

Changes in breeding phenology and population size of birds

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Summary

1. Although the phenology of numerous organisms has advanced significantly in response to recent climate change, the life-history and population consequences of earlier reproduction remain poorly understood.

2. We analysed extensive data on temporal change in laying date and clutch size of birds from Europe and North America to test whether these changes were related to recent trends in population size.

3. Across studies, laying date advanced significantly, while clutch size did not change. However, within populations, changes in laying date and clutch size were positively correlated, implying that species which advanced their laying date the most were also those that increased their clutch size the most.

4. Greater advances in laying date were associated with species that had multiple broods per season, lived in nonagricultural habitats and were herbivorous or predatory. The duration of the breeding season increased for multibrooded species and decreased for single-brooded species. Changes in laying date and clutch size were not related to changes in population size (for resident or migratory species).

5. This suggests that, across a wide variety of species, mismatches in the timing of egg laying or numbers of offspring have had relatively little influence on population size compared with other aspects of phenology and life history.

Key-words: birds, climate change, duration of breeding season, migration, mismatch hypothesis, population trends

Introduction

The life history of organisms is composed of parts that interact in ways that have been moulded by natural selection to maximize reproductive success and survival under given environmental conditions (Roff 2002). Changes in climate not only alter the phenology of numerous organisms, but also affect life-history components such as the number of offspring and breeding attempts per season (Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2007; Dunn & Winkler 2010; Lehikoinen & Sparks 2010). For example, laying (or flowering) date often influences reproductive success, which has significant consequences for recruitment. Both laying date and clutch size are so integrated that some theoretical work treat these as properties of the same life-history character (Rowe, Ludwig &

Schluter 1994). Although many studies have examined the effects of climate change on timing of arrival (for migratory species) or timing of egg laying (laying date), few interspecific studies have investigated the consequences of timing of breeding on subsequent aspects of reproduction and life history. These relationships are important because changes in laying date and clutch size are likely to influence fitness and ultimately population trends.

Using intra- and interspecific variation in birds, we address three general questions about long-term changes in laying date and clutch size, and their subsequent effects on population size. First, are responses at different stages of the reproductive cycle independent, or do effects at early stages feed into subsequent stages? The argument for such an effect is obvious for the timing of migration and timing of breeding, simply because breeding cannot start until breeders have arrived, although early 'delays' in migration may partly be compensated by catching up at later stages. For example, in long-distance migrants,

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the timing of arrival may not change in response to climate change because of lack of cues during winter, which may be spent in tropical regions far away from the breeding grounds (Both & Visser 2001). To compensate for 'late' arrival, selection may favour greater advances in timing of laying or the number of breeding attempts (brood number), which can influence the duration of the breeding season and subsequent autumn migration (Møller *et al.* 2010b). To date, however, it is not known if change in timing of spring arrival is associated with change in timing of laying, and if changes in laying date are associated with changes in clutch size and the duration of the breeding season. Second, what ecological and life-history factors are related to changes in laying date? Several studies have examined ecological correlates of arrival date (Møller, Rubolini & Lehikoinen 2008) and duration of the breeding season (Møller *et al.* 2010b), but to date, there has not been any large-scale comparative study of the timing of laying. Lastly, is population size affected by changes in timing of laying and fecundity (clutch size)? If individuals are unable to track temporal change in the environment caused by climate change, then they may become mismatched with seasonal peaks in food supply or other resources needed for reproduction (Both *et al.* 2006; Saino *et al.* 2011), with negative consequences for changes in population size as reported for breeding birds in Europe (Møller, Rubolini & Lehikoinen 2008; Both *et al.* 2010). Thus, trends in population size ('threat status') of bird species may reflect poor underlying ability to cope with environmental challenges including climate change. Indeed, European species that have shifted their arrival dates the least in response to climate change have declined the most severely in population size during the decade 1990–2000 (Møller, Rubolini & Lehikoinen 2008).

Here, we examine four specific questions. First, are birds that are arriving earlier also starting to lay eggs earlier? If arrival date of migrants constrains the timing of reproduction, then populations that have advanced their spring arrival date the most should also show the greatest advancement in laying date. Similarly, if migration distance constrains the timing of reproduction, then residents (or short-distance migrants) should lay earlier than long-distance migrants. Second, are advances in laying date correlated with increases in clutch size (across populations)? Clutch size is often larger among early breeders, and most species advance their date of laying in warmer springs (reviewed by Dunn 2004), so we might predict that warmer temperatures will lead to both earlier laying and larger clutches. On the other hand, there are a variety of constraints such as the cost of producing more eggs or caring for the young that may limit clutch size increases in warmer springs (Dunn & Winkler 2010). Our third question is what ecological and life-history factors influence the timing of laying? For example, long-distance migration may constrain timing of laying, because it

affects arrival date (Both & Visser 2001; Møller, Rubolini & Lehikoinen 2008). Furthermore, species may differ in timing of laying as a consequence of differences in breeding location (e.g. latitude and habitat), diet and body mass, which affects energy balance and the cost of producing eggs (Stevenson & Bryant 2000). There is also increasing evidence that the response to climate change is influenced by the number of broods laid in a season (Visser *et al.* 2003; Jiguet *et al.* 2007; Møller, Rubolini & Lehikoinen 2008; Møller *et al.* 2010b). Species with two or more clutches per season show a greater advancement in laying date than species with single clutches, and this may allow them more time between clutches (greater interclutch interval), which enhances adult survival (Møller 2007; Møller *et al.* 2010b). Lastly, we ask whether there is an association between changes in laying date or clutch size and recent (1990–2000) population trends. Relatively few intraspecific studies have examined changes in timing of laying and their consequences for population size (Wilson & Arcese 2003; Both *et al.* 2006; Reed *et al.* 2013a,b), so, to date, the broader patterns across species remain unknown. To examine these questions, we made a literature search combined with personal contacts with scientists to establish a data base with information on changes in both laying date and clutch size. We also constructed empirical models to explore possible mechanisms linking changes in laying date to population trends.

Materials and methods

DATA SETS

We made an exhaustive literature search for publications on climate change, laying date and clutch size in birds using Web of Science and Google Scholar combined with our own references on this subject reported in Møller, Fiedler & Berthold (2010a), especially by Dunn & Winkler (2010). When we located publications that had reported change in laying date over time and/or in response to changes in temperature during breeding, we sent the corresponding author an email asking for information on change in mean clutch size over time and/or in response to changes in temperature during breeding. This first request for information was sent out 13 April 2011. If we had not received a response, we sent out a second email on 27 September 2011, followed by a final request on 27 October 2011. Overall, we obtained data from 196 studies (see Data S1 in Supporting information).

PHENOLOGY AND REPRODUCTIVE VARIABLES

Spring arrival date was defined as the first arrival date from time series of arrival dates from Europe (Rubolini *et al.* 2007). For each species, we used mean estimates of change in arrival date per year from a large number of populations as estimates of phenological change, ensuring that most estimates of change were based on multiple estimates, thereby reducing the sampling error in single estimates.

Laying date for each population was estimated as the mean, and change in laying date was estimated as the regression slope of mean laying date for each year against year or mean temperature during the main month of reproduction, respectively. If this information was included in a publication, we extracted this information as reported in the paper. Changes in laying date and clutch size were estimated in the same way. For all estimates of changes in laying date and clutch size, we recorded the number of years for which information was available because a longer time series would be more likely to reveal a significant change in laying date or clutch size.

We estimated change in the duration of the breeding season using information for 20 European species reported by Møller *et al.* (2010b) and seven North American species studied by Dunn *et al.* (2000) and Torti & Dunn (2005). In brief, we estimated duration of the breeding season as the number of days between the 10th and 90th percentiles of breeding dates each year. Then, we regressed this annual estimate against year to obtain a regression slope that represented linear change in the duration of the breeding season per year.

ECOLOGICAL AND LIFE-HISTORY VARIABLES

We examined a variety of ecological and life-history variables that have been associated with changes in breeding phenology or population trends. These included migration distance, northernmost breeding latitude, the number of broods per season, body mass, farmland habitat (coded as agricultural or nonagricultural) and trophic level (primary, secondary or tertiary consumer). Migration distance (in degrees of latitude) was estimated as the difference between the centers of the breeding and wintering ranges (mean of the northernmost and southernmost latitudes of each range) presented in standard references, primarily Cramp & Perrins (1977–1994) for European species and Birds of North America (Poole 2005) for North America. The northernmost latitude of the breeding range was also included in analyses because climate warming is more extreme in northern latitudes (Parmesan & Yohe 2003; IPCC 2007). We excluded three Australian species in these analyses, because it remains unclear whether we should expect similar responses as in northern hemisphere species. Information on the typical number of broods per season (coded as single or multiple), body mass, farmland habitat and trophic level was extracted from standard references.

POPULATION TRENDS

We analysed population trends of breeding birds in Europe during the period 1990–2000, because population trends during this time period were correlated with changes in arrival date (Møller, Rubolini & Lehikoinen 2008). Estimates of population trends were made by Birdlife International (2004) on a seven-point scale ranging from a large decline (–3), a moderate decline (–2), small decline (–1), stable (0), small increase (+1), moderate increase (+2) to a large increase (+3). We estimated a similar breeding population trend for eight of the 15 North American species that were adequately covered by the Breeding Bird Survey for the same time period (1990–2000; Sauer & Link 2011). To make estimates for the North American species comparable with the European estimates, we standardized the per cent change per year estimates in Sauer & Link (2011) and divided them evenly into 7 scores (–3 to +3).

POPULATION MODELS

To explore the mechanisms linking changes in laying date and clutch size with population trends, we constructed models based partly on empirical data from great tits (Reed *et al.* 2013b) and tree swallows (Dunn *et al.* 2011). These two species illustrate the extremes in terms of the effects of mismatching: great tits show reduced reproductive success when most nestlings hatch after the peak of caterpillar abundance (Reed *et al.* 2013a,b), whereas tree swallows show little effect of mismatching on reproductive success, presumably because their food supply is often superabundant and does not have a distinct or predictable seasonal peak (Dunn *et al.* 2011).

For these models, population size (N) in year $t + 1$ was the sum of recruitment and adult survival in year t . Recruitment in year $t + 1$ was the sum of the number of surviving fledglings produced in year t and new immigrants (5% of fledglings). Number of fledglings produced each year was the mean number of eggs hatched minus nestlings lost due to mismatching multiplied by the number of females ($0.5N$). The proportion of nestlings lost due to mismatching (m) was described by: $-0.001 m^2 - 0.001 m$, where m is the number of days between the peak energy demands of nestlings and the peak of food abundance. The shape of this equation was based on data from great tits (Reed *et al.* 2013a) and adjusted so relative fledging success peaked at zero mismatch (i.e. peak food abundance occurred on the same day as the average date of peak nestling energy demand). Thus, fledging success was lower when the peak date of nestling food demand occurred before or after the date of peak food abundance. Other parameters, such as clutch size (six eggs) and per cent hatching success (95%), were constant or chosen randomly from a range of values (fledgling survival varied between 5 and 15%, and adult survival varied between 50 and 65%) to represent stable populations of a typical passerine (Faaborg *et al.* 2010). To model species that showed no effect of mismatching on fledging success, we used a randomly chosen level of nestling mortality from the observed range in tree swallows (14.4–21.8%) to calculate fledging success each year. For both types of models, we estimated the finite rate of population increase (λ) over 1 year for 100 simulated populations and plotted the mean λ in relation to the level of mismatch (m). We considered these our base models.

Next, we examined how population growth rates are changing over the long term in response to changes in laying date and food abundance. In these models, we advanced laying date (using a range of values) and allowed clutch size to respond accordingly for a simulation of 75 years. Change in clutch size was modelled using the observed relationship between clutch size and laying date in tree swallows ($CS = 6.18 + -0.0363 \times \text{laying date}$, where 1 = 1 May; Dunn *et al.* 2011). The extent of mismatching between birds and their food supply will also depend on the rate at which the food peak advances. Here, we assumed the date of peak food supply is advancing at the same rate as the caterpillars studied by Reed *et al.* (2013a; $0.5779 \text{ days year}^{-1}$). Other than advancing the food supply and laying date, which affects clutch size, these models were the same as the base models described in the previous paragraph. As above, we modelled two situations, one in which there was a cost of mismatching and the other without a cost (same as above). Each simulation was run 100 times, and λ was calculated from the slope of the regression of population size on time (over the 75 year simulation). The model may be obtained from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bp3g0>.

STATISTICAL ANALYSES

The entire data set included 196 studies from 89 species. The modal number of studies was one for each species, but 23 species had more than one study (10 species had >2 studies; range: 1–28 studies). Pied flycatchers *Ficedula hypoleuca* ($N = 28$), great tits *Parus major* ($N = 26$) and blue tits *Cyanistes caeruleus* ($N = 20$) had the most studies. Thus, data in the analyses were not independent in terms of phylogenetic history and intraspecific variation. To control for these sources of nonindependence (between and within species), we analysed the data using mixed effects models in the R package MCMCglmm (R Development Core Team 2008; Hadfield 2010). MCMCglmm fits linear models using Monte Carlo methods and Bayesian Markov Chain sampling, and it can use phylogenetic trees to account for nonindependence among populations or species due to evolutionary history. These analyses also included species identity as a random factor to account for the nonindependence of data from different studies of the same species. Most models were analysed with a normal trait distribution (Hadfield 2010), but a Poisson distribution provided a better fit in some analyses of population trend. More details of the MCMCglmm analyses and the phylogenetic tree (Fig. S1 in Supporting Information) we used are presented in the supporting information. All other analyses were conducted in JMP version 10 (SAS 2012).

We made repeatability analyses by using species as a factor for all species with at least two estimates of change in laying date or clutch size (Falconer & Mackay 1996). We found little or no evidence of statistically significant repeatability for different populations of the same species (see Results), implying that there was little phylogenetic signal in the data. This was also verified by the small differences in results between MCMCglmm models that were run with and without phylogenetic effects (see supporting information).

We investigated time series that differed considerably in duration ranging from seven to 103 years with a median of 30 years. It is easier to detect a linear trend in long time series, everything else being equal, so we also included the duration of each study as a covariate in the models. Variables were excluded from final reduced models if they increased DIC (Deviance Information Criterion, Spiegelhalter *et al.* 2002) values >2. Values reported are means or least squares means (LSM) and their SE. The entire data set is reported in the supporting information, and data files, including the models, are also available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bpg30>.

Results

CHANGING LAYING DATE AND CLUTCH SIZE

There was no indication that different populations of the same species showed consistent changes in laying date or clutch size. Estimates of repeatability (R) among species (each with at least two estimates) were not significant for mean change in laying date per year ($F = 1.53$, d.f. = 16,80, $P = 0.11$, $R = 0.21$), or mean change per degree Celsius ($F = 1.82$, d.f. = 14,52, $P = 0.06$, $R = 0.29$). Mean change in clutch size per year was also not significantly repeatable among species ($F = 0.29$, d.f. = 4,15, $P = 0.88$, $R = -0.55$), nor was mean change per degree Celsius ($F = 0.40$, d.f. = 2,13, $P = 0.68$, $R = -0.43$).

Although laying date has advanced, clutch size has not shown any significant change (Table 1). Laying date advanced by an average of 0.23 days per year when we analysed individual studies ('populations'), and 0.19 days per year when we analysed averages for each species (Table 1). For the median study duration of 30 years, this amounts to an advance of about 6 days. Change in laying date in relation to change in temperature advanced by more than 2 days per degree Celsius (Table 1). In contrast, clutch size has not changed over time or in relation to changes in temperature, for either populations or species (Table 1). If we restricted the analyses to populations or species with information on both change in laying date and change in clutch size, the results were qualitatively similar (results not shown).

QUESTION 1: IS EARLIER SPRING ARRIVAL LEADING TO EARLIER LAYING OR LARGER CLUTCHES?

First arrival dates in spring advanced an average (SE) of 0.42 days per year (0.053) in our sample ($N = 49$ species averages). Change in laying date was not significantly related to change in arrival date when change in laying date was estimated as change per year or change per degree Celsius in models that adjusted for phylogeny, duration of the study (in years) and migratory distance (Table 2). Similarly, change in clutch size was not related to change in arrival date when change in clutch size was estimated as change per year or change per degree Celsius (Table 2). Therefore, there was no indication that change in timing of migration affected laying date or clutch size.

QUESTION 2: IS EARLIER LAYING ASSOCIATED WITH INCREASING CLUTCH SIZE?

Across populations and species, laying date is advancing over time (per year) and in relation to temperature change (Table 1). Thus, we tested if change in the timing of laying was also related to change in clutch size. Indeed, species showing a greater increase in clutch size per year were also those that showed a greater advancement in laying date per year (Fig. 1; $P = 0.044$ from phylogenetic MCMCglmm, $P = 0.018$ from nonphylogenetic MCMCglmm; Table 3). However, change in clutch size per degree Celsius was not related to change in laying date per degree Celsius (Table 3).

QUESTION 3: WHAT ECOLOGICAL AND LIFE-HISTORY FACTORS INFLUENCE CHANGES IN THE TIMING OF LAYING?

Larger advances in laying date per year were associated with the number of broods, trophic level and habitat (Table 4). Species with multiple broods per season were advancing laying date [LSM (SE) = -0.352 (0.047) days per year] more than single [-0.216 (0.046)] brooded species (LSM from analyses in JMP controlling for species

Table 1. Change in laying date and clutch size of birds based on estimates for populations or species. Species estimates are based on averages for each species, whereas population estimates are based on individual studies (i.e. there may be more than one study per species). Statistical tests are one-sample *t*-tests for an estimate differing significantly from zero

	Population mean (SE)	<i>N</i>	<i>t</i>	<i>P</i>	Species mean (SE)	<i>N</i>	<i>t</i>	<i>P</i>
Change in laying date year ⁻¹	-0.231 (0.0244)	157	9.46	<0.0001	-0.188 (0.0344)	71	5.48	<0.0001
Change in clutch size year ⁻¹	0.003 (0.0047)	54	0.56	0.57	0.004 (0.0058)	39	0.67	0.51
Change in laying date (°C) ⁻¹	-1.937 (0.1459)	128	13.28	<0.0001	-2.047 (0.2214)	75	9.24	<0.0001
Change in clutch size (°C) ⁻¹	-0.026 (0.0435)	53	0.59	0.56	-0.036 (0.0585)	39	0.61	0.54

Table 2. Change in laying date per year and per °C in relation to first arrival date (FAD), log-transformed migration distance (Migr Dist) and duration of the study (*N* years). Analyses were conducted with MCMCglmm and included species as a random effect to control for the nonindependence of repeated studies of the same species. Analyses 'with phylogeny' adjusted for phylogenetic effects. *P* MCMC is the probability from linear models using Monte Carlo methods and Bayesian Markov Chain sampling. DIC is the Deviance Information Criterion for each model. See Materials and Methods for further details

Dependent variable	Predictors	Posterior mean	95% credibility interval		<i>P</i> MCMC	DIC
			Lower	Upper		
Change in laying date year ⁻¹	Without phylogeny					
	FAD	0.125	-0.069	0.348	0.262	31.33
	<i>N</i> years	0.003	-0.001	0.007	0.144	
	Migr Dist	-0.026	-0.201	0.141	0.796	
	With phylogeny					32.46
	FAD	0.116	-0.088	0.348	0.310	
	<i>N</i> years	0.003	-0.001	0.007	0.132	
Change in laying date (°C) ⁻¹	Migr Dist	-0.023	-0.196	0.179	0.806	
	Without phylogeny					
	FAD	-0.258	-1.533	0.771	0.654	208.91
	<i>N</i> years	-0.010	-0.028	0.008	0.266	
	Migr Dist	0.756	-0.122	1.629	0.098	
	With phylogeny					210.23
	FAD	-0.066	-1.238	1.159	0.928	
	<i>N</i> years	-0.010	-0.030	0.009	0.266	
	Migr Dist	0.758	-0.281	1.649	0.122	

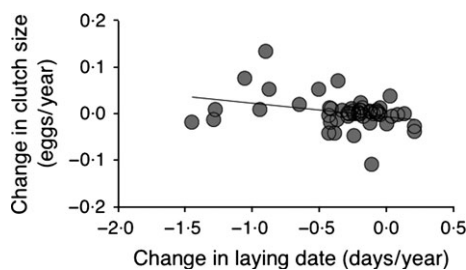


Fig. 1. Change in clutch size per year in relation to change in laying date per year for birds. The line is the linear regression line (Clutch size change/year = $-0.0057 + -0.0292 \times \text{mean laying date change/year}$; $r^2 = 0.10$, SE of slope = 0.0125, $F_{1,49} = 5.45$, $P = 0.024$).

identity). Laying date was also advancing at a slower rate among secondary consumers [-0.134 (-0.033) days per year] than primary [-0.403 (0.096)] or tertiary [-0.315 (0.073)] consumers (Tukey's HSD test, $P < 0.05$). The type of habitat (agricultural or not), northernmost breeding latitude and duration of the study were included in the final model, but individually they had nonsignificant effects on laying date ($P = 0.07$ and 0.182 , respectively,

Table 4; supporting information). Larger advances in laying date per degree Celsius were also associated with species that had multiple broods per season ($P = 0.04$, Table 4). Species with multiple broods advanced their laying date by 2.48 days per °C (4.00 - 0.99 95% CI), compared with 1.60 days per °C (2.25 - 0.97 95% CI) for species with single broods (Table 4). No other variables were related to change in laying date per degree Celsius (Table S1, Supporting information).

Species with multiple broods per season may be advancing their laying dates more than single-brooded species because the duration of the breeding season is increasing. Consistent with this hypothesis, the breeding season has been increasing in length for multibrooded species [LSM (SE) = 0.320 (0.085)] days per year, $N = 17$ species), and shortening for single-brooded species [LSM (SE) = -0.146 (0.115) days per year, $N = 10$ species; $F_{1,24} = 9.72$, $P = 0.005$]. This model controlled for the duration of the study (longer studies show a greater shortening of the breeding season; $F_{1,24} = 6.42$, $P = 0.019$) and northernmost breeding latitude (seasons are lengthening more at northern latitudes, $F_{1,24} = 5.33$, $P = 0.030$). The other ecological and life-history variables (Table 4)

Table 3. Change in clutch size per year and per °C in relation to change in laying date (per year and per °C), and duration of the study (*N* years). Analyses used MCMCglmm to control for the nonindependence of repeated studies of the same species and to adjust for phylogenetic effects. See Table 2 legend for more details

Dependent variable	Predictors	Posterior mean	95% credibility interval		<i>P</i> MCMC	DIC	
			Lower	Upper			
Change in clutch size year ⁻¹							
	Without phylogeny	Laydate year ⁻¹	-0.033	-0.059	-0.008	0.018	-210.43
		<i>N</i> years	0.000	0.000	0.001	0.330	
	With phylogeny	Laydate year ⁻¹	-0.031	-0.059	<-0.001	0.044	-208.71
		<i>N</i> years	<0.001	<-0.001	0.001	0.378	
Change in clutch size (°C) ⁻¹							
	Without phylogeny	Laydate °C ⁻¹	0.006	-0.027	0.034	0.688	-46.73
		<i>N</i> years	-0.002	-0.005	0.001	0.294	
	With phylogeny	Laydate °C ⁻¹	0.002	-0.026	0.035	0.874	-46.16
		<i>N</i> years	-0.002	-0.005	0.002	0.294	

Table 4. Change in laying date per year and per °C in relation to ecological and life-history variables. Variables in the initial full model included duration of the study (*N* years), number of broods per season (*N* Broods; one or at least two), northernmost latitude of breeding range (Latitude), trophic level (Trophic; three levels), habitat (farm or other), body mass and log-transformed migration distance (Migr Dist). Shown is the best reduced MCMCglmm for each dependent variable based on DIC values without adjustment for phylogenetic effects. See the supplementary information for additional analyses, including those adjusting for phylogeny. Analyses included species as a random effect to control for the nonindependence of repeated studies of the same species

Dependent variables	Predictors	Posterior mean	95% credibility interval		<i>P</i> MCMC
			lower	upper	
Change in laying date year ⁻¹ DIC = 34.23	Intercept	18.593	6.486	32.069	0.004
	<i>N</i> years	-0.005	-0.012	0.003	0.182
	<i>N</i> Broods (two +)	-0.121	-0.236	-0.017	0.044
	Latitude	0.008	0.000	0.017	0.080
	Trophic (secondary)	0.263	0.057	0.467	0.018
	Trophic (tertiary)	0.074	-0.185	0.324	0.566
	Habitat (other)	-0.136	-0.284	0.006	0.072
	First year of study	-0.010	-0.017	-0.004	0.002
Change in laying date (°C) ⁻¹ DIC = 421.52	Intercept	-1.599	-2.252	-0.972	<0.001
	<i>N</i> Broods (two +)	-0.880	-1.752	-0.027	0.041

did not provide an improvement in explanatory ability (delta AICc > 2) when added to this model. In this analysis, we only had one estimate of the duration of the breeding season for each species (*N* = 27 species).

QUESTION 4: ARE CHANGES IN LAYING DATE OR CLUTCH SIZE ASSOCIATED WITH RECENT POPULATION TRENDS?

Temporal changes in laying date (Table S2, Supporting information) and clutch size (Table S3, Supporting information) were not related to changes in population size during 1990–2000 (*P* > 0.96). Migration distance was also not related to population trends in either the full model or a reduced model (Table S4, Supporting information). Thus, we removed these variables from the analysis and used a reduced data set to investigate other ecological variables that might be related to recent population trends

(Table 5). Here, we found that single brooded and smaller (lower mass) species were more likely to be declining in the 1990s. Single-brooded species had a median population trend of -2 (i.e. 'moderately declining'; *N* = 73 studies), whereas double-brooded species had a median trend of 0 ('stable'; *N* = 109 studies). The reduced model also suggested that more northern species and those in agricultural habitat were more likely to be declining, but these effects were not significant on their own (Table 5).

POPULATION MODELS

Using our simulation model, we explored several possible explanations for the lack of relationship between changes in laying date and population size in published studies. In our base models, when mismatching was costly, population growth (lambda) decreased with increasing mismatch, as expected (Fig. 2a; dashed line). However, even when

Table 5. Population trends of birds (1990–2000) in relation to ecological and life-history variables. The data set contained 78 species (one value per species). Shown are the best reduced MCMCglms with (DIC = 268.52) and without (DIC = 267.70) adjustment for phylogenetic effects. A Poisson trait distribution was used in these analyses. See the supplementary information for analyses with laying date (Table S2, Supporting information) and clutch size (Table S3, Supporting information) change per year. Trophic level was not included in this model because there were too few data across all other categorical variables

		95% credibility interval		
	Posterior mean	Lower	Upper	<i>P</i> MCMC
Model without phylogeny				
Intercept	1.310	−0.344	2.862	0.128
Broods 1 or 2 (two+)	0.321	0.006	0.683	0.046
Latitude	−0.014	−0.036	0.012	0.260
Habitat (nonfarm)	0.304	−0.067	0.694	0.120
Body mass	0.000	0.000	0.001	0.034
Model with phylogeny				
Intercept	1.376	−0.196	2.946	0.100
Broods 1 or 2 (two+)	0.318	−0.028	0.679	0.088
Latitude	−0.014	−0.037	0.010	0.224
Habitat (nonfarm)	0.296	−0.093	0.720	0.164
Body mass	0.000	0.000	0.001	0.068

there was substantial nestling mortality (14–22%) that was unrelated to the timing of peaks in food abundance (i.e. mismatching *per se* was not costly), then lambda was not related to the level of mismatch (Fig. 2a; solid line). Using these models as a base, we next examined changes in population growth in relation to long-term changes in the timing of laying and food supply.

We modified the base models above by assuming a range in advancement of laying date (from 0.1 to 1 day per year) over a 75-year simulation. Based on data from a great tit population, we also assumed that the date of peak food abundance was advancing $0.5779 \text{ days year}^{-1}$ (Reed *et al.* 2013b). Under these conditions, if mismatching was costly, then populations were only stable when they were advancing laying date at about the same rate as the food supply (0.5–0.7 days per year; Fig. 2b – dashed line). At lower rates of advancement (<0.5), lambda was lower because of both the greater nestling mortality from producing young after the peak of food abundance and the slower rate of increase in clutch size over the 75-year simulation. At higher rates of advancement (>0.7), clutch size increased with earlier laying dates, but here there was also an increased nestling mortality cost from producing young before the peak of food abundance. In our second model, we did not include significant costs of mismatching (Fig. 2b, solid line), as in tree swallows. In this case, lambda increased linearly with advancing laying date, primarily because of increases in clutch size (nestling mortality did not change). Note that these models were not designed to be predictive of any particular species, but rather to simply illustrate the potential effects of

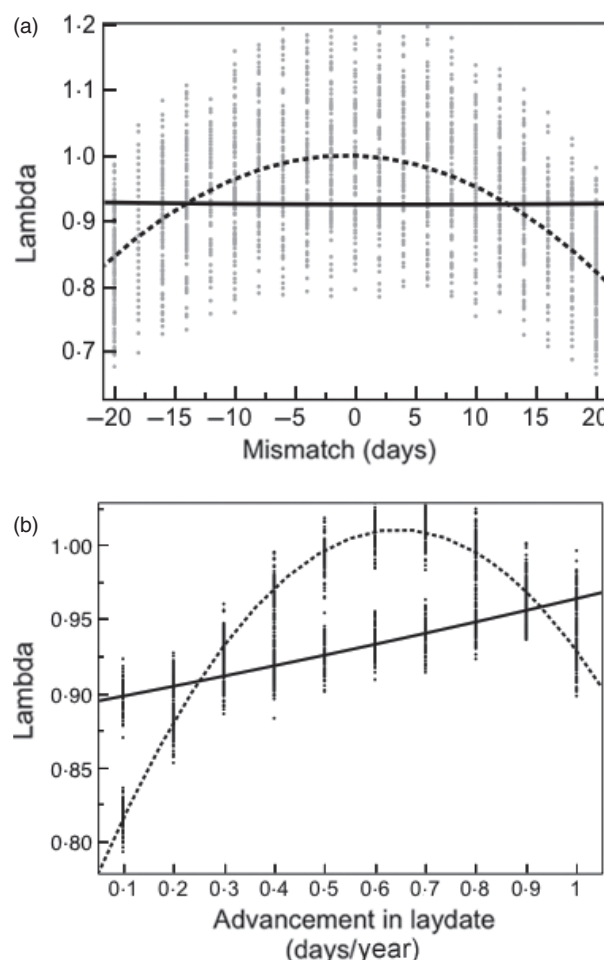


Fig. 2. Predicted rates of population increase (lambda) of model species under varying levels of mismatch between timing of laying and food supply (a) and advancement in laying date (b). Lines are from quadratic (dashed) and linear (solid) regressions through simulated lambda values for model species with (dashed) and without (solid) a cost of mismatching. For clarity, only individual lambda values (points) are shown for the mismatch model (dashed line) in panel a. See Methods and Supplemental Material for the models and additional explanation.

mismatching and changes in laying date using realistic parameters. As a consequence, we only interpret their general patterns.

Discussion

Global mean temperature has increased by more than $0.75 \text{ }^{\circ}\text{C}$ during the last century (IPCC 2007), and this general increase in temperature has advanced the phenology of a diverse array of organisms (Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2007; Dunn & Winkler 2010; Lehikoinen & Sparks 2010; Thackeray *et al.* 2010). Our survey of the literature attempted to find linkages between changes in phenology and population trends. Although arrival date has been linked to population trends (Jiguet *et al.* 2007; Møller, Rubolini & Lehikoinen 2008), we did

not find correlations between arrival date and laying date or clutch size, which might lead to changes in productivity and, ultimately, population trends. We did, however, find that laying date has advanced over time in response to increasing temperatures, and change in laying date was greater in species that had multiple broods per season, lived in nonagricultural habitats and were herbivorous or predatory (primary and tertiary consumers, respectively). Change in laying date was also negatively associated with change in clutch size, but neither of these variables was related to population trends. Thus, our comparative approach suggests that in most species mismatches in the timing of egg laying or the number of offspring have relatively little influence on population size compared with other aspects of phenology, ecology and life history.

On average, laying date in birds has advanced by 0.16 days per year (SE = 0.03) in our survey ($N = 71$ species; Table 1), but across all species, there was no consistent change in clutch size (Table 1). It may seem inconsistent, then, that there was a negative relationship between change in clutch size and change in laying date (Fig. 1). However, this relationship occurred because species with relatively large advances in laying date (>0.5 days per year) increased their clutch size, whereas most species have shown relatively little change in both laying date and clutch size (Fig. 1). Birds generally lay earlier in warmer springs (Dunn 2004), so if temperatures continue to warm, then we predict that more species will advance their laying dates and the average clutch size will start to increase for those species.

Although migratory birds are arriving earlier on the breeding grounds from their winter quarters, it does not seem to be affecting laying date (Table 2). Likewise, Rubolini, Saino & Møller (2010) showed that first song date (and hence the date when the reproductive season started as reflected by attempts of males to attract a mate) was responding more strongly to local change in temperature than migration distance. Change in laying date seems to be influenced more by other life history and ecological factors, such as diet and the number of broods, after controlling for when the study started (older studies have shown more change, Table 4). Laying date was advancing more for species that were herbivorous or predatory (primary and tertiary consumers) rather than insectivorous (secondary consumers). The implication is that species that eat insects (all of our secondary consumer species) are not experiencing as strong shifts in breeding resources or are less responsive to those shifts. A recent review of phenological change in 726 plant and animal taxa in the United Kingdom (between 1976 and 2005) also found that secondary consumers were advancing more slowly than primary producers or primary consumers (Thackeray *et al.* 2010). Other studies of phenological changes across trophic levels have been more variable with different rates of change at different trophic levels depending on the location (Visser & Both 2005; Primack *et al.* 2009). In terms of tertiary consumers (predators),

some previous single-population studies of sparrowhawks *Accipiter nisus* indicate that they are shifting their breeding dates more slowly than the insectivorous birds that they eat (Nielsen & Møller 2006; Both *et al.* 2009), which might be interpreted as an insufficient response by higher trophic levels to changing phenology of lower levels. However, we found the opposite; it was the higher trophic levels that were responding faster. In our sample, sparrowhawks had a relatively slow response (-0.049 days year $^{-1}$) compared with the average predatory species (-0.232 days year $^{-1}$).

Previous studies have found that double-brooded species differ from single-brooded species, particularly in terms of early arrival (Møller, Rubolini & Lehikoinen 2008; Vegvari *et al.* 2010; but see Van Buskirk, Mulvihill & Leberman 2009), earlier start of song activity (Rubolini, Saino & Møller 2010), laying earlier (in tit populations; Visser *et al.* 2003) and exhibiting positive population trends (Jiguet *et al.* 2007). We found that both laying date (Table 4) and duration of the breeding season have changed the most in species with a larger number of clutches. It is thought that double-brooded species advance their laying dates more than single-brooded species, because their reproductive success depends more on the duration of the entire season, rather than synchronizing their laying date with the peak of insect abundance, which is more important to single-brooded species (Crick, Gibbons & Magrath 1993; Møller, Rubolini & Lehikoinen 2008; Møller *et al.* 2010b). Indeed, in recent years, barn swallows *Hirundo rustica* have advanced the laying date of first clutches and the interval between first and second clutches has increased (Møller 2007). As a consequence, parents with longer intervals between clutches were able to rear more offspring, and females with two clutches per year survived better when the interval between clutches was long, while males survived less well (Møller 2007). Thus, a longer breeding season should benefit double-brooded species more than single-brooded species. Consistent with this hypothesis, Jiguet *et al.* (2007) found that population trends of 71 terrestrial species in France (based on field surveys) were positively associated with the number of broods per year. We found the same pattern, even though our analysis used a different method of estimating population trends (Birdlife International 2004) and combined data from 71 terrestrial and aquatic species from throughout Europe and 8 species from North America.

A longer breeding season and increased productivity for double-brooded species might ultimately result in larger or more stable populations, and, indeed, we found that most populations of double-brooded species were stable in recent years (1990–2000), whereas most populations of single-brooded species were declining. Previous studies of migratory birds in Europe have found that declining species have not been advancing their spring arrival date as much as species that are stable or increasing in size (Møller, Rubolini & Lehikoinen 2008). Declining species have also been arriving on the breeding grounds later in the season when it is warmer (more accumulated

degree-days; Saino *et al.* 2011). If arrival date is tied to ecological mismatching and population declines, then we would also expect to see mismatching in terms of laying date and, possibly, clutch size. Indeed, it is the timing of egg laying that is most often discussed in terms of synchronizing the energetic needs of growing nestlings with the food supply. However, we did not find any association between changes in arrival date and changes in laying date (or clutch size), nor any association between them and population trend.

One notable difference between this study and previous surveys is that we included both migratory and resident species in the analysis of population trends [we analysed 19 resident species ($N = 79$) compared with four in the study of Møller, Rubolini & Lehikoinen 2008 and none in Saino *et al.* 2011]. However, migration distance was not a significant predictor of population size trend when added to our final model (Table S4, Supporting information), and it is possible for both resident and migratory species to mistime their reproduction in a changing environment (reviewed by Both 2010). Our population trend estimates primarily came from the same source as previous studies (Birdlife International 2004) and our sample sizes were also similar to previous studies ($N = 148$ for change in laying date and population trends).

There was little evidence of phylogenetic effects in our analyses of phenology or population trends. MCMCglmm models that did not include phylogenetic effects, based on DIC values, were as informative, if not more so, than models that did include phylogenetic effects, and the repeatability of estimates among species was weak and nonsignificant. Thus, species and populations appear to respond to climate change independently of phylogenetic history. Previous studies of arrival dates (Van Buskirk, Mulvihill & Leberman 2009) and population trends (Møller, Rubolini & Lehikoinen 2008) have also found weak phylogenetic effects.

Mismatches between the timing of breeding and the resources needed to produce offspring have become widely cited as one of the negative consequences of climate change, because they should lead to lower productivity and smaller population size. However, most of the evidence comes from long-term studies of just a few species: pied flycatchers (Both *et al.* 2006; Both 2010) and great tits (Reed *et al.* 2013b; Vedder, Bouwhuis & Sheldon 2013). In great tits, mismatches can lead to lower reproductive success, but this appears to lead to lower density in the autumn and increased survival overwinter, and, as a consequence, subsequent breeding population size remains stable (Reed *et al.* 2013b). Thus, our comparative study draws attention to an important question: why is phenological mismatch apparently detrimental to reproductive success and population size in some populations but not in others?

Variation between populations may be related to the assumptions of the mismatch hypothesis (Durant *et al.* 2007), including strong seasonality of resources and 'bottom-up' control of population size (i.e., food

resources limit population size, rather than predators [top-down] or weather). As a consequence, the mismatch hypothesis predicts that when broods are mistimed, there will be less food available and, as a consequence, reproductive success will be lower. However, this focus on timing ignores the abundance of food, which also affects reproductive success. For example, it is possible for even a mistimed brood to be successful if food is superabundant during most of the breeding season (Dunn *et al.* 2011). Thus, the lack of relationship between changes in laying date or clutch size and population trend could be due to: (1) little cost of mismatching (as in tree swallows; Dunn *et al.* 2011), or (2) a cost of mismatching, but compensatory demographic mechanisms, such as density-dependent survival that buffer changes in population size (as in great tits; Reed *et al.* 2013b). Our models (Fig. 2) and the model of Reed *et al.* (2013b) show that stable populations can occur under both of these scenarios. Interestingly, there is considerable variation in the extent of mismatching between species (Review in Table 3 in Dunn *et al.* 2011), and even populations, implying that there is scope for further comparative analyses.

Our results for a variety of species suggest that mistiming of laying (and potentially nonoptimal clutch sizes, as a consequence) are not related to recent population trends. This suggests that recent correlations between population trends and arrival dates (Møller, Rubolini & Lehikoinen 2008) or spring degree-days (Saino *et al.* 2011) are not operating through changes in laying date or clutch size as assumed by the mismatch hypothesis. Instead, these correlations could occur as a consequence of warmer weather during other times of the year that affect survival or reproduction. In any case, our results caution that changes in population size caused by climate change are complex (reviewed by Adahl, Lundberg & Jonzen 2006) and may require different hypotheses for different types of species (e.g. single vs. double-brooded).

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bp3g0> (Dunn & Møller 2014).

References

- Adahl, E., Lundberg, P.E.R. & Jonzen, N. (2006) From climate change to population change: the need to consider annual life cycles. *Global Change Biology*, **12**, 1627–1633.
- Birdlife International B (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. Birdlife International, Cambridge, UK.

- Both, C. (2010) Food availability, mistiming and climatic change. *Effects of Climate Change on Birds* (eds A.P. Møller, W. Fiedler & P. Berthold), pp. 129–147. Oxford University Press, Oxford, UK.
- Both, C. & Visser, M.E. (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, C.M. & Visser, M.E. (2006) Climate change and population declines in a long distance migratory bird. *Nature*, **441**, 81–83.
- Both, C., van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.
- Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. & Foppen, R.P.B. (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London B*, **277**, 1259–1266.
- Cramp, S. & Perrins, C.M. (1977–1994) *The Birds of the Western Palearctic*. Oxford University Press, Oxford, UK.
- Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (1993) Seasonal changes in clutch size in British birds. *Journal of Animal Ecology*, **62**, 263–273.
- Dunn, P. (2004). Breeding dates and reproductive performance. *Birds and Climate Change* (eds A.P. Møller, W. Fiedler & P. Berthold), pp. 69–87. Elsevier, Amsterdam, The Netherlands.
- Dunn, P.O. & Winkler, D.W. (2010) Effects of climate change on timing of breeding and reproductive success in birds. *Effects of Climate Change on Birds* (eds A.P. Møller, W. Fiedler & P. Berthold), pp. 113–128. Oxford University Press, Oxford, UK.
- Dunn, P.O., Thusius, K.J., Kimber, K. & Winkler, D.W. (2000) Geographic and ecological variation in clutch size of tree swallows. *The Auk*, **117**, 215.
- Dunn, P.O., Winkler, D.W., Whittingham, L.A., Hannon, S.J. & Robertson, R.J. (2011) A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? *Ecology*, **92**, 450–461.
- Durant, J.M., Hjermann, D.Ø., Ottersen, G. & Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A. *et al.* (2010) Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*, **80**, 3–48.
- Falconer, D.S. & Mackay, T.F.C. (1996) *Introduction to Quantitative Genetics*, 4th edn. Longman, New York, NY.
- Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.
- IPCC. (2007) Climate Change 2007: The Physical Science Basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor & H.L. Miller) Cambridge University Press, Cambridge, UK.
- Jiguet, F., Gadot, A.S., Julliard, R., Newson, S.E. & Couvet, D. (2007) Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology*, **13**, 1672–1684.
- Lehikoinen, E. & Sparks, T.H. (2010) Changes in migration. *Effects of Climate Change on Birds* (eds A.P. Møller, W. Fiedler & P. Berthold), pp. 89–112. Oxford University Press, Oxford, UK.
- Møller, A.P. (2007) Interval between clutches, fitness and climate change. *Behavioral Ecology*, **18**, 62–70.
- Møller, A.P., Fiedler, W. & Berthold, P. (eds.) (2010a) *Effects of Climate Change on Birds*. Oxford University Press, Oxford, UK.
- Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences USA*, **105**, 16195–16200.
- Møller, A.P., Flensted-Jensen, E., Klarborg, K., Mardal, W. & Nielsen, J.T. (2010b) Climate change affects the duration of the reproductive season in birds. *Journal of Animal Ecology*, **79**, 777–784.
- Nielsen, J.T. & Møller, A.P. (2006) Effects of food abundance, density and climate change on reproduction in the sparrowhawk *Accipiter nisus*. *Oecologia*, **149**, 505–518.
- Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860–1872.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–40.
- Poole, A. (ed.) (2005) The Birds of North America Online: <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/BNA/>. Cornell Laboratory of Ornithology, Ithaca, NY.
- Primack, R.B., Ibáñez, I., Higuchi, H., Lee, S.D., Miller-Rushing, A.J., Wilson, A.M. *et al.* (2009) Spatial and interspecific variability in phenological responses to warming temperatures. *Biological Conservation*, **142**, 2569–2577.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, T.E., Jenouvrier, S., Visser, M.E. & Roulin, A. (2013a) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, **82**, 131–144.
- Reed, T.E., Grotan, V., Jenouvrier, S., Sæther, B.E. & Visser, M.E. (2013b) Population growth in a wild bird is buffered against phenological mismatch. *Science*, **340**, 488–491.
- Roff, D.A. (2002) *Life History Evolution*. Sinauer Associates, Sunderland, MA.
- Root, T.R., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Rowe, L., Ludwig, D. & Schluter, D. (1994) Time, condition, and the seasonal decline of avian clutch size. *American Naturalist*, **143**, 698–772.
- Rubolini, D., Saino, N. & Møller, A. (2010) Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, **42**, 45–55.
- Rubolini, D., Møller, A.P., Rainio, K. & Lehikoinen, E. (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, **35**, 135–146.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenza, A., Huppert, K. *et al.* (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society of London B*, **278**, 835–842.
- SAS (2012) *JMP Version 10*. SAS Institute Inc., Cary, NC.
- Sauer, J.R. & Link, W.A. (2011) Analysis of the North American breeding bird survey using hierarchical models. *Auk*, **128**, 87–98.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B*, **64**, 583–639.
- Stevenson, I.R. & Bryant, D.M. (2000) Climate change and constraints on breeding. *Nature*, **406**, 366–367.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R. *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.
- Torti, V.M. & Dunn, P.O. (2005) Variable effects of climate change on six species of North American birds. *Oecologia*, **145**, 486–495.
- Van Buskirk, J., Mulvihill, R.S. & Leberman, R.C. (2009) Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biology*, **15**, 760–771.
- Vedder, O., Bouwhuis, S. & Sheldon, B.C. (2013) Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biology*, **11**, e1001605.
- Végvári, Z., Bókonyi, V., Barta, Z. & Kovács, G. (2010) Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology*, **16**, 1–11.
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London B*, **272**, 2561–2569.
- Visser, M.E., Adriaenssens, F., Van Balen, J.H., Blondel, J., Dhondt, A.A., Van Dongen, S. *et al.* (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London B*, **270**, 367–372.
- Wilson, S. & Arcese, P. (2003) El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Sciences USA*, **100**, 11139–11142.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Phylogenetic tree of 89 species.

Table S1. Change in laying date per °C in relation to ecological and life-history variables.

Table S2. Population trends of birds (1990–2000) in relation to ecological and life-history variables, including change in laying date

(per year).

Table S3. Population trends of birds (1990–2000) in relation to ecological and life-history variables, including change in clutch size (per year).

Table S4. Population trends of birds (1990–2000) in relation to ecological and life-history variables, including migration distance.

Data S1. File with data on changing phenology and population size of birds ($N = 196$ studies).