THE ROYAL SOCIETY

Received 6 January 2003
Accepted 13 March 2003
Published online 30 May 2003

Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants

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As a response to increasing spring temperature in temperate regions in recent years, populations of many plant and animal species, including migratory birds, have advanced the seasonal start of their reproduction or growth. However, the effects of climate changes on subsequent events of the annual cycle remain poorly understood. We investigated long-term changes in the timing of autumn migration in birds, a key event in the annual cycle limiting the reproductive period. Using data spanning a 42-year period, we analysed long-term changes in the passage of 65 species of migratory birds through Western Europe. The autumn passage of migrants wintering south of the Sahara has advanced in recent years, presumably as a result of selection pressure to cross the Sahel before its seasonal dry period. In contrast, migrants wintering north of the Sahara have delayed autumn passage. In addition, species with a variable rather than a fixed number of broods per year have delayed passage, possibly because they are free to attempt more broods. Recent climate changes seem to have a simple unidirectional effect on the seasonal onset of reproduction, but complex and opposing effects on the timing of subsequent events in the annual cycle, depending on the ecology and life history of a species. This complicates predictions of overall effects of global warming on avian communities.

Keywords: climate change; migrating birds; timing of migration; migration

1. INTRODUCTION

Over the past two decades, spring temperatures in temperate regions have increased (Easterling *et al.* 1997; Anon. 2001) and the phenology of the vegetation and of many insects has advanced in the Northern Hemisphere (Myneni *et al.* 1997; Roy & Sparks 2000; McCarty 2001). Apart from effects on distribution and population size (Burton 1995; Thomas & Lennon 1999; McCarty 2001; Walther *et al.* 2002), this may affect the finely tuned timing of annual processes in migratory birds. Most bird species investigated (see Crick *et al.* 1997; Bairlein & Winkel 2001), but not all (see Visser *et al.* 1998; Both & Visser 2001), have advanced the start of egg-laying. However, there is hardly any information about the effects of global warming on subsequent events of the annual cycle of migratory birds (see Bairlein & Winkel 2001; Walther *et al.* 2002). Evidence for a prolonged breeding season or for delayed or advanced autumn migration is equivocal (Gatter 1992; Moritz & Vogel 1995; Sokolov *et al.* 1999; Gatter 2000; Bairlein & Winkel 2001).

We analysed changes in the timing of autumn peak passage in Western Europe of 64 migratory bird species and one distinct subspecies over three periods: 1958–1969, 1970–1982 and 1988–1999. We used data from 344 496 birds caught at the Alpine pass Col de Bretolet, Switzerland, at 1920 m above sea level. Col de Bretolet is a pure passage site for most species, so our data were not confounded by non-migratory movements of locally breeding conspecific birds. Birds caught originate from a wide area northeast of Col de Bretolet (Fennoscandia, Central and Eastern Europe).

The timing of autumn migration is governed mainly by three factors:

(i) the end of the annual reproductive period;
(ii) the conditions in the breeding area after the breeding season; and
(iii) the expected conditions in the passage and wintering grounds.

Recent climate changes may have altered the relative importance of these three factors, resulting in an advance or a delay of autumn migration. Spring temperatures, which have increased strongly in Europe (Easterling *et al.* 1997; Walther *et al.* 2002), may have an indirect effect on autumn migration by affecting the timing of reproduction. Autumn temperatures, which have increased much less in Europe (Easterling *et al.* 1997), may directly or indirectly affect autumn migration.

We examined the following three predictions:

(i) Long-distance migrants wintering south of the Sahara and passing through areas with seasonally deteriorating ecological conditions (i.e. the onset of the dry season in the Sahel from September onwards) leave earlier in autumn; they can do so because breeding starts and terminates earlier. They thus achieve a higher survival rate during migration. In contrast, short-distance migrants wintering north of the Sahara pass through, and winter in, areas offering better conditions resulting from global warming. They may delay autumn migration or even winter

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DOI 10.1098/rspb.2003.2394

in the breeding grounds (Berthold 1990). Because migration is risky (Sillett & Holmes 2002), they thus achieve higher survival rates and/or obtain higher-quality breeding territories by arriving earlier in spring (Berthold 1990).

(ii) Species with a variable number of broods per year prolong the breeding season (i.e. there is a higher proportion of pairs with more than one brood), achieve a higher reproductive output and delay autumn migration.

(iii) Especially among short-distance migrants, seed eaters might be expected to delay autumn migration, while insectivorous species might not. Insect abundance in autumn generally declines dramatically after a cold spell, making it more risky for insectivorous species to delay migration.

2. MATERIAL AND METHODS

(a) *Study site and data collection*

Trapping data spanning 42 years were obtained at Col de Bretolet, a mountain pass in the Swiss–French Alps (47°09′ N, 6°47′ E; altitude 1920 m). Birds were trapped in mist nets day and night from early July until early November for 33 years between 1958 and 1999 (for details see Jenni (1984); for logistical reasons, not all years could be covered). Their breeding grounds extend in a broad northeast-directed fan from areas in Switzerland to Fennoscandia and Russia. To have appreciable sample sizes for most species, we grouped the 33 studied years into three periods containing 11, 10 and 12 years: 1958–1969 (1958–1966, 1968, 1969), 1970–1982 (1970–1974, 1976, 1977, 1980–1982) and 1988–1999. These groups were so chosen to yield compact time periods with similar numbers of years with data.

The beginning and end of the capture season varied between years owing to the variable onset of winter snowfall and for organizational reasons. The number of birds caught per species and standardized 5-day interval (starting at 1 January) was divided by the number of years during which the trapping station was operating for each of the 5-day intervals. This yielded migration density data that were typically unimodal and symmetrical. However, in some species, a distinct pre-migratory peak corresponded to non-directed post-breeding dispersal rather than true, directional migration and this was cut off (Jenni 1984). The cut-off point was confirmed to represent the start of true migration in 20 species by a sudden transition from birds mainly in old plumage (before or during the post-juvenile or post-breeding moult) to birds mainly in fresh plumage (after moult) and by the occurrence of nocturnal migrants (Jenni 1984).

(b) *Estimation of peak passage*

The trapped birds were a truncated sample of the actual population that migrated across Col de Bretolet, either because premigratory movements were cut off or because the station had to be closed down for winter before their passage was complete. To estimate peak passage for each period (1958–1969, 1970–1982, 1988–1999), we fitted a truncated normal distribution to the trapping densities per 5-day interval. We used an iterative algorithm to obtain the maximum-likelihood estimate of the mean of the distribution (corresponding to the estimated peak passage) and its standard error (Johnson *et al.* 1994). The parameter estimates for each species and period are given in the electronic Appendix, available on The Royal Society's Publications Web site. Both truncation points were specified from the observational record. The lower truncation point was the 5-day interval starting on 30 June (or 5 July during the period 1988–1999) or the start of true, directional migration for those species where post-breeding dispersal captures had been excluded from the data. The upper truncation point was the 5-day interval ending on 1 November.

Our dataset comprised estimated peak passage data for the three periods for 65 taxa (60 species and one distinct subspecies of passerines, four species of small non-passerines). In the case of four species we had estimates for only two periods. Our data were based on 344 496 captures and, depending on species and period, between 5 and 54 230 captures per period.

(c) *Analysis of time shifts*

To test for time shifts and effects of the biology of the species on the timing of migration, we fitted a mixed model with a random effect for species to the estimated peak passage. Because these are estimates of uneven precision, we weighted each data point by its precision. We used iterative weighted least squares to obtain the maximum-likelihood estimates of model parameters in the presence of the known component of variance provided by the standard error of the estimates (McCullagh & Nelder 1989). We first ran the model with the reciprocal of the squared standard error of the estimate as a weight and obtained an initial estimate of residual variance. We then re-ran the model weighted with the reciprocal sum of the residual variance and the squared standard error of the estimates obtained from the fit of the normal distribution. We thus obtained a new estimate of the residual variance component and iterated until convergence.

We considered the following fixed factors: period (1958–1969, 1970–1982, 1988–1999), migration mode, number of broods, and food outside the breeding season. Migration mode contrasts long-distance (trans-Sahara) versus short-distance migrants. If a species winters both north and south of the Sahara, we considered the area where most of the central European population winters. The number of broods is a measure of the potential to lengthen the reproductive season. We distinguished between species with one regular brood (and possibly replacement broods), species with variable proportions of a population attempting a second brood and species that regularly have 2 or more broods. These data were taken from Glutz von Blotzheim & Bauer (1980–1997). Main food type during the non-breeding season was taken from Cramp (1985–1994) and contrasted species feeding on seeds (including a few insects), those feeding on fruits and a few insects, and those feeding mainly on insects.

We used a step-wise backwards elimination procedure to identify the factors with a significant effect. At each step, the factor with statistical significance closest to 1 was dropped from the model until only factors with $p < 0.05$ remained. Our starting model contained the main effects of the above factors and all two-way interactions between period (1958–1969, 1970–1982, 1988–1999) and the other factors. To test if the significant interaction between period and migration mode (see table 1) was a result of significant and opposing time shifts in both short- and long-distance migrants, we also conducted the same analysis separately for both short- and long-distance migrants and fitted a linear effect of period in each case. We obtained significantly positive and negative slopes in the analysis of short- and long-

Table 1. Mixed model analysis of the estimated peak autumn passage time of 65 bird taxa (64 species and one distinct subspecies) at Col de Bretolet (Switzerland) during the three periods analysed (1958–69, 1970–82 and 1988–99).
(Species identity was modelled as a random effect. The table gives Wald χ^2-test data for the following significant fixed effect factors and interactions: period, migration mode (long- versus short-distance migrants), food type (seeds, mainly fruit, mainly insects), number of broods per year (1, variable 1 or 2, 2 or more). The analysis is based on 191 estimated peak autumn passage times (see electronic Appendix). Estimated variance component for species: 4.008 (s.e. 0.792), residual error variance: 0.415 (s.e. 0.054).)

source	d.f.	Wald χ^2	p
period	2	7.2	0.028
migration mode	1	199.5	< 0.001
food type outside the breeding season	2	6.7	0.035
number of broods per year	2	6.6	0.036
period × migration mode	2	20.8	< 0.001
period × no. of broods per year	4	12.3	0.015

distance migrants, respectively. All analyses were conducted with GenStat 5.4.1. (Payne *et al.* 1993).

Our study focuses on long-term changes in most of the small migrating bird species in Western Europe. To be able to include most such species, a study so far not undertaken, we had to group the data into three periods of 10–12 years. This prevented the analysis of single-year data for correlations with temperature or North Atlantic Oscillation. The results of several studies on single or a few species have shown that the timing of spring migration or the beginning of the reproductive season is correlated with spring temperature of the particular year and, considered over several years, they generally show an advance (see, for example, Crick *et al.* 1997; Bairlein & Winkel 2001; Forchhammer *et al.* 2002).

3. RESULTS

At Col de Bretolet, long-distance migrants had their migration peak considerably earlier than short-distance migrants (figure 1). Long-distance migrants have advanced their peak passage time significantly in recent years, whereas short-distance migrants have significantly delayed it (table 1, figure 1). Among all long-distance migrants, 20 species advanced their peak passage time from the period 1958–1967 to 1988–1999, whereas five species delayed it. Among all short-distance migrants, 28 species delayed their peak passage time, whereas 12 species advanced it. Among the latter, there were three of all four irruptive species in our study. Irruptive species may thus be affected differently by global warming than non-irruptive species.

Changes in the timing of autumn migration differed significantly between species according to the number of broods that they make and its variability (table 1). Long-distance migrants with a variable number of 1 or 2 broods did not show a shift toward earlier autumn migration, whereas long-distance migrants with only one brood did (figure 1; there were no long-distance migrants that regularly have 2 or more broods per year in our study). Short-distance migrants with a variable number of 1 or 2 broods tended to delay their autumn peak passage more than short-distance migrants with one brood or with two or more broods (figure 1). The main food type outside the breeding season affected the date of peak passage. Species that predominantly feed on berries and on insects migrated 8.5 days earlier than seed eaters. There was no effect of food type on temporal changes of peak passage.

4. DISCUSSION

Consistent with our first prediction, long-distance migrants have generally advanced their autumn peak passage through Western Europe during the past 40 years. These long-distance migrants winter south of the Sahara and pass through the Sahel area at the beginning of the dry season. This suggests a selection pressure to cross the Sahel as early as possible before the onset of the dry season. In single-brooded long-distance migrants, this is possible because breeding starts and terminates earlier. In contrast, the short-distance migrants generally delayed their autumn passage. They winter in the Mediterranean area or partly in the breeding grounds that offer milder conditions owing to global warming. There are several advantages to a delay in autumn passage. Short-distance migrants may increase their survival rate, because migration is risky (Sillett & Holmes 2002). They may obtain higher-quality breeding territories by arriving earlier in spring (Berthold 1990). They may prolong the breeding season.

Consistent with our second prediction, species with a variable number of 1 or 2 broods tended to delay their autumn peak passage more than species with one brood or with two or more broods. This resulted in no change in peak passage in long-distance migrants but a more pronounced delay over the years in short-distance migrants. Species with a variable number of 1 or 2 broods presumably prolong the breeding season, with a higher proportion of the population attempting second or replacement broods.

Contrary to our third prediction, we did not detect an effect of food type on changes in autumn peak passage. This could be the result of the few long-distance migrant species feeding on seeds.

Although global warming has a unidirectional effect on the onset of reproduction (a smaller or larger seasonal advance; Crick *et al.* 1997; Visser *et al.* 1998; Bairlein & Winkel 2001; Both & Visser 2001), here we show that effects on the timing of subsequent events of the annual cycle may be complex and opposite. The direction (advance or delay) and its extent vary according to the

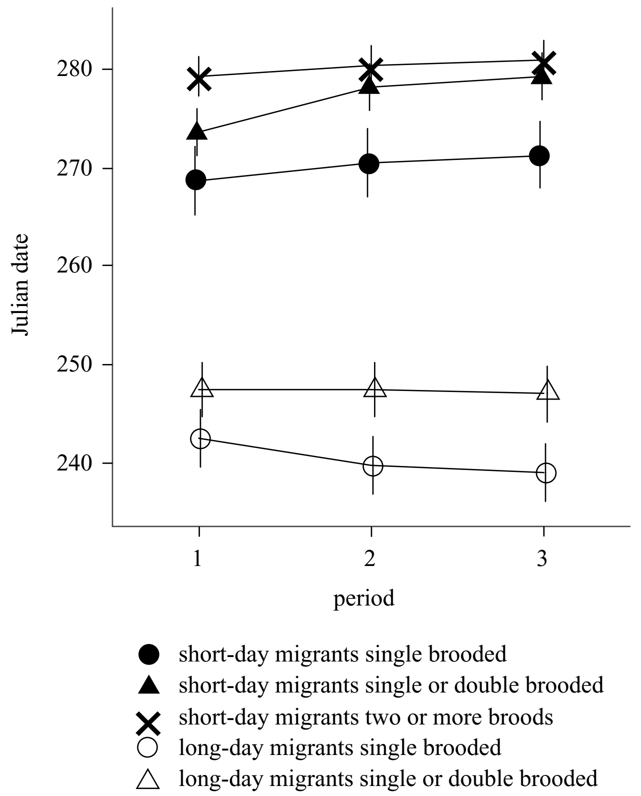

Figure 1. Mean peak of autumn passage (with 1 s.e.m.) at the Alpine pass Col de Bretolet, Switzerland, of 40 taxa of short-distance migrant birds (39 species and one distinct subspecies; wintering north of the Sahara) and 25 species of long-distance migrants (wintering south of the Sahara) during the three periods 1958–69, 1970–82 and 1988–99. Long-distance migrants with a variable number of 1 or 2 broods per year did not change their peak passage time, while those with one brood advanced it. Short-distance migrants with a variable number of 1 or 2 broods per year delayed their peak passage time more than those with one or two broods. Taken together, long-distance migrants passed on average 2.5 days earlier during the period 1988–1999 than during the period 1958–1969. Short-distance migrants showed the opposite trend and crossed the Col de Bretolet 3.4 days later on average in the later period (see table 1 for statistical test results).

ecology and life history of a particular species. This complicates predictions of the effect of global warming on the temporal organization of the annual cycle and its fitness consequences, and on avian communities.

Short-distance migrants may benefit from global warming in several respects: earlier start of reproduction, increased reproductive output owing to a prolonged breeding season (more than 1 brood), better conditions in the breeding area after the breeding season, shortening of migration distance, and fewer migratory individuals in partial migrant species (see Berthold 1990, 1991; Pulido *et al.* 1996). In contrast, long-distance migrants may not obtain the same benefits from global warming. The start of their reproduction is constrained by a less variable spring arrival date, dictated by an endogenous rhythm (Both & Visser 2001), and their autumn migration is probably constrained by the onset of the dry season in the Sahel rather than by conditions in the breeding grounds. Consequently, their breeding season may not be prolonged. There is, therefore, likely to be a considerable asymmetry in the effects of recent climate changes on long- and short-distance migrants, with an increasing advantage for short-distance migrants. Global warming may thus be a serious threat to some long-distance migrants and one reason for their decline in Europe (Berthold 1991; Schmid *et al.* 2001).

Many persons set up, managed and ran the ringing station at Col de Bretolet, most prominently A. Schifferli, G. de Crousaz, J. Aubert (deceased) and R. Winkler, until L.J. took over in 1980. Even more persons helped with trapping and ringing. The community of Champéry and F. Marclay kindly allowed us to work at the site. Hardy Brun and Guido Häfliger built the database containing the data for all birds ringed. David Baird generously provided us with GenStat code to fit a truncated normal distribution and discussed various points of the analysis. William A. Link advised us on iterative weighted least squares analysis. B. Bruderer, M. Kestenholz, R. Spaar and N. Zbinden commented on earlier drafts.

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