Ecological and life history correlates of changes in avian migration timing in response to climate change

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ABSTRACT: Spring migration of birds in many parts of the world has advanced as the climate has become warmer. Variation in advancement among species has been proposed to correlate with geography and life history features, but individual studies have reported variable results, and general patterns have been elusive. In a quantitative review of data from 389 bird species sampled at 69 European and 23 North American localities, we evaluated associations between change in the timing of migration and life history (body size, molt, broodedness), ecology (habitat, diet, nest position), and geography. We confirmed that spring migration advanced: -0.214 d yr^{-1} (95% CI: -0.266, -0.162) for first-arriving individuals and -0.104 d yr^{-1} (-0.139, -0.071) for the median date of passage. The rate of change in autumn was more variable: 0.090 d yr^{-1} (0.002, 0.176) delay for median passage and 0.019 d yr^{-1} (-0.175, 0.204) delay for the date of last departure. The response during spring was weaker in the far north and in species that migrate long distances to the wintering area. Autumn migration became increasingly delayed in species that are large-bodied, molt before departure, and that feed on seeds, insects, or fruits. Variation among species, especially during autumn, was associated in part with constraints surrounding the timing of the postnuptial molt. The results suggest that ecological and life history features of species may influence their ability to respond to climate change.

KEY WORDS: Bird · Body size · Broodedness · Diet · Latitude · Migration · Molt · Phenology

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1. INTRODUCTION

Changes in avian breeding and migration phenology are among the best known examples of the biotic impacts of recent climate change (Parmesan 2006, Knudsen et al. 2011). The consequences of phenological shifts in birds and many other taxa are a topic of lively discussion (Both et al. 2010, Miller-Rushing et al. 2010, Cleland et al. 2012). One likely consequence relates to changes in the timing of life cycle events in multiple interacting species relative to one another. For example, it has been proposed that the breeding seasons of predators may no longer match the maximum availability of their prey, or that mutualisms between pollinators and flowering plants could be disrupted by differential responses in the participants (Visser & Both 2005, Carey 2009, Hegland et al. 2009, Saino et al. 2011). To evaluate the consequences of phenological change, we need quantitative assessments of the magnitude of change and a clear idea of how responses depend on geography and species traits. This study provides such an assessment in an analysis of data on recent changes in the timing of avian migration. Although previous reviews have firmly established links between environmental change and bird migration (Lehikoinen et al. 2004, Gienapp et al. 2007, Gordo 2007, Rubolini et al. 2007, Lehikoinen & Sparks 2010, Knudsen et al. 2011), here we focus on quantifying associations between the observed change and features of species that reflect their life history and ecology. These associations may help reveal underlying mechanisms governing the responses of individual species, and these in turn could guide the way to a general understanding of the consequences of changing phenology.

The need for a quantitative review stems partly from the extensive variation among species reported in nearly all previous studies of this topic (Rubolini et al. 2007, Van Buskirk et al. 2009, Lehikoinen & Sparks 2010). While the overall trend across many species is toward earlier spring migration, there is highly significant heterogeneity among species (Van Buskirk et al. 2009). Some species have shown no change or have begun migrating later even though temperatures have become warmer. Is this a mal-adaptive response to climate change? An empirical review could shed light on this by indicating which species have changed the most and the least; differential responses in distinct groups of species might reflect adaptive variation associated with particular life history traits or ecologies.

Previous work suggests several factors and traits that may correlate with long-term trends in avian phenology. Most are related to geography and the life history of the species. For example, more northern species and populations are expected to exhibit stronger shifts in migration timing because recent increases in temperature have been highest at northern latitudes (Rosenzweig et al. 2008, IPCC 2013). This pattern would arise if birds adjust the rate of spring migration in response to increasingly warm conditions along the way (Hüppop & Hüppop 2003, Marra et al. 2005, Saino & Ambrosini 2008). Many studies have found that the relative locations of breeding and wintering areas predict the degree of advancement of spring migration, with short-distance migrants reacting most strongly (Lehikoinen et al. 2004, Tryjanowski et al. 2005, Thorup et al. 2007, Végvári et al. 2010). Two explanations for this finding are that the onset of migration in long-distance migrants is determined by endogenous mechanisms rather than by environmental conditions (Berthold 1996, Gwinner 1996), and that long-distance migrants are unable to detect the changing conditions on their Northern Hemisphere breeding area because they spend the winter far to the south (Lehikoinen et al. 2004). Migration distance is reported to be more important for North American than European species, although the causes are not known (Gienapp et al. 2007, Van Buskirk et al. 2009). In addition, it has been argued that insectivorous birds inhabiting forests are especially likely to track changing climate conditions: their habitats are relatively seasonal and their diet makes them particularly vulnerable to a mismatch between spring arrival date and the availability of food for nestlings (Visser et al. 1998, Both et al. 2010). Body size could be indirectly associated with the response to climate change through its impacts on mi-

gratory speed or duration of molt (Hedenström 2006, Knudsen et al. 2011). Finally, the number of broods that a female can potentially produce within a single season (broodedness) has been proposed to influence the reaction to climate change, because adding an additional brood may delay autumn departure or encourage advanced spring arrival (Jenni & Kéry 2003, Végvári et al. 2010, Townsend et al. 2013).

Here, we evaluated the importance of each of these factors using a quantitative analysis of published data on changes in the timing of bird migration in the Northern Hemisphere. We asked whether long-term shifts in spring and autumn migration phenology are associated with life history or ecological characteristics of the birds or with geographic features of the locality in which birds were sampled. Although the data come from diverse sources and are of variable quality, a quantitative review such as this can detect patterns in spite of uneven seasonal coverage, different types of data, broad scope of geographic coverage, and diverse species with heterogeneous ecologies, life histories, and apparent responses to climate change.

2. METHODS

2.1. Literature search

We located studies by executing the following search in the ISI Web of Science database through 1 September 2013: '(bird* or avian) AND (migr* or arrival or departure) AND climate'. Studies were included if they reported the slope from a simple linear regression of a measure of migration timing against year, or presented figures from which the slope could be calculated. To minimize reporting bias, we excluded those studies that included results only for species having significant regressions. We did not perform meta-analysis on correlation coefficients (e.g. Borenstein et al. 2009) because the correlation between timing and year was available for only 25% of cases. Nevertheless, the slope against year is a measure suitable for comparison among studies and species because it represents the magnitude of the observed phenological change and has the same units in all studies (d yr^{-1}; Root et al. 2003, Borenstein et al. 2009).

Two kinds of studies were represented in our database. Dedicated birdwatchers and local bird clubs have compiled observations of migrating birds, sometimes extending back to the early 20th century. These records usually include data on the first-arriving individuals in spring, and sometimes on the

latest-departing individuals in autumn. They have been criticized because they are subject to sources of bias that may overestimate phenological change (Sparks et al. 2001, Miller-Rushing et al. 2008, Lehikoinen & Sparks 2010), but there have been efforts to account for some of those biases (Sparks et al. 2007, 2008). The second data source is observatories that capture birds using standard methods over many years. In this case, the data are of higher quality, although not without potential biases (e.g. long-term change in habitat; Remsen & Good 1996). In the end, we complied a database of 69 localities in Eurasia (56 with data only from spring migration, 5 with data only from autumn, and 8 from both seasons) and 23 localities in North America (18 spring migration, 2 autumn, and 3 in both seasons). Maps showing the localities are provided online in Supplement 1 (www.int-res.com/articles/suppl/c061p109_supp.pdf); lists of species and studies are given in Supplement 2.

2.2. Response variable and covariates

Our aim was to understand causes of variation in the regression slope of migration timing against year. Four measures of timing appeared sufficiently often in the literature to support analysis: first arrival date in spring, date on which the median or mean bird was detected in spring and autumn, and the last departure date in autumn. In analyses of autumn last departure, we included a few studies that reported the date by which 90% of individuals had passed. Many studies reported more than 1 timing measure and included more than 1 species, and therefore contributed multiple entries to the dataset.

The geographic, life history, and ecological features of species and localities that may influence the observed change in migration phenology over time (as described in the Introduction) were included as covariates at the level of locality or species (Table 1).

Geographic covariates were defined by the location of the study site and whether the species was a long- or short-distance migrant. Eurasian long-distance migrants overwinter south of the Sahara Desert or in southern Asia, whereas North American long-distance migrants overwinter in the Caribbean or Central or South America. Short-distance migrants spend the winter primarily within Europe/North Africa or North America. Although longitude is known to affect avian phenology in Europe (Both et al. 2006, Rubolini et al. 2007), this covariate was not included because it has different geographic implications on the 2 continents.

Table 1. Features of species and study sites that were entered as covariates in the analyses. Long-distance migrants are those that overwinter south of the Sahara or in southern Asia, the Caribbean, or Central or South America; species that can produce >2 broods yr^{-1} were assigned a value of 3; species that molt during migration were listed as 'after'; diet items were scored as 'yes' if they are included in the diet at any time of year. The 12 ecological variables were subjected to principal component analysis to produce just 3 ecological covariates (Hill & Smith 1976; Supplement 3)

Category Covariate	Levels or range
Geography	
Continent	Europe, North America
Latitude of study site (°N)	29.6–64.1
Migration distance	Long, short
Life history	
Number of broods	1, 2, 3
Postnuptial molt	After, before migration
Body mass (g)	3.3–7200
Ecology	
Forest habitat	No, yes
Grassland habitat	No, yes
Wetland habitat	No, yes
Invertebrate diet	No, yes
Seed diet	No, yes
Fruit diet	No, yes
Plant diet	No, yes
Fish diet	No, yes
Carnivorous diet	No, yes
Nest on ground	No, yes
Nest in cavity	No, yes
Nest in bushes or trees	No, yes

Life history covariates reflected the body mass of the species, whether it is capable of producing more than 1 brood yr^{-1}, and whether the postnuptial (prebasic) molt occurs before or after/during the autumn migration (Table 1).

We defined 12 ecological traits, obtained from Bauer et al. (2005) and Poole (2008), to describe the year-round diet, breeding habitat, and position of the nest for each species. To reduce dimensionality, the 3 groups of ecological traits were subjected to 3 separate principal components analyses (PCAs) for categorical variables (Hill & Smith 1976, Dray et al. 2007). The first component from each PCA was included as an ecological covariate in the analyses, hereafter called Diet, Habitat, and Nest. The PCAs were performed separately for each timing measure because different sets of species were involved, but interpretation of the components was similar for the 4 measures (Supplement 3). Diet usually represented a contrast between carnivory or piscivory and grani-

vory or insectivory; Habitat was a contrast between species living in forests and those in wetlands; and Nest reflected placement of the nest on the ground or in trees and bushes.

Correlations among covariates, reported in Supplement 4, were not high enough to cause severe multicollinearity in the analyses (Glantz & Slinker 2001): 79% of all correlations were between −0.3 and +0.3. The highest correlations, above ±0.50, were between body mass and ecology (diet or habitat).

Supplement 2 lists the 389 species, their ecological and life history traits, and the timing measures for which data are available. The data set contains a broad representation of avian taxa, including 35 species of Anseriformes, 31 raptors, 62 species of Charadriiformes, 37 parulid warblers, 23 cardueline finches, and 37 species of Sylvioidea.

2.3. Statistical analyses

The analysis proceeded in 2 steps. The first step evaluated which covariates should be retained for inclusion within the second step, which involved comparing candidate models to explain the rate of phenological change. The initial step was necessary because models with all 8 covariates and their interactions were overparameterized and often converged poorly. Both steps employed hierarchical mixed-effects models to properly account for correlations among repeated observations of the same species or of different species sampled at the same site, and because covariates were associated with different hierarchical levels (i.e. species, study site, or the individual observation). Observations were not weighted because a measure of the variation in slope was available for only 53% of cases. Models were fit by maximum likelihood to enable model comparison using likelihood ratio tests and Akaike's information criterion (AIC).

In the first step, we fitted 3 separate models for each measure of migration timing: 1 for geographic covariates, 1 for life history covariates, and 1 for the ecological covariates. All models included the duration of the study as a fixed effect, because prior information indicated that very long studies never reported steep changes in migration timing (Supplement 5). The studies ranged in duration from 11 to 198 yr, but 97% of cases were <70 yr long and 78% were <50 yr. The harmonic mean was 35.3 yr. The study duration, number of broods, latitude (by continent), and the natural logarithm of body mass were centered. Continent, migration distance, and molt were categorical fixed effects (Table 1). All 2-way

interactions were included. If the covariate, or an interaction involving the covariate, was significant at a conservative threshold of $\alpha = 0.2$, then it was retained for inclusion in the second step. Significance was assessed by inspecting the 80% profile-likelihood confidence intervals of the parameters (Cox & Hinkley 1974, Venzon & Moolgavkar 1988). Species and study sites were modeled as crossed random effects. The results of this first step are presented in Supplement 6.

A consequence of the initial step of selecting variables for further consideration is that different combinations of covariates were evaluated for each measure of migration timing. This complicates comparison of the effect of the same covariate at different times of year. Furthermore, because interactions between covariates in different categories were not considered in the initial step, analyses did not explore the entire space of possible models. These points should be kept in mind when interpreting the results.

In the second step, we used AICc, a small-sample version of AIC (Burnham & Anderson 1998), to compare all possible models constructed from the covariates that survived the first step, along with all 2-way interactions for which the 80% CI did not include 0. In most cases, the model set consisted of many thousands of models. Models were fit by maximum likelihood and included the same random structure as in the first step. We then used model-averaging based on AIC weights to calculate parameter estimates and confidence intervals from among all models that fell within 2 AICc units of the best model (Burnham & Anderson 1998). The threshold of 2 AICc units was selected as a compromise between the desire to account for model uncertainty and the need to base conclusions on well-supported models. In the end, the exact threshold made only small differences in parameter estimates. We chose this data-dredging approach, rather than comparison among a small set of *a priori* models, because previous information outlined in the Introduction suggested that all covariates could be important, and interactions among all of them were plausible. It should be remembered, however, that data-dredging is accompanied by a risk of overfitting. In this case, the 4 global models fit the data fairly well, judging from their R^2 values (Table 2) and residuals that showed modest leptokurtosis (Supplement 7).

We also fitted phylogenetic mixed-effects models, in which the variance–covariance structure for the random effect of species was specified by the phylogenetic relatedness of taxa (Hadfield & Nakagawa 2010). This is mathematically equivalent to the so-

Table 2. Summary of 4 analyses testing the effects of covariates on the slope of migration timing against year (d yr^{-1}). Models were fit by maximum likelihood to accommodate model selection and likelihood ratio tests. Entries in the table are model-averaged parameter estimates for fixed effects (multiplied by 100; SE in parentheses), variance components for random effects (×100), and sample sizes at the bottom. Model R^2 is the variance explained by both fixed and random factors in the full model used for model averaging (Nakagawa & Schielzeth 2013). **Bold**: estimates for which the 95% CI of the profile likelihood CI of the parameter did not include 0 (fixed effects) or for which a likelihood ratio test revealed significance at α = 0.05 (random effects; df = 1; *p < 0.01). Duration is time in years from the beginning to end of the study, mass is the log of body mass in grams, molt indicates whether adults of the species molt before or after the autumn migration, and diet, habitat, and nest placement are principal components reflecting variation in ecology at the level of species (Table 1; Supplement 3). Continuous variables were centered. – : effect not included in model

Source	Level	Spring		Autumn	
		First arrival	50% passage	50% passage	Last departure
Fixed effects (×10^{-2})					
Duration (yr)		**0.298 (0.075)***	0.191 (0.081)	−0.249 (0.271)	0.642 (0.365)
Continent	North America	–	**6.237 (2.075)***	−1.151 (6.764)	8.862 (30.45)
Latitude		0.419 (0.464)	**0.621 (0.199)***	–	**2.921 (1.310)**
Migration distance	Short	**−9.415 (2.960)***	−1.479 (2.260)	15.331 (19.198)	–
No. of broods		−3.909 (2.037)	–	–	–
Postnuptial molt	Before	−1.277 (3.363)	–	7.405 (7.336)	**18.341 (8.764)**
Mass (g)		−0.468 (1.571)	–	**4.693 (1.655)***	9.857 (12.032)
Diet		**−7.814 (3.778)**	–	5.449 (2.341)	−4.547 (3.540)
Habitat		2.467 (1.598)	−0.666 (0.840)	–	2.751 (2.886)
Nest location		–	−2.220 (1.411)	−2.219 (1.460)	1.460 (10.938)
Continent × Latitude	North America	–	**−2.363 (0.752)***	–	–
Continent × Migration distance	North America, short	–	**17.661 (7.520)**	–	–
Continent × Molt	North America, short	–	–	–	−45.65 (24.34)
Continent × Diet	North America	–	–	−4.531 (3.164)	–
Continent × Nest	North America	–	3.305 (1.533)	–	–
Latitude × Migration distance	Short	–	**2.899 (0.801)***	–	–
Latitude × Mass		**1.063 (0.176)***	–	–	–
Latitude × Diet		−0.268 (0.199)	–	–	–
Latitude × Habitat		**0.629 (0.244)***	**0.338 (0.155)**	–	–
Latitude × Nest		–	0.228 (0.139)	–	–
Migration distance × Molt	Short, before	–	–	−35.007 (20.512)	–
Migration distance × Mass	Short	**−4.929 (2.032)**	–	–	–
Migration distance × Diet	Short	−4.400 (2.395)	–	–	–
Migration distance × Habitat	Short	−3.990 (2.425)	–	–	–
Migration distance × Nest	Short	–	−2.553 (1.572)	–	–
Broods × Mass		**3.469 (1.276)***	–	–	–
Molt × Mass	Before	–	–	–	**−21.89 (9.51)**
Molt × Diet	Before	7.957 (3.394)	–	–	–
Molt × Nest	Before	–	–	–	**−20.44 (9.89)**
Mass × Diet		1.796 (0.720)	–	–	–
Mass × Habitat		–	–	–	**−4.791 (2.337)**
Mass × Nest		–	–	**2.534 (0.961)***	–
Nest × Habitat		–	−0.944 (0.621)	–	**5.099 (1.862)***
Random effects (×10^{-2})					
Sites		**1.538***	0.0	0.315	**0.916***
Species		**1.479***	**0.284**	**1.740***	1.164
Model R^2		0.395	0.352	0.429	0.381
Sample sizes					
Number of sites		74	19	12	9
Number of species		343	132	182	119
Number of observations		1274	286	272	197

called 'animal model' in quantitative genetics, except that inbreeding coefficients are replaced by phylogenetic branch lengths. We used the strict consensus phylogeny downloaded from the Avian Supertree Project (Davis & Page 2014). Species not present on the supertree were added by reference to recent literature; estimated dates for some nodes have been published, and all others were placed at equal intervals between dated divergences. Supplement 8 includes the phylogeny, and describes details of the branch length estimates. Results showed that phylogenetic mixed-effects models were poorly supported

by the data for all 4 measures of migration timing, in comparison with models having species and study sites but no phylogenetic structure. Values of the deviance information criterion (DIC) were always much lower (i.e. better) for the model with no phylogenetic effect (spring first arrival: DIC = 610.46 for the model with phylogeny and sites, and DIC = 548.81 with only species and sites; spring 50% passage: −297.01 and −310.01; fall 50% passage: 72.06 and 53.32; fall last departure: 643.06 and 552.42). Models without the random effects of study sites or species were always less well supported. Therefore, results presented here come from models with species and sites entered as crossed random effects, fitted by maximum likelihood.

Mixed-effects models were fit with the MCMCglmm package in R 2.15 (Bayesian phylogenetic approach; Hadfield 2010) and the lme4 package (likelihood; Baayen et al. 2008); multi-model inference was implemented in package MuMIn (Barton 2009).

3. RESULTS

Across all studies and species, there was strong evidence for advancement in the timing of spring migration and no net change in autumn migration. These conclusions came from mixed-effects models including only a fixed intercept and study duration (centered), with species and sites as random effects. The site/species-level mean change in timing was −0.214 d yr^{-1} for spring first arrival (profile-likelihood 95% CI: −0.266, −0.162), −0.104 d yr^{-1} (−0.139, −0.071) for spring median passage, 0.090 d yr^{-1} (0.002, 0.176) for autumn 50% passage, and 0.019 d yr^{-1} (−0.175, 0.204) for autumn last departure. Sample sizes are given in Table 2.

The significant variance components for species in all analyses indicated that the change in migration timing was heterogeneous among species (Table 2). Variance among study sites was usually less important.

There was a positive relationship between the change in timing and the duration of the study (Supplement 5). Very long studies never reported highly negative or positive values. In conventional meta-analyses this might be interpreted as evidence of publication bias, but in this case short-term studies may report larger slopes for valid biological or statistical reasons. For example, phenological change could be more rapid in recent years, or perhaps no species is capable of sustaining a rapid rate of change over many decades.

3.1. Spring migration

Although both measures of spring migration timing shifted earlier, the first arrivals and the 50% quantile of migrants did not behave the same. First-arrival data supported models in which migration distance, latitude, diet, and body mass were important, whereas change in the timing of the midpoint of the distribution varied between continents, across latitudes, and with several interactions (Table 2). For the first-arriving individuals in spring, species that migrate short distances accelerated their timing significantly faster than long-distance migrants; this was not true for the median passage date (Fig. 1). The broodedness-by-body mass interaction in first arrival arose because large size was associated with strong advancement of migration in species that produce only a single brood, but the association with body size disappeared or was reversed for multiple-brooded species. Latitude also interacted with body size: the rate at which the date of first arrival became earlier was greatest for large-bodied species sampled at southern sites and small-bodied species sampled in the north (Fig. 2). The molt-by-diet interaction indicated that species that enter the postnuptial molt after autumn migration advanced their first arrival date only if their diet is granivorous or insectivorous, whereas species that molt before migration have advanced arrival date regardless of their diet (Supplement 9).
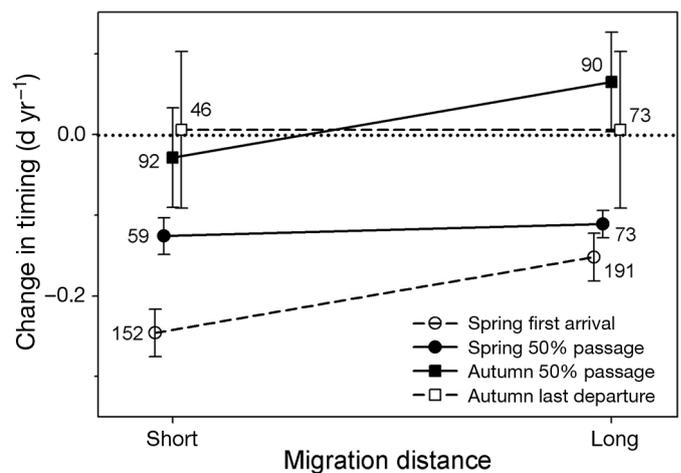

Fig. 1. Long-term change in migration phenology for short- and long-distance migrants sampled in spring and autumn. Long-distance migrants winter in sub-Saharan Africa (for European species) or south of the US–Mexican border (for North American species). Points depict means ± 1 SE; sample sizes are the number of species within each category. The estimated effect of migration distance in model-averaging was significant only for spring first arrival (Table 2)
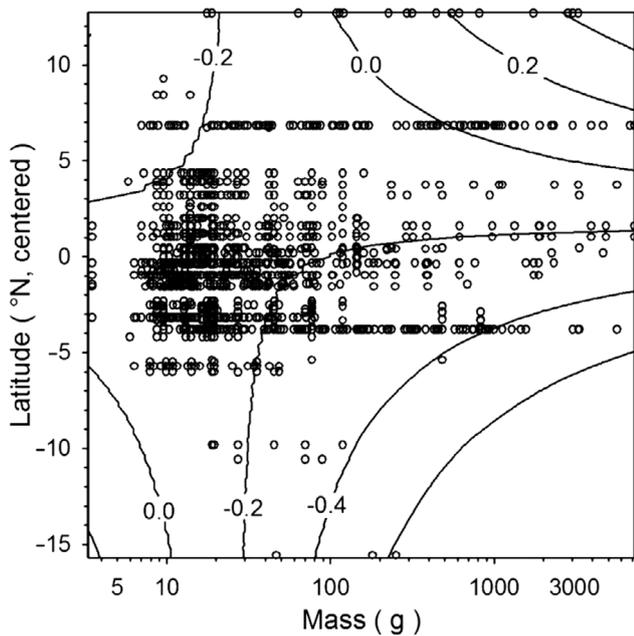
Fig. 2. Change in the date of first arrival in spring depended on an interaction between body size and the latitude of the study site. The surface was fitted using model-averaged parameter estimates in Table 2. Contour intervals are the change in timing (d yr^{-1}), and symbols depict the distribution of 343 species sampled at 74 study sites. Latitude was centered by continent

For the 50% passage date in spring, effects of continent and latitude of the study site were important: the change in timing was most pronounced in the south, and was 0.062 d yr^{-1} greater in Europe than in North America (Table 2). Here again, significant interactions require these generalities to be qualified. The difference between continents was present for ground-nesting species but nearly absent for species that nest in trees and bushes (Fig. 3A). The latitudinal effect was especially strong for short-distance migrants on both continents, but was much weaker for long-distance migrants in Europe and completely reversed for those in North America (Fig. 3B).

3.2. Autumn migration

Phenological change in autumn, although not different from 0 overall, was significantly related to life history and ecological covariates (Table 2). For the 50% quantile, large-bodied species have shifted toward later passage and small species have shifted earlier, but this was primarily true for ground-nesting birds (Fig. 4A). Species with a granivorous/insectivorous/frugivorous diet are departing slightly later,

whereas carnivores are departing earlier (Supplement 9). An interaction between continent and migration distance arose because in Europe—but not in North America—the long-term trend in timing depended on migration distance (Fig. 4B). There was no overall difference associated with continent or migration distance.

For the timing of final departure in autumn, the barely significant positive effect of latitude indicated
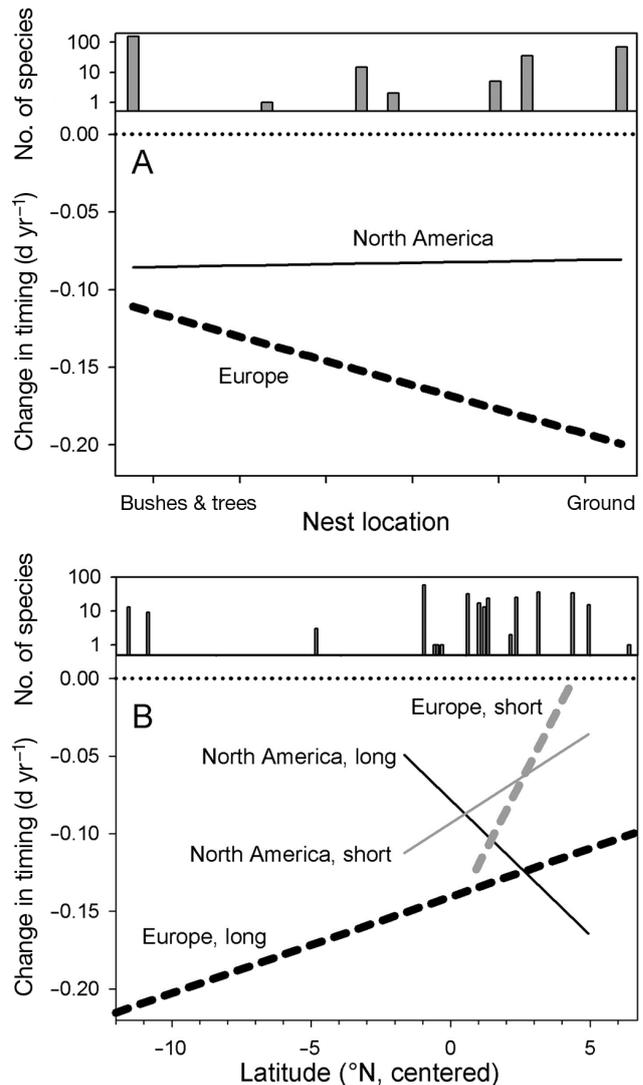

Fig. 3. Change in the date at which 50% of spring migrants passed was influenced by interactions between (A) nest location and continent and (B) migration distance, continent, and latitude of the study site. Relationships were fitted using parameters estimated from model-averaging (Table 2). Nest location came from a principal components analysis of 3 variables (Supplement 3). Latitude was centered by continent (a value of zero corresponds to the average latitude). The frequency distribution of species values is shown at the top of each panel; in (B), 1 additional site with 1 species recorded is at −23.7° N
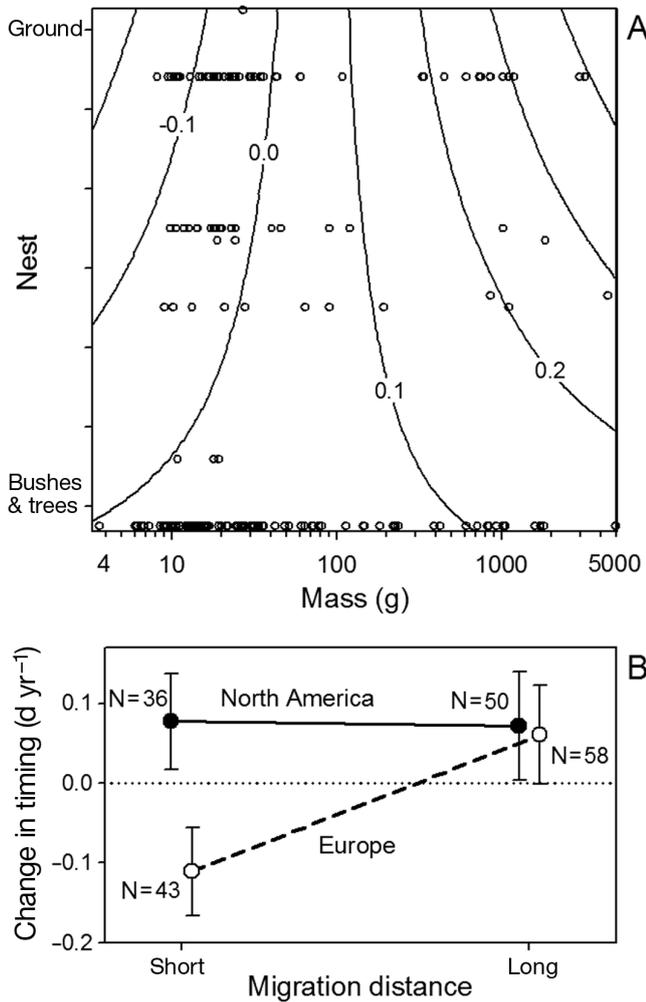
Fig. 4. Change in date at which 50% of autumn migrants were recorded was influenced by interactions between (A) body mass and nest placement and (B) continent and migration distance. Symbols in (A) represent 182 species sampled at 12 study sites, and the surface was fitted using parameters estimated from model-averaging (Table 2); contour intervals represent the change in date at which 50% of migrants were recorded in d yr^{-1}. Nest location came from a principal components analysis of 3 variables (Supplement 3). Symbols in (B) are means ± 1 SE; sample sizes are the number of species. Long-distance migrants winter in sub-Saharan Africa or southern Asia (for Eurasian species) or south of the US–Mexican border (for North American species)

that high-latitude sites have recorded a delay while departure has advanced at low-latitude sites (see Supplement 10). This pattern would require the last migrants to increase their rate of southward travel in recent years. Fig. 5A illustrates that the trend toward a delay in departure decreased with body size in species that molt before migration, whereas it increased with body size in species that molt after migration. A strong interaction between habitat and nest occurred
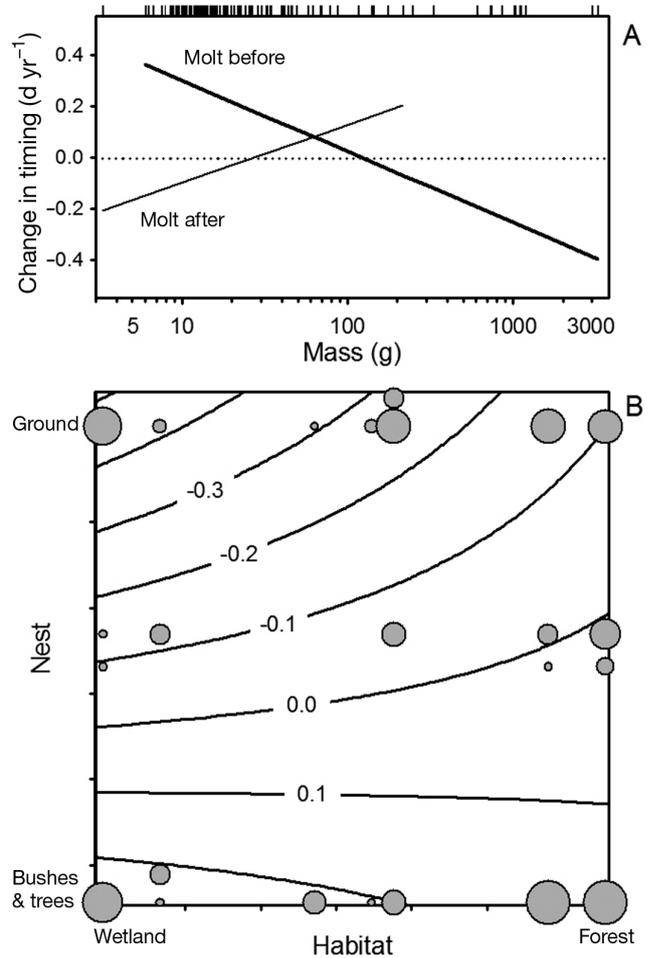

Fig. 5. Long-term change in the date of last departure in autumn depended on an interaction between (A) body size and the timing of the postnuptial molt and (B) habitat and nest location. In (A), symbols along the upper edge are the body masses of 119 species sampled in 9 sites; lines represent predicted relationships using model-averaged parameter values (Table 2). In (B), the diameter of the bubbles is proportional to the logarithm of the number of species (range 1–30 species per habitat–nest combination)

because species that nest on the ground and occupy wetland habitats tended to advance the date of departure whereas habitat was unimportant for species that nest in trees (Fig. 5B). Migration distance was unrelated to changes in autumn migration (Fig. 1).

4. DISCUSSION

The results of this quantitative review confirm previous observations of long-term change in avian migration timing associated with climate change, except that the estimated response during spring was smaller than estimates based on more limited

surveys. For the date of the first-arriving individual in spring, changes reported in previous summaries of partially overlapping data sets are −0.37 and −0.28 d yr^{-1} (Rubolini et al. 2007, Lehikoinen & Sparks 2010), both of which exceed the 95% confidence intervals calculated from our dataset (−0.266 to −0.162 d yr^{-1}). For median passage date in spring, previous reviews have calculated values of −0.24, −0.157, and −0.18 d yr^{-1} (Gienapp et al. 2007, Rubolini et al. 2007, Lehikoinen & Sparks 2010), all of which exceed the 95% CI of our estimate (−0.139 to −0.071). The earliest publications in this field may have reported especially strong results, and the earlier reviews may have included publications that reported only significant results or assembled data sets that were restricted for specific reasons. Furthermore, our analyses differ from some earlier approaches in that they account for non-independence among multiple species observed at the same site and repeated observations of the same species. It is therefore safe to conclude that after averaging across several hundred species and more than 90 sampling localities, spring migration in the Northern Hemisphere has advanced an average of 1 d decade^{-1} over the past few decades, and autumn migration has delayed by only slightly less (0.90 d decade^{-1}) but with much more variation among species. On average, the inter-migration interval, i.e. the period of time during the summer between the midpoints of spring and autumn migrations, has lengthened by over 8 d since 1970 (1.9 d decade^{-1}). This did not differ significantly between North American and European species.

Knudsen et al. (2011, p. 941) concluded that 'the search for general patterns has been difficult' with respect to climate change and migration phenology. This is where a quantitative comparison can make a valuable contribution, by incorporating a wide variety of ecological and life historical traits and by combining data collected in many localities. We are now in a position to propose general inferences about some of the factors mentioned in the Introduction that are thought to be associated with avian responses to climate change. While these analyses have enhanced understanding of, and certainty about, the main patterns and correlates of long-term change, we agree with Knudsen et al. (2011) that the mechanisms underlying many of these patterns are poorly understood.

Geographical covariates

There has been much discussion in the literature about the distinction between species that migrate long and short distances between their summer and winter ranges (Tryjanowski et al. 2005, Tøttrup et al. 2006, Van Buskirk et al. 2009, Van Buskirk 2012a). Some have suggested that migration timing in both seasons is endogenously controlled in long-distance migrants, while short-distance migrants can exploit environmental cues because they have access to reliable information about conditions at their destination (Berthold 1996, Butler 2003, Lehikoinen et al. 2004). Knudsen et al. (2011) concluded that previous studies of migration distance have produced mixed results. We find that short- and long-distance migrants differ significantly in their response only for the earliest individuals in spring (Fig. 1). There is little influence of migration distance on changes in the timing of the center of the distribution of migrating individuals. This suggests that even long-distance migrants have access to cues that can trigger earlier spring migration (Gordo et al. 2005, Saino et al. 2007) or that these species have evolved earlier migration (Van Buskirk et al. 2012, Charmantier & Gienapp 2014).

Prior to our study, there was some indication that European and North American species were accelerating spring migration to different extents (Gienapp et al. 2007, Van Buskirk et al. 2009). There are good reasons to expect such a difference. For example, the degree of climate warming has been somewhat greater in Europe than in North America (Hansen et al. 2006, IPCC 2013), and this might cause European species to shift their phenology more strongly. The geographic context of migration differs between the 2 continents, with an east–west range of mountains in Europe and differences in the climatic influence of the North Atlantic Oscillation. The 2 continents also contain phylogenetically distinct groups of species, which might differ in their reactions to climate change for unknown reasons. Our results only weakly confirm the distinction between continents. We found that the change in median spring migration timing in Europe has been about 70% greater than that in North America (−0.146 versus −0.084 d yr^{-1}), but for other migration measures there was little difference between means and only 1 important interaction (Fig. 4B).

We expected that advancement of spring migration would be higher at high latitudes if the pace of climate change has been greater in northern localities and if migrating birds adjust their migration speed according to temperature (Ahola et al. 2004, Marra et al. 2005, Tøttrup et al. 2008). This was not observed except in the case of the first-arriving individuals of species with small body size (Fig. 2). Most influences of latitude were not as expected. For example, large-

bodied species show more delayed dates of first spring arrival at high latitudes, and the median passage of spring migrants has advanced more at low latitudes than in the north (especially for short-distance migrants; Fig. 3B). This may be related to Hurlbert & Liang's (2012) finding that the shift in spring arrival date for a given change in temperature is greater in the southern parts of North America. It is known that the rate of movement accelerates as conditions become warmer (e.g. Schaub & Jenni 2001, Marra et al. 2005, Halkka et al. 2011), and Hurlbert & Liang (2012) showed that this effect is most important at southern localities. As a result, increasing temperatures in recent decades have caused a sharp advancement in arrival dates in the south, even though the rate of continued northward progress has, if anything, declined.

A possible explanation for the enhanced reactions at low latitudes of short-distance migrants and species with large body size is that these birds have shifted their winter distributions northward, for which there is evidence in many species (La Sorte & Thompson 2007, Maclean et al. 2008). If some fraction of the population of a short-distance migrant species now over-winters near or to the north of the sampling site, this would greatly accelerate the apparent onset and mid-point of spring migratory passage. Spring migration farther north should also advance, but the most northern sampling localities may be so far removed from the over-wintering area that a change in arrival dates caused only by the shift in winter distribution is weak or undetectable.

Life history covariates

Climate change has caused a lengthened growing season in many parts of the Northern Hemisphere, and we predicted that this would encourage some facultative multi-brooded species to extend their breeding season and either produce an extra brood or lengthen the interval between broods. The more pronounced advancement of first arrival dates in multi-brooded than in single-brooded species is consistent with this prediction. The fact that multi-brooded species have not begun to migrate later, as noted in several studies (Jenni & Kéry 2003, Møller et al. 2010), does not necessarily contradict the importance of broodedness. First, there may be constraints associated with molt, discussed in the following paragraph, that prevent multi-brooded species from delaying autumn migration. Moreover, several lines of evidence indicate that the extension of summer

weather does not imply that favorable foraging conditions extend into late summer. Selection favoring early breeding has been observed in many birds (Perrins 1970, Verhulst & Nilsson 2008, Gienapp et al. 2013). Studies of insect prey suggest that warmer conditions are correlated with an earlier but shorter peak of caterpillar availability (Smith et al. 2011), and multiple-brooding is strongly associated with early arrival on the breeding grounds in some species (Bulluck et al. 2013, Townsend et al. 2013). In sum, a shift toward earlier spring migration in multi-brooded species is consistent with the notion that broodedness may influence the response to climate change, even though there has been no detectable change during autumn migration.

The postnuptial molt potentially constrains changes in the timing of autumn migration (Gordo 2007). Species that molt before migration cannot initiate migration much earlier without interfering with the molt, whereas those that molt after migration presumably cannot delay their departure too long or they may be interrupted by the molt while still travelling southward. This suggests that delayed autumn migration should be observed only in those species that molt prior to migration. Conducting a convincing test of this hypothesis is challenging because there are relatively few species that molt after migration, especially among short-distance migrants (Supplement 2). Nevertheless, the data are consistent with the idea that molt constrains phenological change. Both measures of autumn migration timing have become more delayed in species that molt prior to migration than in those that molt later (difference of 0.7–1.8 d decade^{-1}; significant only for date of last departure). This result agrees with much evidence that molting is costly and must be achieved in a brief period between 2 other costly activities, viz. breeding and migrating (e.g. Evans Ogden & Stutchbury 1996, Bonier et al. 2007, Mulvihill et al. 2009). Many individuals appear to run short on time, initiating autumn migration while still undergoing molt (Flockhart 2010). Climate change may alleviate this time constraint to some degree, by allowing birds to carry out the molt over a longer period of time or linger somewhat longer before departing on migration.

Ecological covariates

Direct correlations between ecological variables and long-term change in migration timing were infrequent, but there were important interactions involving ecological covariates in both seasons. In autumn, for

example, species that nest in trees or inhabit forests delayed their last departure somewhat while ground-nesting birds in wetland habitats departed earlier (Fig. 5B). Tree-nesting species that forage in vegetation, especially on insects, may be more affected by long-term changes in seasonality because they depend on warm weather to maintain their habitat and food supply. Warmer conditions in autumn seem to encourage the latest individuals to delay their departure. Wetland species are affected less directly by seasonality of their habitat and prey base, so their decisions about departure timing may be influenced more weakly by autumnal weather conditions.

A similar explanation may apply to the negative relationship between the change in first arrival date in spring and diet, and the interaction between diet and timing of molt (Supplement 9). Here, species with the greatest advancement in arrival were those for which warm conditions in spring most strongly affected food availability (diet of seeds, fruit, and insects, as opposed to fish and other animals; see also Butler 2003). The influence of molt on this relationship may be related to time constraints: species that molt prior to autumn migration have pushed their arrival earlier in spring regardless of diet; those that face no molting constraint after breeding have shown only modest changes in timing.

Important ecological constraints should operate similarly in Europe and North America, so it was unexpected that continents differed in the extent to which changes in spring median passage date depended on nest location (Fig. 3A). In Europe, the group of species that showed the greatest advancement in timing were those that nest on the ground, whereas nest location was unimportant in North America. A sampling bias may be at work here: 74% of ground-nesting species included in the North American data set for median spring passage are sparrows or New World warblers, whereas only 24% of European ground-nesting species were ecologically similar buntings or warblers (Supplement 2). So the question may not be why nesting ecology influences phenology differently on the 2 continents, but rather why a heterogeneous collection of Old World groups is reacting relatively strongly while the response of New World warblers and sparrows is not exceptional.

CONCLUSIONS

We have stepped through the list of covariates in some detail here because these findings highlight a key contribution of our work. Many earlier studies discussed the degree and extent of avian phenological response to climate change, and several thorough reviews are available (Lehikoinen et al. 2004, Rubolini et al. 2007, Lehikoinen & Sparks 2010, Knudsen et al. 2011). However, the ecological and life history correlates of climate impacts remain poorly understood, even though they may be especially important for offering insight into causative mechanisms. Our results begin to unveil substantial variation among kinds of species in how they react to climate change: important distinctions include trophic position, timing of molt, body size, and the relative locations of the breeding and wintering distributions. Some of these factors, such as migration distance, have been studied in some detail (Tryjanowski et al. 2005, Tøttrup et al. 2006, Van Buskirk et al. 2009), whereas other factors, such as diet and molt, are less well understood, and may point toward the influences of time constraints and seasonality of resources in dictating avian responses to climate change.

There is indirect evidence that recent shifts in avian phenology cannot compensate for the negative effects of climate change, leading to reduced performance of individuals and negative trends in - population size (Møller et al. 2008, Jones & Cresswell 2010, Saino et al. 2011). But some of the responses discovered here are potentially positive. For example, it may be beneficial for species that molt prior to autumn migration to have more time to undergo the prebasic molt between the completion of breeding and the onset of migration. A few multi-brooded species may be taking advantage of warmer conditions to either increase the number of broods or improve the spacing between broods (which can enhance fledgling success; Jenni & Kéry 2003, Møller 2007, Møller et al. 2010). Most of the other phenological responses described here are probably at least adaptive in the sense that they improve individual performance more than would a lack of response or a weaker response (Menzel et al. 2006, Van Buskirk 2012a,b). We clearly need a better understanding of the causes of species differences to properly anticipate the implications of climate change and phenological responses for individuals and populations.

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