

Populations of migratory bird species that did not show a phenological response to climate change are declining

Anders Pape Møller*[†], Diego Rubolini^{†‡}, and Esa Lehikoinen[§]

*Laboratoire de Parasitologie Evolutive, Centre National de la Recherche Scientifique Unité Mixte de Recherche 7103, Université Pierre et Marie Curie, F-75252 Paris Cedex 05, France; [†]Dipartimento di Biologia, Università degli Studi di Milano, I-20133 Milano, Italy; and [§]Department of Biology, University of Turku, FI-20014, Turku, Finland

Edited by May R. Berenbaum, University of Illinois, Urbana, IL, and approved August 27, 2008 (received for review April 21, 2008)

Recent rapid climatic changes are associated with dramatic changes in phenology of plants and animals, with optimal timing of reproduction advancing considerably in the northern hemisphere. However, some species may not have advanced their timing of breeding sufficiently to continue reproducing optimally relative to the occurrence of peak food availability, thus becoming mismatched compared with their food sources. The degree of mismatch may differ among species, and species with greater mismatch may be characterized by declining populations. Here we relate changes in spring migration timing by 100 European bird species since 1960, considered as an index of the phenological response of bird species to recent climate change, to their population trends. Species that declined in the period 1990–2000 did not advance their spring migration, whereas those with stable or increasing populations advanced their migration considerably. On the other hand, population trends during 1970–1990 were predicted by breeding habitat type, northernmost breeding latitude, and winter range (with species of agricultural habitat, breeding at northern latitudes, and wintering in Africa showing an unfavorable conservation status), but not by change in migration timing. The association between population trend in 1990–2000 and change in migration phenology was not confounded by any of the previously identified predictors of population trends in birds, or by similarity in phenotype among taxa due to common descent. Our findings imply that ecological factors affecting population trends can change over time and suggest that ongoing climatic changes will increasingly threaten vulnerable migratory bird species, augmenting their extinction risk.

conservation | extinction risk | migration phenology | population trends

Climate change during the second half of the twentieth century has resulted in a mean increase in global temperatures by 0.6°C, with particularly large changes during spring in temperate and Arctic regions of the world (1). Plants and animals have responded to this change by markedly advancing their annual cycles, including timing of reproduction (2–4).

While the phenology of plants and insects has advanced with increases in spring temperature (2–4), many consumers of plants and insects and higher-level predators have responded to a lesser extent or not at all, thus causing a mistiming in reproduction relative to peak availability of food (5, 6). The consequences of such mistiming in reproduction are reduced reproductive output, with diminished recruitment rate and ultimately a decline in population size (7), which possibly can affect the risk of extinction.

Previous studies of migratory birds have shown rapid advances in timing of spring migration during the last 4 decades, associated with advancement of spring and warming of spring weather (8). Considerable heterogeneity in advancement in timing of spring migration among species (8, 9) may be due in part to spatial heterogeneity in climate change across Europe, with spring temperatures increasing in some regions but not in others (10).

However, despite such heterogeneity, spring phenological responses to climate change are species-specific and consistent in different populations, making an investigation of predictors of species-specific variation in change in migration timing, considered as an indicator of the phenological response to climate change, meaningful (9).

The ability of many species to respond to climate change has been a major concern, because species unable to advance their annual cycle will suffer from increased mistiming of reproduction, with potential consequences for the risk of extinction (11). To date, however, there have been no attempts to assess how a phenological response to climate change relates to bird population trends, although previous studies have identified farmland breeding habitat, migration distance, body mass, northernmost distribution limit, ecological specialization, number of broods, thermal maximum (i.e., temperature at the hot edge of the species-specific climate envelope), natal dispersal, and relative brain size as significant predictors of interspecific differences in breeding population trends (12–19).

In this comparative study, we related changes in mean/median (“mean” hereinafter) timing of spring migration of 100 European migratory bird species since 1960, which was considered a cue as to the ability of a given species to show a phenological response to recent climate warming, to their population trends during two separate periods, 1970–1990 and 1990–2000 (20). We predicted that migratory bird species that did not anticipate timing of spring migration (i.e., that did not show a phenological response to climate change) should demonstrate declining populations, while taking into account several variables previously shown to be associated with population trends (see above and 12–19) or response to climate change. Among variables potentially affecting the phenological response to climate change, we considered migration distance, intensity of sexual selection, and total population size; a small population size, and thus lack of genetic variation, potentially could explain lack of response to climate change (8, 9, 21, 22). All analyses were performed while accounting for phylogenetic relatedness among species by using phylogenetically independent linear contrasts (23).

Population trends of European birds were obtained from a qualitative assessment conducted by BirdLife International, expressed on a seven-point scale ranging from a large population decline to a large population increase (20). We deliberately avoided using change in first arrival dates as a cue to phenology.

Author contributions: A.P.M. designed research; A.P.M. and D.R. performed research; A.P.M., D.R., and E.L. analyzed data; and A.P.M., D.R., and E.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[†]To whom correspondence may be addressed. E-mail: amoller@snv.jussieu.fr or diego.rubolini@unimi.it.

This article contains supporting information online at www.pnas.org/cgi/content/full/0803825105/DCSupplemental.

© 2008 by The National Academy of Sciences of the USA

Table 1. Minimal adequate multiple regression models of population trend of migratory birds during 1970–1990, population trend of migratory birds during 1990–2000, and change in mean spring migration date of migratory birds 1960–2006, obtained by step-down removal of nonsignificant predictors (see *Methods*)

Variables	F	df	P	Estimate (SE)
Population trend during 1970–1990				
Species-specific values				
Body mass	21.13	1,95	<0.001	0.724 (0.157)
Farmland habitat	5.19	1,95	0.025	−0.886 (0.389)
Independent contrasts				
Body mass	8.36	1,92	0.005	1.263 (0.437)
Farmland habitat	8.80	1,92	0.004	−1.164 (0.393)
Northernmost breeding latitude	5.54	1,92	0.021	−0.081 (0.035)
Population trend during 1990–2000				
Species-specific values				
Change in migration date	27.19	1,96	<0.001	−2.801 (0.537)
Independent contrasts				
Change in migration date	31.48	1,94	<0.001	−2.656 (0.473)
Change in migration date, 1960–2006				
Species-specific values				
Population trends 1990–2000	21.84	1,92	<0.001	−0.069 (0.015)
Migration distance	7.70	1,92	0.007	0.111 (0.040)
Number of broods	5.21	1,92	0.025	−0.052 (0.023)
Independent contrasts				
Population trends 1990–2000	23.33	1,90	<0.001	−0.079 (0.016)
Migration distance	5.00	1,90	0.028	0.110 (0.049)
Number of broods	5.69	1,90	0.019	−0.072 (0.030)

Statistics for excluded terms are reported in [Table S1](#).

ical response to climate change, because this phenological datum is strongly dependent on sampling effort and may be affected by changes in population size (8, 9).

Results

The analysis of population trends during 1970–1990 based on species-specific values identified body mass and farmland breeding habitat as main predictors of population trends, whereas the effects of other variables were not significant [Table 1 and [supporting information \(SI\) Table S1](#)]. Specifically, population trends of large species and those not breeding in agricultural habitats were more favorable than those of small species breeding mainly in farmland (Table 1). The additional effects of habitat specialization [−0.321 (standard error [SE], 0.468), $F_{1,34} = 0.47$, $P = 0.50$] and thermal maximum [−0.178 (0.189), $F_{1,34} = 0.89$, $P = 0.35$] were not significant, neither were those of relative brain size [1.069 (1.377 SE), $F_{1,60} = 0.60$, $P = 0.44$] and natal dispersal [0.162 (0.383 SE), $F_{1,41} = 0.18$, $P = 0.67$]. The inclusion in the initial model of a categorical predictor identifying species wintering in Africa versus other species (instead of migration distance; see *Materials and Methods*) further showed that species wintering in Africa declined more in this period compared with other species [−0.621 (0.275 SE), $F_{1,94} = 5.11$, $P = 0.026$; [Table S2](#)]. The analyses based on phylogenetically independent contrasts, besides confirming the significant effects of body mass and breeding habitat, revealed that species extending their breeding ranges to more northern latitudes showed the largest population declines (Table 1). The effects of habitat specialization [0.145 (0.090 SE), $F_{1,33} = 2.56$, $P = 0.12$] and thermal maximum [−0.023 (0.041 SE), $F_{1,33} = 0.31$, $P = 0.58$] were not significant, neither were those of relative brain size [0.308 (0.349 SE), $F_{1,57} = 0.78$, $P = 0.38$] and natal dispersal [−0.019 (0.086 SE), $F_{1,38} = 0.05$, $P = 0.82$]. Inclusion of a variable reflecting wintering in Africa in the initial model instead of migration distance confirmed that species wintering in Africa

suffered larger declines compared with other species [−0.781 (0.339 SE), $F_{1,91} = 5.29$, $P = 0.024$; [Table S2](#)].

In contrast, change in migration date was the only predictor of population trends during 1990–2000 (Table 1, Fig. 1). This analysis also revealed an additional effect of habitat specialization, with habitat specialists declining more than habitat generalists [effect of habitat specialization, −0.889 (0.341 SE), $F_{1,35} = 6.80$, $P = 0.013$]. However, the inclusion of habitat specialization did not affect the relationship between population trend and change in migration date [−2.425 (0.504 SE), $F_{1,35} = 23.12$, $P < 0.001$]. Thermal maximum [0.261 (0.150 SE), $F_{1,35} = 3.05$, $P = 0.09$], relative brain size [2.344 (1.387 SE), $F_{1,61} = 2.86$, $P = 0.10$],

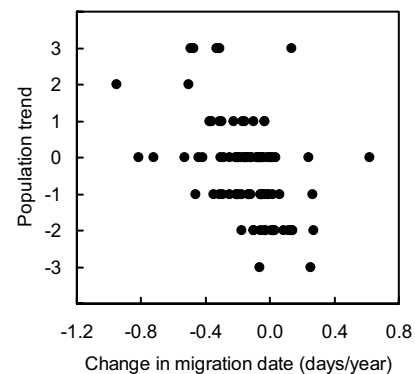


Fig. 1. Recent population trends of European migratory bird species (1990–2000) (negative values: decline; positive values: increase; see *Materials and Methods* and ref. 20) in relation to change in mean spring migration date (days/year) in the period 1960–2006 (9). Change in mean spring migration date for each species was estimated as least square means after accounting for among-sites variance, geographical coordinates and initial year of time series in mixed models (see *Materials and Methods* and ref. 9).

and natal dispersal [0.593 (0.366 SE), $F_{1,41} = 2.64$, $P = 0.11$] did not significantly predict population trends. The analyses based on contrasts confirmed the significant relationship between population trend and change in migration date (Table 1) but showed no additional effects of habitat specialization [0.003 (0.093 SE), $F_{1,31} = 0.00$, $P = 0.98$]. Thermal maximum [0.025 (0.038 SE), $F_{1,31} = 0.46$, $P = 0.50$], relative brain size [0.390 (0.321 SE), $F_{1,56} = 1.48$, $P = 0.23$], and natal dispersal [−0.028 (0.081 SE), $F_{1,40} = 0.12$, $P = 0.73$] did not significantly predict population trends. Inclusion of a variable reflecting wintering in Africa instead of migration distance in initial models did not affect the conclusions for both species-specific and contrast-based analyses (Table S2).

We tested whether the relationship between population trends and the significant predictors of population trends identified by the regression models (see above and Table 1) differed between the two time periods (1970–1990 vs. 1990–2000) by using a mixed model analysis in which population trend was the dependent variable and time period was considered a fixed-effect factor, with change in migration date, farmland breeding habitat, wintering in Africa, northernmost breeding latitude and body mass as covariates. Species identity was considered a random-effect factor, to account for replication of species-specific values between periods. The model was subjected to sequential removal of nonsignificant predictors (see *Materials and Methods*). The interaction term between period and change in migration date was statistically significant ($F_{1,93,8} = 10.29$, $P = 0.002$), implying that the slope of the relationship between population trend and change in migration date differed between the two periods [1970–1990, estimate = −0.558 (0.610 SE), $t = -0.91$, $P = 0.36$; 1990–2000, estimate = −2.772 (0.607 SE), $t = -4.57$, $P < 0.001$]. Similarly, the effect of wintering in Africa on population trends differed between periods [$F_{1,94,5} = 7.96$, $P = 0.006$; 1970–1990, estimate = −0.637 (0.294 SE), $t = -2.16$, $P = 0.032$; 1990–2000, estimate = 0.270 (0.294 SE), $t = 0.92$, $P = 0.36$]. In contrast, the effects of northernmost breeding latitude, farmland breeding habitat, and body mass on population trends did not differ between periods (time period × northernmost breeding latitude, $F_{1,92,1} = 0.99$, $P = 0.32$; time period × farmland habitat, $F_{1,91,4} = 1.01$, $P = 0.32$; time period × body mass, $F_{1,94,3} = 3.66$, $P = 0.06$). The overall effect of northernmost breeding latitude was not significant ($F_{1,92,5} = 2.79$, $P = 0.10$), similar to the analysis of species-specific values reported in Table 1. Moreover, population trends showed a significant decline between 1970–1990 and 1990–2000, suggesting deterioration of the conservation status of European migratory bird species over the past 30 years (least squares means (SE), 1970–1990: 0.15 (0.12); 1990–2000: −0.32 (0.12); $F_{1,94,9} = 10.99$, $P < 0.001$), and the overall effect of farmland habitat on population trends was weakly, but not significantly, negative [−0.597 (0.310 SE), $F_{1,92,7} = 3.70$, $P = 0.057$].

A potential confounding factor of the relationship between population trends during 1990–2000 and change in migration date is that some species included in the present study had resident populations that contributed to the overall population trend (20, 24) but did not contribute to a change in migration phenology. Consequently, we created a binary variable, migration status, with strictly migratory species (i.e., long-distance migrants migrating more than 24° latitude) coded as 1 and all other species, including those with resident populations in Europe, coded as 0. We then tested the effect of the interaction between migration status and change in migration date on population trend. The effects of the interaction [0.915 (1.423 SE), $F_{1,94} = 0.41$, $P = 0.52$] and migration status [0.043 (0.292 SE), $F_{1,94} = 0.02$, $P = 0.88$] were not significant, whereas the effect of change in migration date on the 1990–2000 population trend remained significant [−3.015 (0.701 SE), $F_{1,94} = 12.90$, $P < 0.001$]. Therefore, our conclusions were not confounded by

including in the analyses species that had both resident and migratory populations in Europe.

The analysis of factors affecting long-term phenological trends, besides confirming the relationship between population trends during 1990–2000 and phenological response to climate change, revealed that change in migration date was predicted by migration distance, with short-distance migrants advancing the most, and by number of broods, with species laying more broods advancing migration date the most (Table 1) (see also 9). The results for contrast-based analyses were similar (Table 1). The additional effects of ecological specialization, thermal maximum, relative brain size, and natal dispersal were not significant in analyses based on both species-specific values or contrasts (all P values > 0.11 and > 0.20 , respectively; details not shown). Including wintering in Africa instead of migration distance in initial models did not qualitatively affect any conclusion (Table S2).

Discussion

Our study clearly showed that European migratory bird species with declining breeding populations in Europe in the last decades (1990–2000) responded the least to recent climate change as reflected by the temporal trend in spring migration phenology, or even delayed their timing of spring migration, whereas species with stable or increasing populations advanced migration. This conclusion was independent of potentially confounding variables previously found to predict population trends in a range of extensive studies of this scientific problem and was not confounded by phylogenetic relatedness among species. Interestingly, change in migration date did not predict population trends of migrants in an earlier period (1970–1990), implying that the relevance of climate-mediated phenological changes on population trends could have increased in recent years.

Obviously, future studies may identify other potentially confounding variables, although we consider this possibility unlikely given the extent of research on population trends of birds dating back more than 2 decades and the number of potentially confounding variables that we have taken into account in our analyses. We can exclude the alternative hypothesis that species were simply less easy to detect when their populations declined, because neither body mass nor population size predicted change in migration date (Table S1), although body mass positively predicted population trends during 1970–1990 (see also below). Likewise, we can exclude the hypothesis that it is advantageous to arrive earlier when populations are increasing and less advantageous when they are declining, due to differences in level of competition and hence degree of protandry (25, 26). In fact, sexual dichromatism has been shown to predict protandry (27), but sexual dichromatism did not predict change in migration date or population trend (Table S1). The ability to adjust migration date to changing climatic conditions also may depend on the concomitant variation in winter habitat quality, because of carryover effects (28, 29). If certain winter habitats degraded more than others during the twentieth century [e.g., farmland habitats in Europe, African forests, and open dry savannahs in the Sahel (30, 31)], then variation in the ability to advance migration date among species wintering in different habitats might be expected. Similarly, the breeding population of migrants can be regulated by ecological conditions in winter quarters, and thus population trends may vary according to winter habitat, provided that ecological conditions have changed differentially according to habitat type (31, 32). However, change in migration date or population trends during both periods did not vary in relation to the main wintering habitat (see Table S3) for species wintering or not wintering in Africa (analysis of variance on species-specific values: species not wintering in Africa, all $P > 0.10$; species wintering in Africa, all $P > 0.18$). This also could be the case because, for example,

habitat changes may negatively impact certain species but not others wintering in the same habitat (31). In any case, this result implies that the relationship between population trends during 1990–2000 and change in migration date was not confounded by variation in wintering habitat among species.

Other interesting findings emerge from this study. First, species breeding in farmland habitats declined more than other species during 1970–1990 but not during 1990–2000. This pattern could have been expected, because the effects of agricultural intensification on farmland breeding birds were more severe in the earlier period compared with the subsequent period (12, 20, 33). Alternatively, agricultural intensification during the second half of the twentieth century depleted populations of farmland species to an extent that any additional change in agricultural practices had no further impact on population trends of migrants. Unfortunately, the lack of a differential effect of farmland habitats on population trends between periods, as revealed by the mixed model analysis, complicates the interpretation of this finding.

Second, species wintering in Africa declined more during 1970–1990 compared with 1990–2000. The differential effect of wintering in Africa on population trends during the two periods, a finding confirmed by the mixed model analysis, could be related to the occurrence of prolonged droughts in sub-Saharan Africa during the 1970s, which strongly and negatively affected the breeding populations of several trans-Saharan migrants (31).

Third, species with more northern distributions exhibited larger population declines than those with a more southern distribution during 1970–1990, after controlling for phylogenetic effects. This result is consistent with previous findings (16), and it can be reconciled with the observed stronger effects of climate change on biological diversity at northern latitudes in the boreal region (1, 2). Thus, northern breeding migratory bird species could be more sensitive to climate warming, because of altered environmental conditions and community composition resulting from changes in climate [e.g., suffering increased competition from resident breeding species (34)]. The multiple regression analyses also showed that population trends of larger species were more favorable than those of smaller species during 1970–1990, although we consider this finding to be either a sampling artifact (a few large, unrelated species that increased considerably during 1970–1990 were driving this relationship, see Table S3) or a consequence of the easier detectability of larger species during population increases. This latter explanation is unlikely, however; if it was true, then a similar trend should have been detected in the subsequent period as well.

Overall, our findings indicate that factors affecting population declines of European bird species varied temporally in the second half of the twentieth century. Specifically, farmland breeding habitat, wintering in Africa, and northern breeding latitudes were associated with population declines during 1970–1990, whereas climate-driven change in spring migration phenology was the only significant predictor of population trends in more recent decades. Therefore, an important message of this study is that factors affecting population trends and extinction risk of birds appear to be dynamic over time, and this fact should be taken into account in evaluations of conservation priorities for declining species.

Finally, our analyses also identified ecological and life-history correlates of phenological response of migratory birds to climate change. While controlling for the effect of population trend during 1990–2000, which strongly predicted change in migration timing, we found that long-distance migrants advanced spring migration date the least, and that species laying a greater number of clutches showed a stronger advance in timing of spring migration. A stronger advance in timing of spring migration in short-distance versus long-distance migrants is in accordance with most previous studies [e.g., (8, 9), but see (35)]. This pattern

is indeed to be expected, because short-distance migrants spend the winter closer to the breeding areas compared with long-distance migrants, which may allow such species to better tune the timing of spring migration to concomitant weather conditions (8, 9), and the timing of migration of short-distance migrants may have a stronger environmental component compared with long-distance migrants (8, 36). On the other hand, a greater advance of timing of spring migration in species raising a greater number of broods could occur because spring climate warming (leading to a progressively longer breeding season) may have relaxed constraints affecting interclutch intervals in multi-brooded species. Such a relaxation could have resulted in greater plasticity in migration schedules, and thus in increased ability to adjust the timing of spring migration to climate change in multibrooded versus single-brooded species. Interestingly, warming of spring between 1971 and 2005 resulted in increased interval between clutches in a migratory songbird (37).

The underlying mechanisms responsible for long-term changes in timing of migration remain unknown, although phenotypic plasticity, gene flow, and microevolutionary response constitute the three possibilities (38). Total population size, which may reflect the amount of genetic variation (22), did not explain the relationship between phenological response in mean timing of spring migration and population trends, suggesting that reduced genetic variability did not affect population declines and did not explain lack of changes in migration timing. A possibility is that poor environmental conditions that particularly affect threatened species translate into poor body condition, resulting in reduced maternal effects that may represent important determinants of the phenotype of the next generation. Early maternal effects may have long-lasting consequences for the ability to respond phenotypically to changing environmental conditions (39–41). We hypothesize that such an unavoidable maternal legacy may affect the ability to adjust the timing of spring migration to climate change.

Our findings have important implications for future evaluations of conservation status and for attempts to manage populations of declining species. If migratory bird species do not advance their timing of migration, they may arrive later relative to the phenologically optimal timing of reproduction, because the phenology of primary producers and prey species can advance more rapidly. Mistiming of reproduction results in reduced reproductive output (7), with the reduction in output assumed to increase with increasing degree of mistiming. Therefore, we predict that, under current climate change scenarios, species with a threatened population status and declining breeding populations will suffer further losses. Our findings highlight the importance of investigating heterogeneity among species in response to climate change, while also allowing the identification of a suite of species that is likely to become particularly threatened during the next decades.

Materials and Methods

Change in Migration Dates. We collected 289 estimates of change in mean/median spring migration dates of migratory birds with a minimum duration of 15 years from Europe (west of the Ural Mountains) during 1960–2006, mainly from bird observatories with multiple populations passing during migration (8, 9, 42, 43). Most of these observatories are located in central Europe and southern Fennoscandia, and intercept populations of migratory birds on the way to their breeding grounds (9). This fact prevented us from quantifying change in migration phenology in relation to local climate, because climate during any part of the migratory path could potentially affect change in phenology (44, 45). Therefore, we analyzed change in phenology over time, assuming that such change was due to change in climate, as has been done in other studies (8, 9, 21, 35, 46, 47). Changes in migration dates were the slope of the simple linear regression of migration date on year, expressed as days/year.

We developed mixed models (restricted maximum likelihood method) to quantify variation in change in migration date among species and sites, while

statistically assessing differences related to latitude, longitude, and initial year of time series [see (9) for details]. The data used as the response variable in the present study were species-specific least squares means derived from the model concerning mean/median migration dates presented in table 3 of Rubolini *et al.* (9).

Population Trends. We obtained estimates of European population trends of breeding birds during two separate periods, 1970–1990 and 1990–2000, using an assessment by BirdLife International (20) on a seven-point scale: large decline (–3), moderate decline (–2), small decline (–1), stable (0), small increase (+1), moderate increase (+2), and large increase (+3). The categories “small decrease” and “small increase” were not available for the period 1970–1990 (20). These qualitative assessments were available for a much larger number of species than quantitative estimates of population trends during 1980–2005, estimated as the change in population size from an initial index value of 100, with the European population index based on national indices weighted by the relative size of different national populations (see <http://www.ebcc.info/index.php?ID=148>). However, for the 58 species in our sample that were common to the two data sets, we found a strong positive relationship ($r = 0.77$; $P < 0.001$) between qualitative and quantitative estimates. We used the qualitative rather than the quantitative estimate of population trend as a predictor in the analyses, because this is available for a greater number of species and is representative of all of Europe west of the Urals (20), whereas quantitative estimates are based on long-term data from a limited fraction of European countries. Qualitative population trend estimates for 1990–2000 were significantly, although weakly, correlated with trends of the previous period (1970–1990) ($r_s = 0.38$, $P < 0.001$, $n = 96$ species). Although population trends were expressed on an interval scale, all conclusions remained unaltered when we instead based the analyses on nonparametric rank order correlations or regressions of ranks in the analyses of contrasts (details not shown).

Potential Predictors of Population Trends and Phenological Response. Previous studies indicated that breeding in farmland habitats (12, 48), migration distance (13, 14, 32), northern distribution limit (4, 15, 16), relative brain mass (17), degree of ecological specialization, thermal maximum, number of broods (16, 18), and body mass (19) predicted population trends of common breeding birds. We extracted information on farmland breeding habitat (0 = population mainly breeding in habitats other than farmland; 1 = population mainly breeding in farmland) from appendix 4 of BirdLife International (20). We determined the global northernmost and southernmost latitudes of the breeding and the wintering distributions, respectively, to the nearest tenth of a degree of all species, based on information on breeding and wintering ranges shown on maps by Cramp and Perrins (24). Migration distance was estimated as the mean of the two latitudes during breeding minus the mean of the two latitudes during winter (expressed in absolute values). We also considered a categorical covariate, wintering in Africa (0 = not wintering in Africa; 1 = wintering in Africa) (24, 32), and coded the main wintering habitats of all species according to Cramp and Perrins (24) (see the details of the coding in Table S3).

Information on brain mass was obtained from Garamszegi *et al.* (49), Iwaniuk and Nelson (50), and Mlíkovský (51). Information on ecological specialization and thermal maximum was derived from Jiguet *et al.* (18). In addition, information on natal dispersal was derived from Jiguet *et al.* (18) and Wernham *et al.* (52). Body mass and number of broods (maximum number of broods laid per season) of all species were recorded from Cramp and Perrins (24). Finally, total population size in the western Palearctic (20) also was included in the analyses, because larger populations may give rise to a larger number of heterozygous loci (22, 53, 54), which may facilitate phenological

response to climate change. Information on sexual dichromatism was derived from a standard field guide (55), with all species with a visible sexual difference in coloration receiving a score of 1 and all others receiving a score of 0.

The entire data set is reported in Table S3.

Comparative and Statistical Analyses. Species cannot be treated as statistically independent observations in comparative analyses, because apparent phenotypic correlations may result from species sharing a common ancestor rather than convergent evolution. We controlled for similarity in phenotype among species due to common phylogenetic descent by calculating standardized independent linear contrasts (23), using the CAIC software (56), assuming a gradual evolution model (see *SI Methods* for additional details). The composite phylogeny used for the contrast analyses (Fig. S1) was based on Sibley and Ahlquist (57), combined with several other sources (see *SI Methods* for details).

We log₁₀-transformed migration distance, body mass, total population size, and natal dispersal (by adding 1 to the migration distance). We used farmland habitat, wintering in Africa, and sexual dichromatism as continuous variables, because using dichotomous variables as continuous predictors is similar to using a dummy variable in standard regression analyses (58). The variable wintering in Africa was strongly positively correlated with log (migration distance) ($r = 0.79$, $P < 0.001$), and thus we ran each analysis with either one variable or the other, to avoid collinearity among predictors. To avoid biases in the calculation of relative brain size due to the particular set of species included in the study, we adopted the following procedure. Relative brain size was expressed as the residuals of a linear regression, where the slope was obtained from a log-log phylogenetically corrected regression of brain size on body mass of a large set of 567 bird species for which we were able to retrieve information on the two phenotypic traits (49–51) and to code the phylogeny (details not shown). The slope of this regression (based on phylogenetically independent contrasts) was $\log(\text{brain size}) = 0.581 (0.010 \text{ SE}) \log(\text{body mass})$ ($F_{1,494} = 35.20$, $P < 0.0001$; contrasts with standardized residuals > 1.96 were excluded from the regression analysis). The same procedure was adopted for contrast analyses. In this case, we first calculated contrasts of log (brain size) on log (body mass) for the set of species included in this study, and then calculated the residuals of these contrasts from the aforementioned phylogenetically corrected regression equation.

We used multiple regression to find the minimal adequate model, using the JMP software (59). The minimal adequate model was obtained by step-down removal of nonsignificant predictors (60). We conducted two sets of analyses. In the first set, population trend (during either 1970–1990 or 1990–2000) was the dependent variable, whereas change in migration date was a predictor, thereby hypothesizing that population trends could be affected by change in migration date. In the second set, change in migration date was the dependent variable, and population trends (during both 1970–1990 and 1990–2000) were included as predictors, because it could be argued that this variable has changed more recently than population trend, and we aimed to identify traits of species that could possibly predict the response to climate change.

Besides change in migration date and population trend, in these models we tested the effects of several other variables (i.e., farmland breeding habitat, migration distance or wintering in Africa, northernmost breeding latitude, sexual dichromatism, body mass, European breeding population size, maximum number of broods; see above). The effects of ecological specialization and thermal maximum (18), relative brain size, and natal dispersal were analyzed by adding these variables in turn to the minimal adequate models identified above. This was done because values for these variables were available for only a limited subset of species (see Table S3).

ACKNOWLEDGMENTS. We thank C. Both, L. Z. Garamszegi, N. Saino, and two reviewers for useful comments on previous drafts.

- IPCC (2001) *Climate Change 2001: The Scientific Basis* (Cambridge Univ Press, Cambridge, UK).
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Walther GR, *et al.* (2002) Ecological responses to recent climate change. *Nature* 416:389–395.
- Root TL, *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc Lond B* 265:1867–1870.
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298.
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Lehikoinen E, Sparks TH, Zalakevicius M (2004) Arrival and departure dates. *Adv Ecol Res* 35:1–31.
- Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim Res* 35:135–146.
- Menzel A, *et al.* (2006) European phenological response to climate change matches the warming pattern. *Glob Change Biol* 12:1969–1976.
- Sæther BE, Sutherland WJ, Engen S (2004) Climate influences on population dynamics. *Adv Ecol Res* 35:185–209.
- Fuller RJ, *et al.* (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conserv Biol* 9:1425–1441.
- Hjort C, Lindholm C-G (1978) Annual bird ringing totals and population fluctuations. *Oikos* 30:387–392.
- Baillie SR, Peach WJ (1992) Population limitation in Palearctic-African migrant passerines. *Ibis* 134:120–132.

15. Parmesan C, Root TL, Willig M (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 81:443–450.
16. Julliard R, Jiguet F, Couvet D (2004) Common birds facing global changes: What makes a species at risk? *Glob Change Biol* 10:148–154.
17. Shultz S, Bradbury RB, Evans KL, Gregory RD, Blackburn TM (2005) Brain size and resource specialization predict long-term population trends in British birds. *Proc R Soc Lond B* 272:2305–2311.
18. Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D (2007) Climate envelope, life history traits and the resilience of birds facing global change. *Glob Change Biol* 13:1672–1684.
19. Bennett PM, Owens IPF (2002) *Evolutionary Ecology of Birds* (Oxford Univ Press, Oxford, UK).
20. BirdLife International (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status* (BirdLife International, Cambridge, UK).
21. Spottiswoode CN, Tøttrup AP, Coppack T (2006) Sexual selection predicts advancement of avian spring migration in response to climate change. *Proc R Soc Lond B* 273:3023–3029.
22. Møller AP, Garamszegi LZ, Spottiswoode CN (2008) Genetic similarity, distribution range and sexual selection. *J Evol Biol* 21:213–225.
23. Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15.
24. Cramp S, Perrins CM (1977–1994) *The Birds of the Western Palearctic* (Oxford Univ Press, Oxford, UK).
25. Møller AP (1994) *Sexual Selection and the Barn Swallow* (Oxford Univ Press, Oxford, UK).
26. Kokko H (1999) Competition for early arrival in migratory birds. *J Anim Ecol* 68:940–950.
27. Rubolini D, Spina F, Saino N (2004) Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behav Ecol* 15:592–601.
28. Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
29. Saino N, et al. (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25.
30. Tucker GM, Evans MI (1997) *Habitats for Birds in Europe: A Conservation Strategy for the Wider Environment* (BirdLife International, Cambridge, UK).
31. Newton I (2004) Population limitation in migrants. *Ibis* 146:197–226.
32. Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biol Cons* 131:93–105.
33. Tucker GM, Heath MF (1994) *Birds in Europe: Their Conservation Status* (BirdLife International, Cambridge, UK).
34. Ahola MP, Laaksonen T, Eeva T, Lehikoinen E (2007) Climate change can alter competitive relationships between resident and migratory birds. *J Anim Ecol* 76:1045–1052.
35. Jónzén N, et al. (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961.
36. Berthold P (1996) *Control of Bird Migration* (Chapman & Hall, London).
37. Møller AP (2007) Interval between clutches, fitness and climate change. *Behav Ecol* 18:62–70.
38. Pulido F, Berthold P (2004) Microevolutionary response to climate change. *Adv Ecol Res* 35:151–183.
39. Hørak P, Vellau H, Ots I, Møller AP (2000) Growth conditions affect carotenoid-based plumage coloration of great tit nestlings. *Naturwiss* 87:460–464.
40. Blount JD, et al. (2003) Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. *Proc R Soc Lond B* 270:1691–1696.
41. Koutsos EA, Clifford AJ, Calvert CC, Klasing KC (2003) Maternal carotenoid status modifies the incorporation of dietary carotenoids into immune tissues of growing chickens (*Gallus gallus domesticus*). *J Nutr* 133:1132–1138.
42. Knudsen E, et al. (2007) Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Clim Res* 35:59–77.
43. Both C (2007) Comment on “Rapid advance of spring arrival dates in long-distance migratory birds.” *Science* 315:598b.
44. Ahola M, et al. (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob Change Biol* 10:1610–1617.
45. Both C, te Marvelde L (2007) Climate change and timing of avian breeding and migration throughout Europe. *Clim Res* 35:93–105.
46. Saino N, et al. (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Clim Res* 35:123–134.
47. Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58.
48. Chamberlain DE, Fuller RJ, Bunce RG, Duckworth JC, Shrubbs M (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J Appl Ecol* 37:771–788.
49. Garamszegi LZ, Møller AP, Erritzøe J (2002) Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc R Soc Lond B* 269:961–967.
50. Iwaniuk AN, Nelson JE (2003) Developmental differences are correlated with relative brain size in birds: a comparative analysis. *Can J Zool* 81:1913–1928.
51. Mlikovsky J (1990) Brain size in birds, 4: Passeriformes. *Acta Soc Zool Bohem* 54:27–37.
52. Wernham CV, Toms MP, Marchant JH, Siriwardena GM, Baillie SR, eds (2002) *The Migration Atlas: Movements of the Birds of Britain and Ireland* (T & AD Poyser, London).
53. Nagylaki T (1998) The expected number of heterozygous sites in a subdivided population. *Genetics* 149:1599–1604.
54. Wakeley J (1998) Segregating sites in Wright’s island model. *Theor Popul Biol* 53:166–174.
55. Mullarney T, Svensson L, Zetterström D, Grant PJ (2000) *The Complete Guide to the Birds of Europe* (Harper Collins, London).
56. Purvis A, Rambaut A (1995) Comparative analysis by independent contrasts (CAIC). *Comp Appl Biosci* 11:247–251.
57. Sibley CG, Ahlquist JE (1990) *Phylogeny and Classification of Birds: A Study in Molecular Evolution* (Yale Univ Press, New Haven, CT).
58. Sokal RR, Rohlf FJ (1995) *Biometry* (Freeman, New York), 2nd ed.
59. SAS Institute, Inc (2000) *JMP* (SAS Institute, Cary, NC).
60. Crawley MJ (1993) *GLIM for Ecologists*. (Blackwell, Oxford, UK).