmland species and long-distance migrants between the first two census periods, i.e. 1980-1981 and 1990-1992. In the present analyses, the third census period, i.e. 2000-2002, was included. Thus, it is now possible to analyse population trends for the 20-year time interval 1980-1981 to 2000-2002.

The first objective of the present study was to analyse the long-term population trends of the bird species in the Lake Constance region between 1980-1981 and 2000-2002. For this 20 year time interval, I contrasted the population trends of birds in relation to breeding habitat, latitudinal distribution, species' origin (exotic *versus* indigenous), and migratory behaviour. Second, to test, whether the influence of the respective factor increased or decreased in the course of the last 20 years, the analysis was repeated for the two time periods 1980-1981 to 1990-1992, and 1990-1992 to 2000, separately. Finally, I studied the impact of these factors on the regional abundance, local abundance, and range size of the species within the Lake Constance region because I wanted to test whether changes in regional abundance were caused rather by changes in local abundance, by changes in range size or by changes in both. When analysing the impact of the four factors on abundance and range size, I used both, univariate and multivariate statististical analyses to account for potential interrelationship between the independent factors. Finally, I analysed the number of species going extinct, and colonising the area.

## 5.2 METHODS

### 5.2.1 DATA SET

The Lake Constance bird atlas data were collected in 1980-1981, in 1990-1992, and in 2000-2002 by the Ornithologische Arbeitsgemeinschaft Bodensee. The atlas consists of 303 grid squares of 2 x 2 km, and covers 1212 km$^2$ of German, Austrian and Swiss territory (Schuster et al. 1983; Bauer & Heine 1992, Bauer et al. in press). The Lake Constance region consists of forest, grassland, arable land, orchards, fruit plantations, reed areas, lakes, and settlements in a small scale mosaic. Elevation ranges from 396 m (Lake Constance) to 980 m above sea level (foothill of the Alps).

To collect the bird data, each square was visited five times between the end of March and the middle of June in the early morning by trained observers. Data collection during unfavourable weather conditions was excluded because that might reduce singing activity. During each visit the observer sampled a different 4-km line transect covering an area of 50 m to either site, thus sampling 40 ha (4 km x 100m). Hence, over five visits, half of the square area was sampled. For each square the abundance of each breeding bird species was recorded in a standardized way in one of six abundance classes (1-3, 3-10, 10-30, 30-100, 100-300, 300-1000 breeding pairs). For analyses, I replaced the classes by the mean of the logarithmic abundance class boundaries (1.7, 5.5, 17.3, 54.8, 173.2, 547.7 breeding pairs, respectively) and used these mean values as abundance estimates for each species in each square.

The quality of the bird atlas data was tested by several methods. For example, standard line-transect data were compared with those obtained by territory mapping of the whole square and the same squares were sampled independently by two observers (Schuster et al. 1983, Bauer & Heine 1992, Böhning-Gaese and Bauer 1996). Semi-quantitative breeding bird atlases, like the Lake Constance bird atlas, are a compromise between a large spatial scale and good data quality. Although those atlas data cannot reach data quality of territory mapping, as used in the British Common Bird Census (Marchant et al. 1990), data quality is much better than point-counts like in the North American Breeding Bird Survey.

### 5.2.2 CLASSIFICATION OF SPECIES

To investigate the influence of land-use change, climatic change, the invasion of exotic species and migratory behaviour, on the Lake Constance bird community I contrasted the population trends of birds in relation to their breeding habitat, latitudinal distribution, species' origin, and migratory behaviour (Appendix 1). All 159 bird species recorded during any of the three census periods, were classified into four breeding habitat categories: primarily wetland (open water, reed, water edge); farmland (arable land, dry and damp grassland, pasture, orchards, hedgerows); forest (forest, forest clearings, woods); and urban (city, suburbs, cemeteries, parks, farm houses). For two species, the breeding habitat could not be identified unambiguously (Lesser Whitethroat, *Sylvia curruca*; Craig Martin, *Ptyonoprogne rupestris*). The geographic distribution of each species was quantified by its latitudinal distribution within Europe using the data of the EBCC Atlas of European breeding birds (Hagemeijer & Blair 1997). I determined the latitudinal position of the northern most and southern most edge of the range within Europe, and calculated the mean of these two values. For species' origin I distinguished between exotic and native species. Exotic or non-indigenous species were defined as species that were introduced to Central Europe since 1492 (Gebhardt et al. 1996, Kowarik 2003). Four bird species were defined as exotic: Ruddy Shelduck (*Tadorna ferruginea*), Mandarin Duck (*Aix galericula*), Canada Goose (*Branta candensis*), and Pheasant (*Phasianus colchicus*). Migratory behaviour was classified into three categories: primarily resident; short-distance migrants (wintering in the Mediterranean area); long-distance migrant (wintering south of the Sahara).

### 5.2.3 CHANGES IN BIRD POPULATIONS

I analysed changes in regional abundance, local abundance and range size because changes in regional abundance might have been caused by changes in local abundance, in range size, or in both. For example, if habitat degradation on the wintering grounds in the Sahel zone reduced the number of migratory bird individuals returning in spring, I would expect declines in the regional abundance of the species, mediated mostly through declines in local abundance, but less so in range size. On the other hand, if a species lost parts of its breeding habitat because of urban development, one should observe declines in regional abundance, mostly caused by a decline in range size with little change in local abundance in still-occupied sites.

For each species, regional abundance was calculated as the product of local abundance and range size. Local abundance was defined as the mean number of breeding pairs in occupied squares. Range size was determined as the number of occupied squares. Estimates of regional and local abundance were both based on the original abundance estimates in abundance classes of each species in each square. Thus, the values give only best estimates of the real population sizes for each species. Please note, that the measure used in this study to describe population size were not independent because regional abundance is the product of local abundance and range size.

I calculated changes in regional abundance, local abundance and range size in the same way. In the following, to simplify the terminology, I use the expression “status” to refer to all three of them. Change in status was defined as change = $[\text{status}_{2000} - \text{status}_{1980}] / [(\text{status}_{1980} + \text{status}_{2000})/2]$. For example, the Lapwing (*Vanellus vanellus*) changed in regional abundance by $-1.33 = [171.5 - 849.4] / [(849.4 + 171.5)/2]$. In contrast to the usual calculations of percent change, I used the mean of the status in 1980-1981 and 2000-2002 as denominator, not the status in 1980-1981. The problem with using the 1980-1981 status as denominator is that increases and declines are not symmetrical. The maximum decline a species can archive is –1, the maximum increase >> +1. Using the mean of the status in 1980-1981 and 2000-2002 as the denominator makes increase and declines symmetrical. Maximum decline in the case of extinction was –2, and maximum increase in the case of colonization was +2.

For analyses, changes in status were weighted by the mean status of the species because alterations in rare and abundant species were not equally reliable. The same percent change in a rare species is less significant than in an abundant species. For example, an increase in regional abundance between 1980-81 and 1990-92 of +0.20 was not significant for Little Grebe (*Tachybarptus ruficollis*); mean regional abundance 311 breeding pairs) but was highly significant and therefore more reliable for the collared Dove (*Streptopelia decaocto*; mean regional abundance 2888 breeding pairs). Census data of abundant species were also more precise (Bauer & Heine 1992). In the statistical analysis, I weighted the change in status by the logarithm of the mean status (log [(status$_{1980}$ + status$_{2000}$)/2 + 1]). I added +1 to the mean status because for a species that was detected within a square only for one of the three census periods, for the other two census periods the weight would have been calculated as weight = log (0 + 0/2), a term that is mathematically not defined.

Please note that the paired design used for calculating changes, for example in local abundance, reduced the problems connected with potentially biased estimates of local abundance. Although the local abundance estimates of a species might be biased, the comparison of the abundance of a species between two census periods is statistically valid as long as the bias influences the abundance estimates of the species in both census periods in the same way.

When testing the impact of breeding habitat, latitudinal distribution, species' origin, and migratory behaviour on changes in regional abundance, local abundance and range size, I first tested each factor univariately, using either a univariate ANOVA, or a univariate regression analysis. I then combined the four factors in multivariate ANCOVAs. For each analysis, I first tested the change in status between the two census periods 1980-81 and 2000-2002, and then for the census periods 1980-1981 to 1990-1992 (first decade), and 1990-1992 to 2000-2002 (second decade), separately. All analyses were calculated with JMP (SAS, 2001). Furthermore, I tested all two-way, three-way, and four-way interaction terms. Please note that the univariate ANOVAs testing the impact of breeding habitat and migratory behaviour on changes in regional abundance, local abundance and range size between the census periods 1980-81 and 1990-92 have been published previously (Böhning-Gaese & Bauer 1996). Nevertheless, I decided to include them in the results to aid the presentation and interpretation of the effects.

## 5.3 RESULTS

### 5.3.1 UNIVARIATE ANALYSES

In the univariate analyses, breeding habitat had a significant impact on changes in the regional abundance of the bird species between 1980-1981 and 2000-2002 (Tab. 5.1). Effects of breeding habitat were more significant in the first than in the second decade (Tab. 5.1). Changes were mostly mediated through changes in range size. Between 1980-1981 and 2000-2002, the latitudinal distribution significantly affected changes in the regional abundance of the bird species (Tab. 5.1). This factor was not significant in the first decade, but increased strikingly in importance and became highly significant in the second decade (Tab. 5.1). Again, changes were mostly mediated through changes in range size. The species' origin did not affect the abundance or range size of the species in any of the analyses (Tab. 5.1). Migratory behaviour was significantly related to changes in regional abundance of the species between 1980-81 and 2000-2002 (Tab. 5.1). The effect was slightly stronger in the second than in the first decade and, again, mediated more by changes in range size than by changes in local abundance (Tab. 5.1).

Tab. 5.1: Univariate analyses, testing the influence of breeding habitat, latitudinal distribution, species' origin, and migratory behaviour on changes in regional abundance (RA), local abundance (LA) and range size (RS) of breeding birds in the Lake Constance region between 1980-1981 and 2000-2002, between 1980-1981 and 1990-1992, and between 1990-1992 and 2000-2002. [1] = one-factor-ANOVA; [2] = univariate regression; n = 156.

| *Factor* | | *Model d.f.* | *Error d.f.* | *F* | *t* | *p* | *$R^2$(%)* |
|---|---|---|---|---|---|---|---|
| RA | | | | | | | |
| Breeding habitat[1] | 1980-2000 | 3 | 152 | 7.33 | - | **<0.001** | 12.6 |
| | 1980-1990 | 3 | 146 | 5.00 | - | **0.002** | 9.32 |
| | 1990-2000 | 3 | 151 | 3.78 | - | **0.012** | 6.99 |
| Latitudinal distribution[2] | 1980-2000 | - | - | - | - 3.28 | **0.001** | 6.46 |
| | 1980-1990 | - | - | - | - 1.28 | 0.20 | 1.09 |
| | 1990-2000 | - | - | - | - 4.24 | **<0.001** | 10.4 |
| Species' origin[1] | 1980-2000 | 1 | 156 | 0.56 | - | 0.45 | 0.36 |
| | 1980-1990 | 1 | 149 | 1.65 | - | 0.20 | 1.10 |
| | 1990-2000 | 1 | 155 | 0.05 | - | 0.82 | 0.03 |
| Migratory behaviour[1] | 1980-2000 | 2 | 153 | 8.37 | - | **<0.001** | 9.74 |
| | 1980-1990 | 2 | 147 | 4.22 | - | **0.017** | 5.42 |
| | 1990-2000 | 2 | 154 | 5.05 | - | **0.008** | 6.15 |

Tab. 5.1 continued:

| *Factor* | | *Model d.f.* | *Error d.f.* | *F* | *t* | *p* | *$R^2$(%)* |
|---|---|---|---|---|---|---|---|
| LA | | | | | | | |
| Breeding habitat[1] | 1980-2000 | 3 | 152 | 1.99 | - | 0.12 | 3.78 |
| | 1980-1990 | 3 | 146 | 0.18 | - | 0.91 | 0.36 |
| | 1990-2000 | 3 | 151 | 3.01 | - | **0.032** | 5.65 |
| Latitudinal distribution[2] | 1980-2000 | - | - | - | - 2.51 | **0.013** | 3.88 |
| | 1980-1990 | - | - | - | - 1.71 | 0.09 | 1.91 |
| | 1990-2000 | - | - | - | - 1.65 | 0.10 | 1.72 |
| Species' origin[1] | 1980-2000 | 1 | 156 | 2.20 | - | 0.14 | 1.39 |
| | 1980-1990 | 1 | 149 | <0.01 | - | 0.98 | <0.01 |
| | 1990-2000 | 1 | 155 | 3.00 | - | 0.09 | 1.90 |
| Migratory behaviour[1] | 1980-2000 | 2 | 153 | 3.98 | - | **0.021** | 4.89 |
| | 1980-1990 | 2 | 147 | 1.60 | - | 0.21 | 2.13 |
| | 1990-2000 | 2 | 154 | 1.69 | - | 0.19 | 2.15 |
| RS | | | | | | | |
| Breeding habitat[1] | 1980-2000 | 3 | 152 | 8.48 | - | **<0.001** | 14.30 |
| | 1980-1990 | 3 | 146 | 6.34 | - | **<0.001** | 11.52 |
| | 1990-2000 | 3 | 151 | 2.80 | - | **0.042** | 5.27 |
| Latitudinal distribution[2] | 1980-2000 | - | - | - | - 2.75 | **0.006** | 4.62 |
| | 1980-1990 | - | - | - | - 0.34 | 0.73 | 0.079 |
| | 1990-2000 | - | - | - | - 4.14 | **<0.001** | 9.96 |
| Species' origin[1] | 1980-2000 | 1 | 156 | 0.12 | - | 0.73 | 0.76 |
| | 1980-1990 | 1 | 149 | 0.09 | - | 0.77 | 0.058 |
| | 1990-2000 | 1 | 155 | 0.08 | - | 0.78 | 0.51 |
| Migratory behaviour[1] | 1980-2000 | 2 | 153 | 5.01 | - | **0.008** | 6.08 |
| | 1980-1990 | 2 | 147 | 2.36 | - | 0.10 | 3.11 |
| | 1990-2000 | 2 | 154 | 2.81 | - | 0.06 | 3.52 |

### 5.3.2 MULTIVARIATE ANALYSES

In the multivariate analyses, changes in the regional abundance of the species between 1980-1981 and 2000-2002 were significantly influenced by the factors breeding habitat (Fig. 5.1), latitudinal distribution (Fig. 5.2), and migratory behaviour (Fig. 5.3, Tab. 5.2). Again, the origin of the species had no influence on population trends (Tab. 5.2). In the first decade, changes in regional abundance were influenced by breeding habitat and migratory behaviour, in the second decade by latitudinal distribution and migratory behaviour (Fig. 5.1-5.3, Tab.

5.2). Thus, in the multivariate analysis, breeding habitat became marginally non-significant and latitudinal distribution the most significant factor in the second decade.

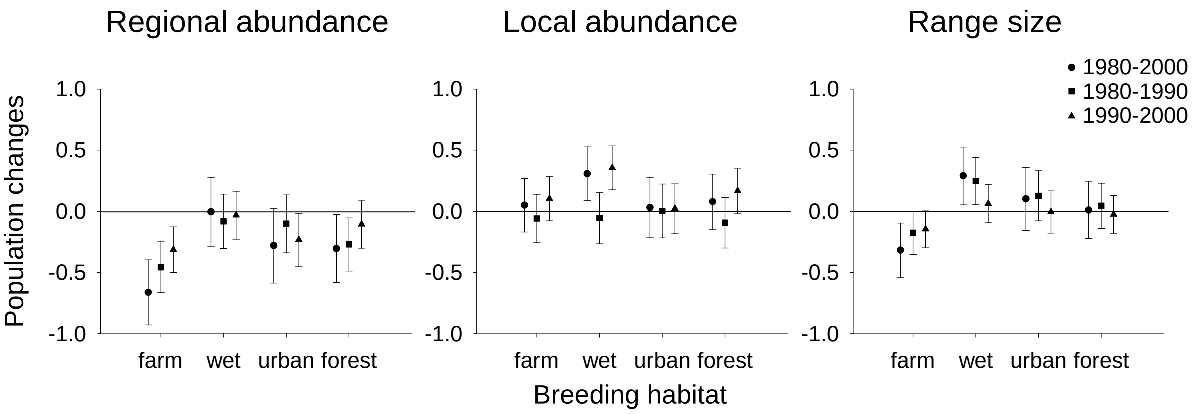


Fig. 5.1: Mean (± 1 SE) changes in regional abundance, local abundance, and range size of groups of species that differ in breeding habitat. Least mean squares after controlling for latitudinal distribution, species' origin, and migratory behaviour (SAS 2001). Farmland species (farm) are species that breed in grassland, arable land, fields, hedgerows, and orchards; wetland species (wet) are species that breed in reed and along water edge; urban species are species that breed in settlements, parks, and cemeteries; and forest species are species that breed in forest and woods.

The influence of breeding habitat on changes in regional abundance were mediated mostly through declines in range size of farmland species, and increases in local abundance and range size of wetland species (Fig. 5.1). The latitudinal distribution of the species had an effect almost exclusively on range size, with increases in range size of species with a southern geographical distribution, and decreases in range size of northern species (Fig. 5.2). Long-distance migrants declined both in range size and in local abundance, while short-distance migrants and residents increased more in local abundance than in range size (Fig. 5.3). None of the interaction terms between the factors breeding habitat, latitudinal distribution, species' origin, and migratory behaviour was significant in any of the models.

Tab. 5.2: ANCOVAs testing the combined effect of breeding habitat, latitudinal distribution, species' origin, and migratory behaviour on changes in regional abundance (RA), local abundance (LA) and range size (RS) of breeding birds in the Lake Constance region between 1980-1981 and 2000-2002, between 1980-1981 and 1990-1992, and between 1990-1992 and 2000-2002 .

| *Factor* | *Model d.f.* | *Error d.f.* | *F* | *P* | *$R^2$ (%)* |
|---|---|---|---|---|---|
| | | *1980-2000* | | | |
| RA | | | | | |
| Model | 7 | 148 | 6.76 | **<0.001** | 24.2 |
| Breeding habitat | 3 | | 5.40 | **0.002** | |
| Latitudinal distribution | 1 | | 9.68 | **0.002** | |
| Species' origin | 1 | | 0.79 | 0.37 | |
| Migratory behaviour | 2 | | 6.90 | **0.001** | |
| LA | | | | | |
| Model | 7 | 148 | 2.65 | **0.013** | 11.14 |
| Breeding habitat | 3 | | 1.74 | 0.16 | |
| Latitudinal distribution | 1 | | 2.96 | 0.09 | |
| Species' origin | 1 | | 1.26 | 0.26 | |
| Migratory behaviour | 2 | | 3.83 | **0.024** | |
| RS | | | | | |
| Model | 7 | 148 | 5.49 | **<0.001** | 20.6 |
| Breeding habitat | 3 | | 6.55 | **<0.001** | |
| Latitudinal distribution | 1 | | 6.01 | **0.015** | |
| Species' origin | 1 | | 0.05 | 0.82 | |
| Migratory behaviour | 2 | | 3.09 | **0.048** | |
| RA | | | | | |
| Model | 7 | 142 | 3.49 | **0.002** | 14.7 |
| Breeding habitat | 3 | | 3.74 | **0.013** | |
| Latitudinal distribution | 1 | | 1.26 | 0.26 | |
| Species' origin | 1 | | 1.26 | 0.26 | |
| Migratory behaviour | 2 | | 3.48 | **0.034** | |
| LA | | | | | |
| Model | 7 | 142 | 1.00 | 0.43 | 4.69 |
| Breeding habitat | 3 | | 0.25 | 0.86 | |
| Latitudinal distribution | 1 | | 3.08 | 0.08 | |
| Species' origin | 1 | | <0.01 | 0.95 | |
| Migratory behaviour | 2 | | 1.78 | 0.17 | |
| RS | | | | | |
| Model | 7 | 142 | 3.06 | **0.005** | 13.1 |
| Breeding habitat | 3 | | 5.35 | **0.002** | |
| Latitudinal distribution | 1 | | <0.01 | 0.98 | |
| Species' origin | 1 | | <0.01 | 0.96 | |
| Migratory behaviour | 2 | | 1.29 | 0.28 | |

Tab. 5.2 continued:

| *Factor* | *Model d.f.* | *Error d.f.* | *F* | *P* | *R² (%)* |
|---|---|---|---|---|---|
| | | *1990-2000* | | | |
| RA | | | | | |
| Model | 7 | 147 | 5.11 | **<0.001** | 19.6 |
| Breeding habitat | 3 | | 2.30 | 0.08 | |
| Latitudinal distribution | 1 | | 16.2 | **<0.001** | |
| Species' origin | 1 | | 0.16 | 0.69 | |
| Migratory behaviour | 2 | | 3.94 | **0.022** | |
| LA | | | | | |
| Model | 7 | 147 | 2.10 | **0.047** | 9.11 |
| Breeding habitat | 3 | | 2.71 | **0.047** | |
| Latitudinal distribution | 1 | | 0.041 | 0.64 | |
| Species' origin | 1 | | 2.03 | 0.16 | |
| Migratory behaviour | 2 | | 1.34 | 0.26 | |
| RS | | | | | |
| Model | 7 | 147 | 3.85 | **<0.001** | 15.5 |
| Breeding habitat | 3 | | 1.68 | 0.17 | |
| Latitudinal distribution | 1 | | 14.36 | **<0.001** | |
| Species' origin | 1 | | 0.13 | 0.72 | |
| Migratory behaviour | 2 | | 1.98 | 0.14 | |

### 5.3.3 EXTINCTIONS AND COLONIZATIONS

In the 20 years between 1980-1981 and 2000-2002, four species went regionally extinct (Hoopoe, *Upupa epops*; Sedge Warbler, *Acrocephalus schoenobaenus*; Great Grey Shrike, *Lanius excubitor*; and Woodchat Shrike, *Lanius senator*). Each of them was already rare in 1980-1981 with less than seven breeding pairs. Three species, that were present in 1980-81, but missed in 1990-1992, re-colonized the Lake Constance region in the second decade: Purple Heron (*Ardea purpurea*), Corncrake (*Crex crex*), and Meadow Pipit (*Anthus pratensis*). One species, the Northern Wheatear (*Oenanthe oenanthe*) colonized the region in the first decade with less than four breeding pairs and went extinct in the second decade.

During the same period (1980-1981 to 2000-2002) 16 species colonized the Lake Constance region (Mandarin Duck, Greylag Goose, *Anser anser*; Hazel Grouse, *Bonasa bonasia*; Canada Goose, White Stork, *Ciconia ciconia*; Rock Bunting, *Emberiza cia;* Peregrine, *Falco peregrinus*; Melodious Warbler, *Hippolais polyglotta*; Mediterranean Gull, *Larus melanocephalus*; Yellow-legged Gull, *Larus michahellis*; Eagle Owl, *Bubo bubo*; Cormorant, *Phalacrocorax carbo*; Crag Martin; Penduline Tit, *Remiz pendulinus*; Ruddy Shelduck, and Ring Ouzel, *Turdus torquatus*). Three of these species, Mandarin Duck, Canada Goose, and Ruddy Shelduck, have been defined as exotic species. As more species colonised the region than went extinct, the total number of species increased from 141 species in 1980-1981 to 146 species in 1990-1992, and 154 species in 2000-2002.

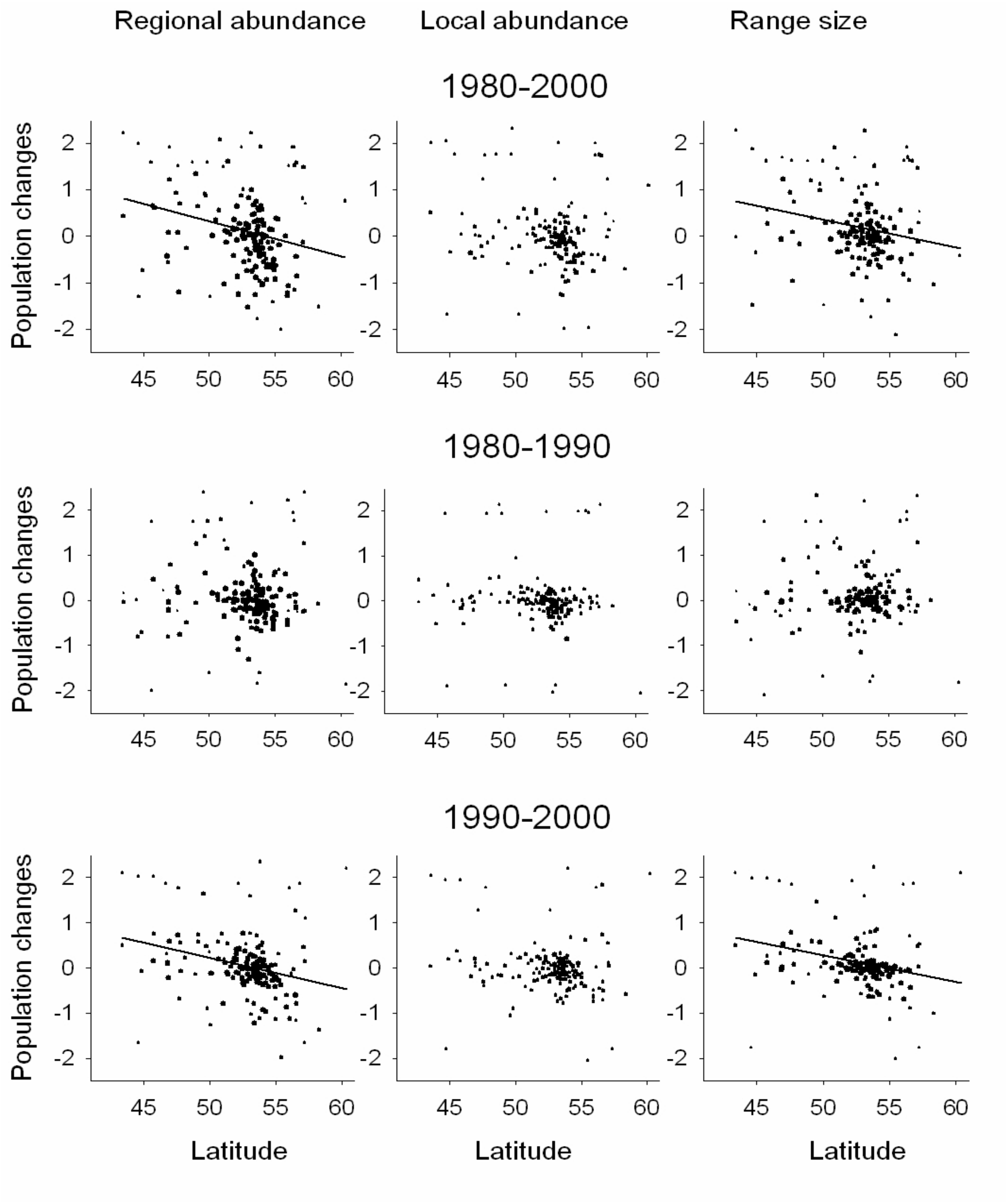


Fig. 5.2: Influence of latitudinal distribution (in °N) on population changes in regional abundance, local abundance, and range size of species. Leverage plot after controlling for breeding habitat, species' origin and migratory behaviour (SAS 2001). The census area in the Lake Constance region lies at 47°39''N latitude. Circle size determined by weight of status.

## 5.4 DISCUSSION

Changes in the regional abundance of 159 coexisting Central European bird species from 1980-1981 to 2000-2002 were influenced by their breeding habitat, latitudinal distribution, and migratory behaviour. Although only two time intervals were compared, I am, nevertheless, confident that these changes reflected long-term trends in bird abundances and not only annual fluctuations. Firstly, each of the census periods consisted of two or three years, which should reduced the probability that only year-to-year population fluctuations were analysed. Secondly, population trends were calculated by averaging over many species. Thus, it is unlikely that particularly low or high population densities of a specific species in a specific year had a strong impact on the results.

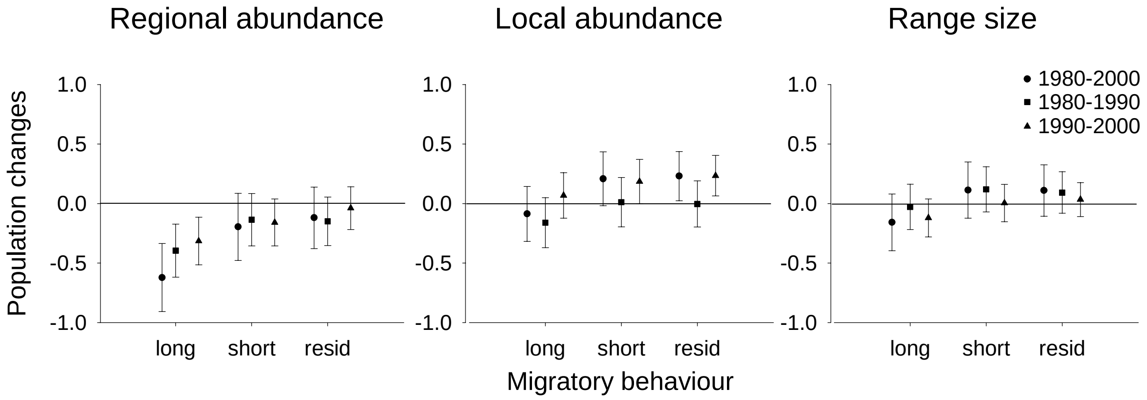


Fig. 5.3: Mean (± 1 SE) changes in regional abundance, local abundance, and range size of groups of species that differ in migratory behaviour. Least mean squares after controlling for breeding habitat, latitudinal distribution, and species' origin (SAS 2001). Long-distance migrants (long) are species that winter south of the Sahara; short-distance migrants (short) are species that winter in the Mediterranean area; and residents (resid) are species that winter in the breeding area.

The influence of breeding habitat on changes in the regional abundance of the species was highly significant between 1980-1981 and 2000-2002. The effect of breeding habitat was significant in the first and second decade in the univariate analyses (Tab. 5.1), and significant in the first, but marginally non-significant in the second decade in the multivariate analysis (Tab. 5.2). Changes in regional abundance in relation to breeding habitat were primarily mediated through range expansions and contractions, whereas the mean abundance in occupied squares stayed approximately constant.

The strongest declines within the four breeding habitat categories were found for farmland species (Fig. 5.1). Again, the declines in regional abundance were mainly caused by declines in range size, with little change in local abundance (Fig. 5.1). The declines of farmland birds in the Lake Constance region reflect a trend that can be observed European-wide and can be linked to increased agricultural intensification and yields connected to EU policies (Fuller et al. 1995, Pärt & Söderström 1999, Chamberlain et al. 2000, Donald et al. 2001, Donald et al.2002, BirdLife International 2004). Although declines are found for both decades, declines in the second decade appear to have been weaker than in the first decade. This suggests that programs aimed at diminishing the negative impacts of agricultural intensification on farmland birds, e.g. the set-aside area program (Buckingham et al. 1999, Henderson et al. 2000, Van Buskirk & Willi 2004) and other more regional conservation programs (e.g., Wiesenbrüter-Programm, Randstreifen-Programm) slowly became effective and slowed down the declines. Nevertheless, it has to be noted that although these programs are effective since the early 1990 (Buckingham et al. 1999, Henderson et al. 2000), farmland birds still showed declines between 1990-1992 and 2000-2002. This demonstrates that these programs are not efficient enough and further efforts to develop a better integration of bird protection requirements and agricultural policies have to be undertaken.

In addition, the fact that declines in farmland species are mediated mostly through loss of range size suggests that other factors besides agricultural intensification had a negative impact on farmland birds as well. One of these processes might be urbanization, increases in land area occupied by human settlements and roads, mostly at the cost of agricultural land (Jobin et al. 1996, Titeux et al. 2004). In the Lake Constance region the land area covered by urban areas (including city, suburbs, cemeteries, parks, and farm houses) increased from 16.3 % in 1980-1981 to 20.7 % in 1990-1992 (Böhning-Gaese 1998). Further increases up to today can be observed in the region but have not been quantified. Thus, a second incentive to protect farmland birds is to reduce the area lost to urban development.

A positive development in the Lake Constance region is increases in regional abundance, local abundance and range size of wetland species. These increases are probably caused by the fact that relatively large nature reserves in the Lake Constance region protect wetland habitats (e.g. Wollmatinger Ried, Konstanzer Bucht, Randecker Maar, Lauteracher Ried, Mindelsee). These nature reserves have been well managed (e.g. naturalization of riverbeds, facilitation of alluvial forests) and many threatened wetland species increased in abundance (e.g. Red-crested Porchard, *Netta rufina*; Common Tern, *Sterna hirundo;* Gadwall, *Anas strepera;* Kingfisher, *Alcedo atthis;* and White-throated Dipper, *Cinclus cinclus*). The positive trends resulting from these conservation efforts seem to have continued in both decades.

The latitudinal distribution of the species significantly influenced changes in abundance and range size between 1980-1981 and 2000-2002 (Fig. 5.2). The relationship between regional abundance and latitudinal distribution of the species was not significant in the first decade, but increased in importance and was highly significant in the second decade (Fig. 5.2). Changes in regional abundance in relation to geographic distribution were mostly mediated through changes in range size. Southern distributed species increased in range size, whereas species with a rather northern distribution decreased in range size. Several species declining between 1980-1981 and 2000-2002 in the Lake Constance region had a more northern distribution (e.g., Mute Swan, *Cygnus olor*; Teal, *Anas crecca*; Pochard, *Aythya ferina*; Wheatear; Sedge Warbler; Lapwing; Snipe, *Gallinago gallinago*; Tree Pipit, *Anthus trivialis*; Redstart, *Phoenicurus phoenicurus*). Accordingly, several southern distributed species increased in the same time (Purple Heron; Ruddy Shelduck; Red-crested Pochard; Black Kite, *Milvus migrans*; Peregrine; Skylark, *Alauda arvensis*; Sand Martin, Rock Bunting; Melodius Warbler; Crag Martin).

Global climate change is one important factor discussed to lead to range shifts in northern directions (Thomas & Lennon 1999, Böhning-Gaese & Lemoine 2004). Temperatures of the coldest month in the Lake Constance region increased by 2.1° C from -1.6° C in 1980-81 to 0.5°C in 2000-2002. These increases in, especially, winter temperature appeared to have allowed range expansions of species whose northern range limit lied in the Lake Constance region and whose northern distribution appeared to have been limited by low mean winter temperature. The declines of species with more northern distributions are more difficult to explain. One explanation might be increasing heat stress (Hayworth & Weathers 1984, Hampe & Petit 2005), pathogen pressure (Epstein et al. 1998, Walker 1998, Benning et al. 2002, Buckley et al. 2003, Higgs et al. 2004) or competition with colonising and rising populations of more southern species in increasingly species-rich communities. A similar relationship between changes in abundance and latitudinal distribution were found for common bird species that breed in France. Species with a more northern breeding distribution tended to have a lower annual population growth rate than species with a more southern distribution (Julliard et al. 2003). In addition to these studies, my results indicate that the impact of climate change on bird populations has increased in importance between 1990-1992 and 2000-2002 and is now more significant than any other tested factor, even more so than breeding habitat.

Among the 159 bird species recorded in the Lake Constance region in at least one of the three census periods, only four species were determined as exotic species (Ruddy Shelduck, Mandarin Duck, Canada Goose, and Pheasant). Two of them, the Mandarin Duck and the Ruddy Shelduck, colonized the Lake Constance region in the second decade and had a mean regional abundance of 1.7 breeding pairs in 2000-2002. The Canada Goose colonized the region in the first decade and remained stable with a mean of 5.5 breeding pairs in the second decade. The Pheasant, introduced in Central Europe in the 14th century, declined from about 1980 breeding pairs in 1980-1981 to about 1660 breeding pairs in 1990-1992 to about 380 breeding pairs in 2000-2002. Three of these species had only very small range sizes with quite low abundances. Currently, there seems to be no threat of exotic species to the native avifauna in the Lake Constance region. However, as exotic species represent only 2.5% of the Lake Constance species, it is not surprising that the impact of these species is currently of minor importance. In other regions, especially on oceanic islands, the impact of non-indigenous species became a major threat to native species (e.g. Williamson 1996, Huxel 1999, Sakai et al. 2001, Duncan et al. 2003). Still, among the 16 species newly colonising the Lake Constance region, three (18.8%) were exotic. Thus, with further increases in temperature, exotic species might pose a more significant threat to the indigenous avifauna in Central Europe in the future.

The impact of migratory behaviour on population trends was highly significant between 1980-1981 and 2000-2002 with a similar significance in the first and second decade (Tab. 5.2). These changes were, similar to the results of Böhning-Gaese & Bauer (1996), mainly caused by declines in the regional abundance of long-distance migrants. In Europe in general, long-distance migrants are declining at a threatening rate. The overall trends for long distance migrants were significantly worse than for short-distance migrants or residents at the EU and Pan-European level (BirdLife International 2004).

The causes for the declines of long-distance migrants are difficult to evaluate. One factor might be global climate change acting on the breeding ground, leading to higher survival of resident birds in winter, increasing competitive pressure on migrants, resulting in declines of long-distance migrants (Lemoine & Böhning-Gaese 2003). The significant declines of the long-distance migrants in the Lake Constance region in the first decade were of a magnitude that can be quantitatively predicted by the observed climate change in the Lake Constance region (Lemoine & Böhning-Gaese 2003). In addition, the population sizes of migratory birds, unlike those of resident species, are influenced not only by conditions on the breeding grounds but also in other parts of the world (Greenberg & Marra 2005). Therefore, declines in the abundance of long-distance migrants can be caused by changing habitat quality on the wintering grounds south of the Sahara (Sears et al. 1993, Marra et al. 1998, Bearhop et al. 2004, Norris 2005). The destruction and degradation of migrant stopover habitat is another potential cause for migrant declines (Rappole & Warner 1976; Moore et al. 1995). Long-distance migrants may also be endangered by increasing physiological difficulties in passing the expanding Sahara desert.

To conclude, while long-distance migrants showed declines both between 1980-1981 and 1990-1992 and between 1990-92 and 2000-2002, the relative influence of changes in land-use and climate on population trends of birds seemed to have shifted their importance during those two decades. Breeding habitat was, besides migratory behaviour, the most significant predictor of population trends during the time period 1980-1982 to 1990-1992. During this time period the latitudinal distribution of the species was not related to population trends. In the second decade from 1990-92 to 2000-2002, however, breeding habitat was marginally non-significant (in the multivariate analysis) and latitudinal distribution became the most significant predictor of population trends. This demonstrates that climate and not land-use change might currently be the most important threat for birds in Europe.

### 5.5 SUMMARY

While it is known, that changes in land use, climate and the spread of exotic species have an impact on ecological communities, it is unclear, which of these factors is currently of most importance. The aim of this study was, therefore, to determine which of these factors has currently the strongest influence on population trends of Central European birds. I examined the impact of these factors by contrasting the population trends of groups of birds, differing in breeding habitat, latitudinal distribution, origin (exotic *versus* native) and migratory behaviour. Using data from the semi-quantitative breeding bird atlas “Lake Constance” from

1980-1981 to 2000-2002, I demonstrated that changes in the regional abundances of the 159 coexisting bird species were influenced by their breeding habitat, latitudinal distribution, and migratory behaviour. I could not detect an impact of exotic species on population trends. The separate analysis of the time periods from 1980-1981 to 1990-1992, and from 1990-1992 to 2000-2002, demonstrated that the relative influence of land-use and climate on population trends seemed to have shifted in importance. While breeding habitat was more significant in the first than in the second decade, latitudinal distribution was not significant in the first decade and became the most significant predictor of population trends in the second decade. These results suggest that climate change is currently more important than land-use change in determining the population trends of birds in Central Europe.

# 6 GENERAL CONCLUSIONS

Everything in the Earth's flora and fauna is aligned with environmental conditions. Animal and plant species were exposed to changes in the environmental conditions at all times and at all places. Nevertheless, the present changes in habitat, climate, and the ecological community composition are of an exceeding magnitude. Habitat conversion, climate change and the invasion of new species influence the indigenous communities with unexpected consequences. A factor with expanding importance for biodiversity is global warming (McCarthy et al. 2001), because it is increasingly influencing the phenology, abundance, range size and range position of plant and animal species, resulting in observable changes from the level of individuals to whole communities (Peñuelas & Filella 2001, McLaughlin et al. 2002, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003). Birds have proved to be good indicators for environmental changes and were, therefore, the focus of my thesis.

In a first approach, I collected information about changes in the birds' ranges and communities. The most interesting conclusion of this review was, so far, that only few effects of climate change on ranges and communities have actually been reported using field data. This is surprising because strong effects of climate change on the phenology, reproductive success and population dynamics of birds are well documented (Lehikoinen et al. 2004, Dunn 2004). This is also surprising because birds are one of the few groups of organisms for which good, long-term data exist. The reasons for this lack of effects are difficult to judge. One possibility might be that changes in ranges and communities are not as strong as often predicted and these (negative) results have not been published. In addition, it is possible that the regions for which the best data sets exist are not the regions in which climate had changed so far.

My second study dealt with the impact of climate change on bird community composition in Europe. For this macroecological study my analyses indicated that observed changes in bird community composition could be explained by climate change. I did not find any significant influence of spatial autocorrelation or of alternative factors on the changes in bird community composition. Predictions for future changes in the composition of bird communities in Europe indicated no negative changes in the proportion of migratory bird species for most regions of Europe. Only in the northern part of Europe declines can probably be expected.

Finally, I analysed a regional bird community in central Europe on a small spatial scale to detect the main factors currently influencing population trends. Changes in the regional abundance of 159 coexisting central European bird species from 1980-1981 to 2000-2003 were influenced by their breeding habitat, their migratory behaviour, and their latitudinal distribution. Significant declines were found in farmland species and in long-distance migrants. The highest increases were detected for wetland and for resident species. The impact of exotic species on the indigenous avifauna seems to be currently of minor importance, but with increasing temperatures it might become more relevant in the future. Despite the ongoing declines in farmland species in Central Europe during the last decade, the impact of global warming seems to be stronger than the influence of habitat degradation. Moreover, persisting declines in long-distance migrants and declines especially in species with northern distributions indicate that climate change might be currently the most important threat for birds in Europe.

In chapter 3 of the thesis I reviewed the impact of climate change on the ranges of birds and on avian communities according to the literature. The current state of research led to the question if changes in bird communities could be observed, which can be explained by global climate change. Accordingly, I analysed the relationship between the bird community composition and climate change first on a broad scale (chapter 4). Secondly I tested for a central European bird community the main factors currently influencing the community structure (chapter 5) on a small spatial scale. Analysing the broad scale impact of climate change on the bird community composition I was able to detect a general pattern global climate change probably causes in European bird communities. This macroecological approach had the advantage that the large amount of detailed information about bird species did not superpose the general pattern. Nevertheless, I made the assumption, that migratory behaviour was a fixed trait within a bird species over the whole range of the species within Europe. Neither intraspecific variation in the migratory behaviour of migrants nor evolutionary changes of migratory behaviour were included into the analyses. However, several species of partial and short-distance migrants do not migrate anymore and have become "more resident" (Berthold 1999, 2000). Such changes could not be detected with this approach.

For the bird community in the Lake Constance region a very good data-set exist containing standardised abundance and range size data for three different census periods. Therefore, the data set of the Lake Constance region was exceedingly appropriate to evaluate the results of the broad scale analyses for a single bird community and to analyse the impact of climate change in relation to the influence other environmental factors have on the bird community structure. The analysis of the Lake Constance data-set also dealt with a fixed status for breeding habitat and migratory behaviour. However, within a single bird community these traits might be less variable within a species than for all bird communities within Europe. The results of the chapter 5 are, on the one hand, more detailed than the results of chapter 4. On the other hand, the results of chapter 5 without the broad scale approach would be rather less representative for Europe. Therefore, the combined approach of a macroecological correlation of changes in bird communities with isochronic climate change and a detailed investigation of the main factors influencing a single bird community provided an opportunity to scrutinise the broad scale pattern on a smaller level.

Generally, climate change seems to be the most important factor presently influencing bird communities and, therefore, it can be expected that also numerous other animal and plant species might be, to a certain degree, controlled by this phenomenon. In several studies range expansions of birds were predicted and observed that lead to increases in species richness in many temperate, boreal, and Arctic regions and at high altitudes. The question arises if high Arctic and Alpine species are threatened by these processes because their life-zones might contract. In contrast, range contractions and a loss of species richness with increasing temperatures and decreasing precipitation can probably be expected especially for arid subtropical and tropical regions. Thus, conservation efforts have to focus more on the high-temperature, low-precipitation part than on the low-temperature part of the latitudinal gradient.

Furthermore, centres of species richness are expected to shift or even to contract (Erasmus et al. 2002). This has severe consequences for conservation efforts. Currently, international conservation efforts focus on areas with many endemic or threatened bird species. With the predicted changes in ranges it can be expected that many threatened species move out of the areas that receive highest conservation efforts. The new ranges might then be placed in areas with high human population density or areas with conflicting land-use (Erasmus et al. 2002). Therefore, the results obtained in this thesis have important implications for the conservation of birds.

Apart from climate change, habitat conversion continuously threatens especially farmland birds. These declines can be observed European-wide and are linked to increased yields driven by agricultural practices in the EU (BirdLife International 2004). Therefore, it is a key challenge to develop better integration of bird protection requirements into agricultural and other policies. To conclude, the results presented in this thesis demonstrate that the lingering pressure on the environment mainly manifests itself in habitat conversion and especially in climate change.

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# 8 APPENDIX

Appendix 1: Breeding habitat, latitudinal distribution, species' origin, migratory behaviour, and changes in regional abundance, local abundance, and range size from 1980-1981 to 2000-2002 for 159 coexisting bird species in the Lake Constance region.

| | *B*[a] | *L*[b] | *O*[c] | *M*[d] | *Regional abundance* | | | *Local abundance* | | | *Range size* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Name* | | | | | *1980* | *2000* | *change* | *1980* | *2000* | *change* | *1980* | *2000* | *change* |
| Little Grebe<br>(*Tachybaptus ruficollis*) | w | 51.1 | n | r | 269.8 | 384.5 | 0.35 | 3.4 | 4.6 | 0.31 | 80 | 83 | 0.04 |
| Great Crested Grebe<br>(*Podiceps cristatus*) | w | 52.4 | n | r | 956.0 | 1478.4 | 0.43 | 11.5 | 14.9 | 0.26 | 83 | 99 | 0.18 |
| Black-necked Grebe<br>(*P. nigricollis*) | w | 48.6 | n | s | 11.0 | 165.9 | 1.75 | 5.5 | 9.8 | 0.56 | 2 | 17 | 1.58 |
| Cormorant<br>(*Phalacrocorax carbo*) | w | 56.3 | n | s | 0.0 | 60.3 | 2.00 | 0.0 | 30.2 | 2.00 | 0 | 2 | 2.00 |
| Little Bittern<br>(*Ixobrychus minutus*) | w | 47.3 | n | l | 14.0 | 29.3 | 0.71 | 2.3 | 2.0 | -0.18 | 6 | 15 | 0.86 |
| Grey Heron<br>(*Ardea cinerea*) | w | 53.8 | n | r | 79.3 | 257.1 | 1.06 | 19.8 | 9.5 | -0.70 | 4 | 27 | 1.48 |
| Purple Heron<br>(*A. purpurea*) | w | 45.2 | n | l | 1.7 | 3.4 | 0.67 | 1.7 | 1.7 | 0.00 | 1 | 2 | 0.67 |
| White Stork<br>(*Ciconia ciconia*) | f | 49.7 | n | l | 0.0 | 39.5 | 2.00 | 0.0 | 1.9 | 2.00 | 0 | 21 | 2.00 |
| Mute Swan<br>(*Cygnus olor*) | w | 54.7 | n | r | 313.2 | 246.0 | -0.24 | 2.9 | 2.5 | -0.15 | 110 | 100 | -0.10 |
| Greylag Goose<br>(*Anser anser*) | w | 56.3 | n | r | 0.0 | 24.1 | 2.00 | 0.0 | 4.8 | 2.00 | 0 | 5 | 2.00 |
| Canada Goose<br>(*Branta canadensis*) | w | 55.4 | e | r | 0.0 | 5.1 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 3 | 2.00 |
| Ruddy Shelduck<br>(*Tadorna ferruginea*) | w | 45.9 | e | r | 0.0 | 1.7 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 1 | 2.00 |
| Mandarin Duck<br>(*Aix galericulata*) | w | 51.4 | e | r | 0.0 | 1.7 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 1 | 2.00 |
| Gadwall<br>(*Anas strepera*) | w | 53.3 | n | r | 42.4 | 99.9 | 0.81 | 2.7 | 3.7 | 0.33 | 16 | 27 | 0.51 |
| Teal<br>(*A. crecca*) | w | 58.1 | n | r | 10.6 | 3.4 | -1.03 | 2.7 | 1.7 | -0.44 | 4 | 2 | -0.67 |
| Mallard<br>(*A. platyrhynchos*) | w | 54.2 | n | r | 1890.9 | 1666.4 | -0.13 | 7.7 | 6.6 | -0.15 | 245 | 252 | 0.03 |
| Garganey<br>(*A. querquedula*) | w | 53.8 | n | l | 19.5 | 11.9 | -0.48 | 2.8 | 1.7 | -0.48 | 7 | 7 | 0.00 |
| Shoveler<br>(*A. clypeata*) | w | 54.5 | n | s | 5.1 | 6.8 | 0.29 | 1.7 | 1.7 | 0.00 | 3 | 4 | 0.29 |

Appendix 1 continued:

| | B[a] | L[b] | O[c] | M[d] | Regional abundance | | | Local abundance | | | Range size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Name* | | | | | *1980* | *2000* | *change* | *1980* | *2000* | *change* | *1980* | *2000* | *change* |
| Red-crested Pochard<br>(*Netta rufina*) | w | 47.3 | n | s | 204.2 | 336.9 | 0.49 | 5.2 | 5.4 | 0.02 | 39 | 63 | 0.47 |
| Pochard<br>(*Aythya ferina*) | w | 53.6 | n | r | 31.3 | 19.1 | -0.48 | 4.5 | 2.1 | -0.71 | 7 | 9 | 0.25 |
| Ferruginous Duck<br>(*A. nyroca*) | w | 47.4 | n | r | 0.0 | 3.4 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 2 | 2.00 |
| Tufted Duck<br>(*A. fuligula*) | w | 55.6 | n | r | 88.3 | 145.2 | 0.49 | 6.3 | 3.8 | -0.49 | 14 | 38 | 0.92 |
| Honey Buzzard<br>(*Pernis apivorus*) | fo | 53.1 | n | l | 44.2 | 13.6 | -1.06 | 1.7 | 1.7 | 0.00 | 26 | 8 | -1.06 |
| Black Kite<br>(*Milvus migrans*) | fo | 51.8 | n | s | 256.9 | 332.3 | 0.26 | 2.0 | 1.7 | -0.12 | 131 | 191 | 0.37 |
| Red Kite<br>(*M. milvus*) | fo | 47.5 | n | s | 39.1 | 120.7 | 1.02 | 1.7 | 1.7 | 0.00 | 23 | 71 | 1.02 |
| Marsh Harrier<br>(*Circus aeruginosus*) | w | 52.2 | n | s | 1.7 | 10.2 | 1.43 | 1.7 | 1.7 | 0.00 | 1 | 6 | 1.43 |
| Goshawk<br>(*Accipiter gentilis*) | fo | 53.1 | n | r | 22.1 | 64.6 | 0.98 | 1.7 | 1.7 | 0.00 | 13 | 38 | 0.98 |
| Sparrowhawk<br>(*A. nisus*) | fo | 53.3 | n | r | 49.3 | 183.6 | 1.15 | 1.7 | 1.7 | 0.00 | 29 | 108 | 1.15 |
| Common Buzzard<br>(*Buteo buteo*) | fo | 52.7 | n | r | 453.4 | 604.6 | 0.29 | 2.0 | 2.3 | 0.11 | 222 | 264 | 0.17 |
| Kestrel<br>(*Falco tinnunculus*) | f | 53.3 | n | r | 413.3 | 395.3 | -0.04 | 1.9 | 2.0 | 0.07 | 223 | 199 | -0.11 |
| Hobby<br>(*F. subbuteo*) | fo | 53.8 | n | l | 76.5 | 107.1 | 0.33 | 1.7 | 1.7 | 0.00 | 45 | 63 | 0.33 |
| Peregrine Falcon<br>(*F. peregrinus*) | f | 53.6 | n | r | 0.0 | 11.9 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 7 | 2.00 |
| Hazel Grouse<br>(*Bonasa bonasia*) | w | 55.8 | n | r | 0.0 | 1.7 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 1 | 2.00 |
| Grey Partridge<br>(*Perdix perdix*) | f | 53.3 | n | r | 154.8 | 10.2 | -1.75 | 2.5 | 1.7 | -0.38 | 62 | 6 | -1.65 |
| Common Quail<br>(*Coturnix coturnix*) | f | 50.9 | n | l | 71.7 | 61.5 | -0.15 | 2.3 | 2.5 | 0.06 | 31 | 25 | -0.21 |
| Common Pheasant<br>(*Phasianus colchicus*) | f | 52.2 | e | r | 1978.8 | 376.3 | -1.36 | 9.0 | 4.1 | -0.76 | 221 | 93 | -0.82 |
| Water Rail<br>(*Rallus aquaticus*) | w | 51.8 | n | s | 279.6 | 176.2 | -0.45 | 4.7 | 3.2 | -0.39 | 60 | 56 | -0.07 |
| Spotted Crake<br>(*Porzana porzana*) | w | 52.4 | n | s | 3.4 | 5.1 | 0.40 | 1.7 | 1.7 | 0.00 | 2 | 3 | 0.40 |
| Corncrake<br>(*Crex crex*) | f | 54.0 | n | l | 3.4 | 14.0 | 1.22 | 1.7 | 2.3 | 0.31 | 2 | 6 | 1.00 |
| Moorhen<br>(*Gallinula chloropus*) | w | 52.0 | n | r | 434.3 | 193.7 | -0.77 | 3.8 | 2.7 | -0.34 | 113 | 71 | -0.46 |
| Coot<br>(*Fulica atra*) | w | 53.6 | n | r | 1496.7 | 1713.7 | 0.14 | 10.3 | 10.1 | -0.02 | 145 | 169 | 0.15 |
| Little Ringed Plover<br>(*Charadrius dubius*) | w | 52.7 | n | s | 17.0 | 15.3 | -0.11 | 1.7 | 1.7 | 0.00 | 10 | 9 | -0.11 |
| Lapwing<br>(*Vanellus vanellus*) | f | 54.2 | n | s | 849.4 | 171.5 | -1.33 | 7.8 | 3.5 | -0.76 | 109 | 49 | -0.76 |
| Snipe<br>(*Gallinago gallinago*) | f | 56.3 | n | s | 164.2 | 31.8 | -1.35 | 4.1 | 2.7 | -0.43 | 40 | 12 | -1.08 |
| Black-tailed Godwit<br>(*Limosa limosa*) | f | 56.7 | n | s | 10.6 | 1.7 | -1.45 | 2.7 | 1.7 | -0.44 | 4 | 1 | -1.20 |
| Curlew<br>(*Numenius arquata*) | f | 57.4 | n | s | 46.2 | 30.1 | -0.42 | 2.9 | 2.7 | -0.05 | 16 | 11 | -0.37 |
| Common Sandpiper<br>(*Tringa hypoleucos*) | w | 54.5 | n | s | 5.1 | 1.7 | -1.00 | 1.7 | 1.7 | 0.00 | 3 | 1 | -1.00 |

## Appendix 1 continued:

|  | B[a] | L[b] | O[c] | M[d] | Regional abundance |  |  | Local abundance |  |  | Range size |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Name* |  |  |  |  | *1980* | *2000* | *change* | *1980* | *2000* | *change* | *1980* | *2000* | *change* |
| Mediteranean Gull<br>(*Larus melanocephalus*) | w | 48.4 | n | s | 0.0 | 1.7 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 1 | 2.00 |
| Yellow-legged Gull<br>(*L. michahellis*) | w | 45.2 | n | s | 0.0 | 8.9 | 2.00 | 0.0 | 3.0 | 2.00 | 0 | 3 | 2.00 |
| Black-headed Gull<br>(*L. ridibundus*) | w | 54.5 | n | s | 1423.8 | 1184.2 | -0.18 | 158.2 | 91.1 | -0.54 | 9 | 13 | 0.36 |
| Common Gull<br>(*L. canus*) | w | 56.7 | n | s | 3.4 | 14.4 | 1.24 | 1.7 | 3.6 | 0.72 | 2 | 4 | 0.67 |
| Common Tern<br>(*Sterna hirundo*) | w | 54.7 | n | l | 98.3 | 143.4 | 0.37 | 16.4 | 23.9 | 0.37 | 6 | 6 | 0.00 |
| Rock Dove<br>(*Columba livia*) | u | 53.6 | n | r | 1590.9 | 3077.0 | 0.64 | 23.7 | 18.8 | -0.23 | 67 | 164 | 0.84 |
| Stock Dove<br>(*C. oenas*) | fo | 52.4 | n | s | 62.0 | 176.9 | 0.96 | 1.9 | 2.3 | 0.17 | 32 | 77 | 0.83 |
| Wood Pigeon<br>(*C. palumbus*) | fo | 53.3 | n | s | 2563.3 | 2771.3 | 0.08 | 9.7 | 10 | 0.03 | 264 | 277 | 0.05 |
| Collared Dove<br>(*Streptopelia decaocto*) | u | 53.1 | n | r | 2388.3 | 2128.5 | -0.12 | 11.6 | 9.76 | -0.17 | 206 | 218 | 0.06 |
| Turtle Dove<br>(*S. turtur*) | f | 51.5 | n | l | 31.4 | 83.5 | 0.91 | 2.2 | 2.9 | 0.25 | 14 | 29 | 0.70 |
| Cuckoo<br>(*Cuculus canorus*) | f | 54.2 | n | l | 778.2 | 485.4 | -0.46 | 2.8 | 2.3 | -0.22 | 276 | 214 | -0.25 |
| Barn Owl<br>(*Tyto alba*) | u | 47.3 | n | r | 17.0 | 93.5 | 1.38 | 1.7 | 1.7 | 0.00 | 10 | 55 | 1.38 |
| Eagle Owl<br>(*Bubo bubo*) | f | 53.6 | n | r | 0.0 | 3.4 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 2 | 2.00 |
| Little Owl<br>(*Athene noctu*a) | f | 47.3 | n | r | 19.5 | 8.5 | -0.79 | 2.8 | 1.7 | -0.48 | 7 | 5 | -0.33 |
| Tawny Owl<br>(*Strix aluco*) | fo | 52.0 | n | r | 390.1 | 300.2 | -0.26 | 2.1 | 2.0 | -0.05 | 187 | 152 | -0.21 |
| Long-eared Owl<br>(*Asio otus*) | fo | 54.0 | n | r | 202.6 | 157.5 | -0.25 | 1.9 | 2.1 | 0.09 | 108 | 77 | -0.34 |
| Common Swift<br>(*Apus apus*) | u | 53.3 | n | l | 5105.2 | 3556.0 | -0.36 | 24.3 | 17.5 | -0.32 | 210 | 203 | -0.03 |
| Common Kingfisher<br>(*Alcedo atthis*) | w | 49.5 | n | r | 11.9 | 61.2 | 1.35 | 1.7 | 1.7 | 0.00 | 7 | 36 | 1.35 |
| Hoopoe<br>(*Upupa epops*) | f | 50.2 | n | l | 1.7 | 0.0 | -2.00 | 1.7 | 0.0 | -2.00 | 1 | 0 | -2.00 |
| Wryneck<br>(*Jynx torquilla*) | f | 54.0 | n | l | 275.1 | 114.7 | -0.82 | 2.8 | 1.8 | -0.42 | 99 | 63 | -0.44 |
| Grey-headed Woodpecker<br>(*Picus canus*) | fo | 54.0 | n | r | 300.0 | 274.3 | -0.09 | 2.2 | 2.0 | -0.13 | 134 | 139 | 0.04 |
| Green Woodpecker<br>(*P. viridis*) | fo | 52.4 | n | r | 498.0 | 768.8 | 0.43 | 2.4 | 2.9 | 0.19 | 208 | 266 | 0.24 |
| Black Woodpecker<br>(*Dryocopus martius*) | fo | 53.8 | n | r | 155.1 | 206.9 | 0.29 | 1.7 | 1.8 | 0.03 | 89 | 115 | 0.25 |
| Great Spotted Woodpecker<br>(*Dendrocopos major*) | fo | 53.8 | n | r | 1770.7 | 2941.4 | 0.50 | 6.5 | 10.1 | 0.44 | 274 | 291 | 0.06 |
| Middle Spotted Woodpecker<br>(*D. medius*) | fo | 48.4 | n | r | 35.7 | 32.3 | -0.10 | 1.7 | 1.7 | 0.00 | 21 | 19 | -0.10 |
| Lesser Spotted Woodpecker<br>(*D. minor*) | fo | 54.2 | n | r | 336.1 | 226.3 | -0.39 | 2.2 | 2.0 | -0.09 | 153 | 113 | -0.30 |
| Woodlark<br>(*Lullula arborea*) | f | 51.3 | n | s | 1.7 | 6.8 | 1.20 | 1.7 | 1.7 | 0.00 | 1 | 4 | 1.20 |
| Skylark<br>(*Alauda arvensis*) | f | 53.8 | n | s | 4915.2 | 1286.6 | -1.17 | 22.2 | 13.7 | -0.48 | 221 | 94 | -0.81 |
| Sand Martin<br>(*Riparia riparia*) | w | 53.6 | n | l | 481.0 | 155.2 | -1.02 | 48.1 | 25.9 | -0.60 | 10 | 6 | -0.50 |

Appendix 1 continued:

| | $B^{a}$ | $L^{b}$ | $O^{c}$ | $M^{d}$ | Regional abundance | | | Local abundance | | | Range size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Name* | | | | | *1980* | *2000* | *change* | *1980* | *2000* | *change* | *1980* | *2000* | *change* |
| Crag Martin (*Ptyonoprogne rupestris*) | n | 42.1 | n | s | 0.0 | 5.5 | 2.00 | 0.0 | 5.5 | 2.00 | 0 | 1 | 2.00 |
| Swallow (*Hirundo rustica*) | u | 53.8 | n | l | 10745.8 | 4930.7 | -0.74 | 37.6 | 17.7 | -0.72 | 286 | 279 | -0.02 |
| House Martin (*Delichon urbica*) | u | 53.8 | n | l | 11457.3 | 5725.7 | -0.67 | 46.0 | 24.3 | -0.62 | 249 | 236 | -0.05 |
| Tree Pipit (*Anthus trivialis*) | f | 54.5 | n | l | 2441.6 | 241.2 | -1.64 | 10.7 | 4.2 | -0.88 | 229 | 58 | -1.19 |
| Meadow Pipit (*A. pratensis*) | f | 60.5 | n | s | 3.4 | 5.5 | 0.47 | 1.7 | 5.5 | 1.06 | 2 | 1 | -0.67 |
| Yellow Wagtail (*Motacilla flava*) | f | 54.2 | n | l | 225.5 | 144.5 | -0.44 | 4.4 | 6.6 | 0.39 | 51 | 22 | -0.79 |
| Grey Wagtail (*M. cinerea*) | w | 53.8 | n | s | 188.5 | 193.5 | 0.03 | 3.1 | 2.2 | -0.33 | 61 | 87 | 0.35 |
| Pied/White Wagtail (*M. alba*) | f | 53.8 | n | s | 5040.5 | 3882.4 | -0.26 | 16.8 | 13.0 | -0.25 | 300 | 298 | -0.01 |
| Dipper (*Cinclus cinclus*) | w | 54.2 | n | r | 40.7 | 57.8 | 0.35 | 2.7 | 1.7 | -0.46 | 15 | 34 | 0.78 |
| Wren (*Troglodytes troglodytes*) | fo | 53.1 | n | r | 7454.9 | 11062.3 | 0.39 | 26.1 | 37.1 | 0.35 | 286 | 298 | 0.04 |
| Dunnock (*Prunella modularis*) | fo | 54.7 | n | s | 7792.0 | 4301.3 | -0.58 | 27.2 | 15.8 | -0.53 | 286 | 273 | -0.05 |
| Robin (*Erithacus rubecula*) | fo | 53.8 | n | r | 15994.9 | 15229.9 | -0.05 | 56.1 | 51.5 | -0.09 | 285 | 296 | 0.04 |
| Nightingale (*Luscinia megarhynchos*) | fo | 45.7 | n | l | 192.4 | 257.4 | 0.29 | 2.9 | 3.6 | 0.20 | 66 | 72 | 0.09 |
| Black Redstart (*Phoenicurus ochruros*) | u | 52.0 | n | s | 4795.4 | 7617.0 | 0.45 | 16.2 | 25.3 | 0.44 | 296 | 301 | 0.02 |
| Redstart (*P. phoenicurus*) | f | 54.5 | n | l | 1688.5 | 316.8 | -1.37 | 7.0 | 3.3 | -0.72 | 242 | 96 | -0.86 |
| Whinchat (*Saxicola rubetra*) | f | 53.8 | n | l | 341.3 | 174.9 | -0.64 | 7.8 | 7.6 | -0.02 | 44 | 23 | -0.63 |
| Stonechat (*S. torquata*) | f | 51.1 | n | s | 3.4 | 62.7 | 1.79 | 1.7 | 3.0 | 0.55 | 2 | 21 | 1.65 |
| Ring Ouzel (*Turdus torquatus*) | fo | 56.3 | n | s | 0.0 | 1.7 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 1 | 2.00 |
| Blackbird (*T. merula*) | u | 53.8 | n | r | 46705.7 | 41781.5 | -0.11 | 154.1 | 137.9 | -0.11 | 303 | 303 | 0.00 |
| Fieldfare (*T. pilaris*) | f | 55.6 | n | s | 8624.4 | 5302.6 | -0.48 | 29.7 | 19.6 | -0.41 | 290 | 270 | -0.07 |
| Song Thrush (*T. philomelos*) | fo | 54.9 | n | s | 12078.8 | 7919.1 | -0.42 | 42.8 | 27.6 | -0.43 | 282 | 287 | 0.02 |
| Mistle Thrush (*T. viscivorus*) | fo | 53.6 | n | s | 624.5 | 1525.9 | 0.84 | 5.4 | 8.8 | 0.47 | 115 | 174 | 0.41 |
| Grashopper Warbler (*Locustella naevia*) | w | 54.5 | n | l | 1235.9 | 456.3 | -0.92 | 7.3 | 3.8 | -0.62 | 170 | 119 | -0.35 |
| Savis Warbler (*L. luscinioides*) | w | 48.6 | n | l | 24.6 | 47.9 | 0.64 | 2.5 | 2.8 | 0.14 | 10 | 17 | 0.52 |
| Marsh Warbler (*Acrocephalus palustris*) | f | 52.7 | n | l | 2566.6 | 1383.6 | -0.60 | 11.5 | 7.4 | -0.43 | 224 | 187 | -0.18 |
| Sedge Warbler (*A. schoenobaenus*) | w | 54.9 | n | l | 3.4 | 0.0 | -2.00 | 1.7 | 0.0 | -2.00 | 2 | 0 | -2.00 |
| Reed Warbler (*A. scirpaceus*) | w | 50.9 | n | l | 2666.5 | 2912.1 | 0.09 | 17.7 | 17.1 | -0.03 | 151 | 170 | 0.12 |
| Great Reed Warbler (*A. arundinaceus*) | w | 51.1 | n | l | 74.1 | 77.1 | 0.04 | 3.5 | 3.1 | -0.13 | 21 | 25 | 0.17 |
| Icterine Warbler (*Hippolais icterina*) | fo | 56.5 | n | l | 1396.9 | 358.4 | -1.18 | 6.8 | 3.1 | -0.74 | 205 | 114 | -0.57 |

Appendix 1 continued:

| | B[a] | L[b] | O[c] | M[d] | Regional abundance | | | Local abundance | | | Range size | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Name* | | | | | *1980* | *2000* | *change* | *1980* | *2000* | *change* | *1980* | *2000* | *change* |
| Melodius Warbler (*H. polyglotta*) | w | 44.1 | n | l | 0.0 | 3.4 | 2.00 | 0.0 | 1.7 | 2.00 | 0 | 2 | 2.00 |
| Lesser Whitethroat (*Sylvia curruca*) | ? | 55.1 | n | l | 556.0 | 187.1 | -0.99 | 3.5 | 2.3 | -0.41 | 158 | 81 | -0.64 |
| Whitethroat (*S. communis*) | f | 52.2 | n | l | 1016.7 | 576.0 | -0.55 | 5.7 | 5.1 | -0.13 | 177 | 114 | -0.43 |
| Garden Warbler (*S. borin*) | fo | 54.5 | n | l | 4738.1 | 3953.4 | -0.18 | 16.1 | 14.2 | -0.13 | 295 | 279 | -0.06 |
| Blackcap (*S. atricapilla*) | fo | 54 | n | s | 17952.3 | 20249.5 | 0.12 | 59.3 | 66.8 | 0.12 | 303 | 303 | 0.00 |
| Bonellis Warbler (*Phylloscopus bonelli*) | fo | 44.8 | n | l | 51.2 | 15.7 | -1.06 | 4.3 | 2.2 | -0.62 | 12 | 7 | -0.53 |

[a] Breeding habitat: f = farmland, species breed in grassland, arable land, hedgerows, and orchards; w = wetland, species breed in reed and along water edge; u = urban, species breed in settlements, parks, and cemetries; fo = forest, species breed in forest and woods.

[b] Latitudinal distribution: centre of distribution area (°N).

[c] Species' origin: n = native, indigenous species of Central Europe; e = exotic, species not native to Central Europe.

[d] Migratory behaviour: l = long-distance migrant wintering south of the Sahara; s = short-distance migrants wintering in the Mediterranean area; and r = resident.