

Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology

Marketa Zimova¹  | David E. Willard² | Benjamin M. Winger³  | Brian C. Weeks¹ 

¹School for Environment and Sustainability,
University of Michigan, Ann Arbor, MI, USA

²Gantz Family Collection Center, The Field
Museum, Chicago, IL, USA

³Museum of Zoology and Department of
Ecology and Evolutionary Biology, University
of Michigan, Ann Arbor, MI, USA

Correspondence

Marketa Zimova

Email: mzimovaa@umich.edu

Funding information

Institute for Global Change Biology at the
University of Michigan

Handling Editor: Elizabeth Derryberry

Abstract

1. Advancements in phenology and changes in morphology, including body size reductions, are among the most commonly described responses to globally warming temperatures. Although these dynamics are routinely explored independently, the relationships among them and how their interactions facilitate or constrain adaptation to climate change are poorly understood.
2. In migratory species, advancing phenology may impose selection on morphological traits to increase migration speed. Advancing spring phenology might also expose species to cooler temperatures during the breeding season, potentially mitigating the effect of a warming global environment on body size.
3. We use a dataset of birds that died after colliding with buildings in Chicago, IL to test whether changes in migration phenology are related to documented declines in body size and increases in wing length in 52 North American migratory bird species between 1978 and 2016. For each species, we estimate temporal trends in morphology and changes in the timing of migration. We then test for associations between species-specific rates of phenological and morphological changes while assessing the potential effects of migratory distance and breeding latitude.
4. We show that spring migration through Chicago has advanced while the timing of fall migration has broadened as a result of early fall migrants advancing their migrations and late migrants delaying their migrations. Within species, we found that longer wing length was linked to earlier spring migration within years. However, we found no evidence that rates of phenological change across years, or migratory distance and breeding latitude, are predictive of rates of concurrent changes in morphological traits.
5. These findings suggest that biotic responses to climate change are highly multidimensional and the extent to which those responses interact and influence adaptation to climate change requires careful examination.

KEYWORDS

adaptation, biotic responses, body size, climate change, migration speed, migratory birds, museum collections, wing length

1 | INTRODUCTION

Changes in morphology, life history and geographical range in response to anthropogenic climate change have been recorded across a wide range of taxa (Parmesan & Yohe, 2003; Root et al., 2003; Scheffers et al., 2016; Thackeray et al., 2016; Walther et al., 2002). Shifts in these three axes of adaptation are predicted to be widespread responses to global warming (Gardner et al., 2011). Although changes in each of these dimensions are often explored independently in relation to warming temperatures, the interactions among them are likely complex. For example, there is some evidence of a coupled relationship between phenological and morphological changes (Eastman et al., 2012; Ozgul et al., 2010; Van Gils et al., 2016). Other studies have found that changes in phenology could mitigate the need for changes in geographical range (Bennett et al., 2015; Socolar et al., 2017). However, owing to the sparsity of long-term datasets that contain data on multiple dimensions of biotic responses to climate change, phenological, biogeographical and morphological changes tend to be studied individually, and the role of interactions among them in facilitating or constraining adaptation to climate change remains poorly understood.

Phenological shifts in seasonal migration are thought to be largely driven by the need to minimize mismatches between the timing of breeding and seasonal pulses in the availability of food as warming temperatures change the phenology of resource bases (Cohen et al., 2018; Kharouba et al., 2018). There is broad evidence that birds have advanced their timing of spring migration, breeding site arrival and clutch initiation in recent decades, though there is also ample interspecific variation in these responses (Bitterlin & Van Buskirk, 2014; Dorian et al., 2020; Gordo & Sanz, 2006; Hällfors et al., 2020; Usui et al., 2017; Van Buskirk et al., 2009). By contrast, shifts in fall migration phenology appear to be less consistent (Bitterlin & Van Buskirk, 2014; Chambers et al., 2014; Jenni & Kéry, 2003; Lehikoinen et al., 2004; Mills, 2005; Van Buskirk et al., 2009). The proximate mechanisms facilitating phenological shifts in migration are often unclear (Horton, Van Doren, et al., 2019; Knudsen et al., 2011). Most studies report individual modification of the speed of migration, a dynamic that could involve adjustments to stopover frequency and duration (Haest et al., 2020; Lameris et al., 2018; Oliver et al., 2020; Schmaljohann, 2018; Schmaljohann & Both, 2017) or flight speed (Corman et al., 2014).

Changes in avian morphology over recent decades, notably in wing shape and length, have largely been ascribed to changing thermoregulatory needs imposed by warming temperatures (Gardner et al., 2014, 2019; Yom-Tov et al., 2006) or selection on birds' dispersal abilities in altered habitats (Desrochers, 2010; Martin et al., 2017; Moreno-Rueda & Rivas, 2007). In migratory birds, there is evidence linking the morphology of the flight apparatus and the phenology of migration, raising the possibility of a connection between shifting phenology and wing morphology. For example, lower wing loading (smaller mass relative to wingspan) and higher wing aspect ratio (longer, more pointed wings) yield more efficient

flight (Claramunt et al., 2012; Kipp, 1958; Pennycuick, 2008). Within species, individuals with higher aspect ratios have been shown to migrate faster or arrive earlier to their breeding grounds in spring (Bowlín, 2007; Cooper et al., 2011; Hahn et al., 2016; Potti, 1998). The documented interactions between morphological traits, flight performance and migration phenology suggest that phenological changes due to climate change may impose selection pressures on morphology to increase flight efficiency. For example, increased selection pressure to migrate faster to arrive earlier on the breeding grounds (Alerstam, 2011; Giery & Layman, 2019; Kokko, 1999; Nilsson et al., 2013; Spottiswoode et al., 2006) might drive morphological shifts towards longer, more-pointed wings or lower wing loading. Such morphological changes could be adaptive if they increase flight speed (Corman et al., 2014) or if they reduce refueling needs on migration due to improved flight efficiency (Bowlín & Wikelski, 2008; Burns, 2003; Lank et al., 2017). However, the extent to which selection to adjust migration phenology has involved adaptive shifts in morphological traits related to flight speed and efficiency is largely unknown, particularly in the context of recent phenological shifts.

Changes in overall body size driven by climate change may also interact with phenological shifts. Body size declines have largely been attributed to increasing temperatures (Audzijonyte et al., 2020; Baudron et al., 2014; Daufresne et al., 2009; Forster et al., 2012; Gardner et al., 2011; Sheridan & Bickford, 2011; Weeks et al., 2020a). In endothermic species, smaller bodies are more efficient at dissipating heat (Speakman & Król, 2010) which is advantageous in a warmer climate (Bergmann, 1847; Mayr, 1956). Recent increases in temperature have been suggested to yield body size reductions in birds through natural selection against larger size (Prokosch et al., 2019; Van Buskirk et al., 2010) or via developmental plasticity that yields smaller adult body size when developing nestlings become heat stressed (Andrew et al., 2017; Cunningham et al., 2013). However, phenological shifts might mitigate this response to climate change. For example, Socolar et al. (2017) suggested that if birds advance their nesting phenology such that broods develop earlier in spring, they may not require geographical range shifts to maintain their thermal niches as climates warm. By similar logic, if advancing migration phenology results in species breeding earlier in the season, this may offset the effect of rising temperatures in the breeding range and reduce the effect of increasing temperature on body size. Yet, the interaction between shifts in migratory phenology and body size are largely unknown.

Here, we test the relationships between shifts in migratory phenology and changes in morphology in 52 species of North American birds. We do this using a four-decade dataset that includes morphological trait and migration phenology data from salvaged window-killed specimens in Chicago, IL (Weeks et al., 2020a). These birds collided with buildings during their spring and fall migrations between their breeding ranges (north of Chicago) and wintering grounds (south of Chicago; Figure 1). From 1978 to 2016, nearly all species experienced both declines in body size (as indicated by tarsus length, mass and a multivariate principal

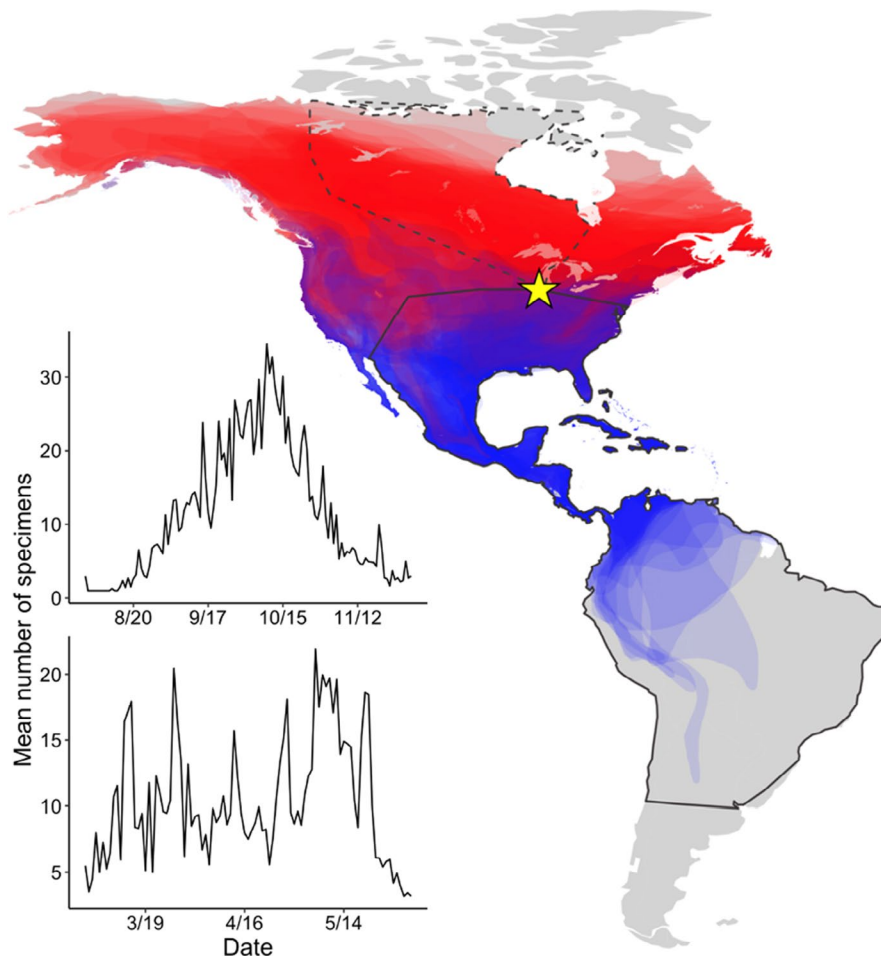


FIGURE 1 The 52 species in this study were collected in Chicago (star) as they migrated between their breeding ranges (red) and wintering grounds (blue). Solid and dashed lines depict likely destinations, based on known migratory paths. Plots show the mean number of specimens collected on each day in fall (top) and spring (bottom) from 1978 to 2016

components-based index) and simultaneous increases in relative wing length (Weeks et al., 2020a). Weeks et al. (2020a) attributed the observed body size reductions to warming summer temperatures on the breeding grounds but did not test for phenological shifts. They also proposed that the increases in wing length may be a result of selection to maintain migration by increasing flight efficiency, as an adaptive compensation for the increased energetic costs of flight as the species got smaller. Here, we test whether increasing wing length could alternatively be explained by selection imposed by advancing migration phenology to increase migration speed.

We take a three-part approach to testing the relationship between shifts in migratory phenology and morphological change. First, to characterize how individual morphology and migration phenology interact, we test whether individuals with longer wing length relative to their body size migrate through Chicago earlier in the year. Based on previous studies (Bowlin, 2007; Cooper et al., 2011; Hahn et al., 2016; Potti, 1998), we predict that longer-winged birds will migrate earlier in the spring. Second, we characterize how the timing of migration through Chicago has changed over the past 40 years, predicting an advancement in spring phenology. Third, we assess whether rates of change in morphology are correlated with rates of change in migration phenology. If selection pressure to advance phenology is driving the observed

increases in wing length, we predict faster increases in wing length in species that have advanced their spring phenology the most. Likewise, if phenological shifts towards earlier breeding season are mitigating the influence of warming summer temperatures on body size, we predict slower rates of body size declines in those species that have advanced their phenology the most. We also test whether the rates of change in fall migration phenology are associated with changes in wing length and body size, though the expected nature of these relationships is less clear than for spring migration (Knudsen et al., 2011).

The magnitude of recent warming has been greater at higher latitudes (IPCC, 2013), suggesting that breeding latitude may influence the degree to which species have advanced phenology or experienced changes in morphology. Additionally, the capacity of species to adjust their migratory phenology or morphology may depend on their migratory distance, as longer-distance migrants are thought to have more limited ability to respond to phenological changes on distant breeding grounds and potentially greater constraints on morphological adjustments given their physiologically demanding journeys (Møller et al., 2017; Rubolini et al., 2010). Therefore, we leverage the diversity of breeding latitudes and migratory distances among the 52 species in this dataset to assess how these variables mediate patterns of phenological and morphological changes.

2 | MATERIALS AND METHODS

2.1 | Dataset

We use a museum dataset from Weeks et al. (2020a) that includes 70,716 bird specimens from 52 species of North American migratory birds, spanning 11 families and 30 genera. Fifty of 52 species are passerines, with one rail *Porzana carolina* and one woodpecker *Sphyrapicus varius* (Table S1). These specimens were salvaged after they died following collisions with buildings in Chicago, IL, which is one of the most dangerous cities in the United States for building collisions driven by artificial light at night (Horton, Nilsson, et al., 2019; Winger et al., 2019). Collision monitoring and collection of individuals were conducted every year from 1978 to 2016 when species fly through Chicago during spring migration (around March 1 to May 31) and again during the fall migration (around August 15 to early November; Figure 1). Specimens were collected the morning after death for nocturnal collisions or within a day of death for diurnal collisions. Therefore, collection date was used as an index of each individual's passage date through Chicago. The date was transformed into Julian day (day 1 = January 1st). We assume that the passage dates through Chicago are a reasonable proxy for relative timing of arrival on the breeding grounds in the spring.

A single person (D.E.W.) measured tarsus length using digital calipers, wing length using a wing rule and mass using a digital scale of each individual carcass prior to preparation as a museum specimen. Weeks et al. (2020a) found that both tarsus and mass declined through time in most species in the dataset, as did the first principal component of a multivariate dataset that also included bill length. The length of the tarsus relative to body size varies widely across bird species depending on their ecology and behaviour and is therefore a poorer proxy than mass for interspecific differences in body size. However, tarsus is a more sensitive indicator of intraspecific variation in body size than mass due to rapid changes in mass that occur throughout migration depending on body condition, energetics and food availability (Rising & Somers, 1989; Senar & Pascual, 1997). Therefore, following Weeks et al. (2020a), we focus on tarsus length as the best index of recent body size change. Individuals were sexed based on gonadal inspection and aged based on skull ossification to Hatch Year (fall birds hatched that summer) and After Hatch Year (all spring birds and all fall birds at least one year old). To model the relationship between phenology and migration, we followed Weeks et al. (2020a) and included only 52 species that had 100 or more specimens with all morphological measurements throughout the study period and at least 10 specimens measured per decade. All results are qualitatively similar when including only species ($n = 22$) that had 500 or more specimens with morphological measurements throughout the study period, with at least 100 measurements per decade (Tables S2–S5).

All species in our dataset are migratory. For each species, migratory distance was calculated as the great-circle distance (or

orthodromic distance; the shortest distance between two points on the surface of a sphere) between their breeding and wintering range centroids (Table S1). The range centroids were based on breeding and wintering ranges (BirdLife International, 2015) that were cropped to exclude unlikely breeding destinations for birds migrating through Chicago, IL (see Weeks et al., 2020a for details; Figure 1).

2.2 | Relationship between wing length and within-year migration phenology

All generalized linear mixed models (GLMMs) were implemented in the MCMCGLMM package (Hadfield, 2010) in R (R Core Team, 2018). To test whether wing length predicts intra-annual variation in spring and fall migration phenology, we modelled Julian day as a function of the logarithm of relative wing length (i.e. $\log(\text{wing length}/\text{tarsus length})$), with sex, age and year (transformed to start at zero in 1978) included as fixed effects. Additionally, we ran an identical set of models but instead of using relative wing length, we included both the logarithm of tarsus and the logarithm of wing length as predictors to test the potential effect of using a ratio in the model. Spring and fall data were modelled separately.

We accounted for phylogenetic relatedness by including phylogeny as a random effect in the models. The phylogenetic variance covariance matrix was based on 1,000 ultrametric trees from the posterior distribution of a global phylogeny of birds (Jetz et al., 2012) based on the backbone phylogeny of Hackett et al. (2008). The posterior distribution was used to generate a 50% majority-rule consensus tree with DendroPy (Sukumaran & Holder, 2010), following Rubolini et al. (2015). In brief, bifurcations were included in the consensus when they occurred in >50% of the trees from the posterior distribution, and if a branching event was not supported in >50% of the trees, a polytomy was formed. Branch lengths were calculated with the SumTrees function in DendroPy (Sukumaran & Holder, 2010), which assigns ages to nodes based on the median ages of those nodes across the posterior distribution of input trees.

All GLMMs were run for 120,000 iterations with a burn-in of 20,000 iterations and a thinning interval of 100 iterations. We used diffuse normal priors for the fixed effects (mean 0, variance 10^8) and an uninformative inverse-Wishart distribution with $V = 1$ and $nu = 0.002$ for the random effect, following the recommendations of Hadfield (2010). We examined trace plots to ensure proper chain mixing and checked for autocorrelation between samples (all values were <0.1). The strength of phylogenetic signal was calculated as the proportion of variance attributable to the phylogenetic relationships (Hadfield & Nakagawa, 2010) which is equivalent to Pagel's λ (Housworth et al., 2004).

2.3 | Shifts in migration phenology across years

To quantify shifts in spring and fall migration phenology, we tested whether the early, median and late dates of migration through

Chicago have changed over the past 40 years using linear mixed-effects models in the `lme4` package (Bates et al., 2015). For each year, we calculated the early, median and late passage dates as 5th, 50th and 95th sample percentiles, respectively, for each species. Next, we modelled those passage dates as a function of year (transformed to start at zero) with a random intercept and slope for year for each species. We included two interaction terms between year and migratory distance and year and mean breeding range latitude in the models to test the effect of migratory distance and breeding range latitude, respectively, on the degree of phenological shifts. Migratory distance and breeding range latitude, both estimated at the species level, were centred and standardized to have a mean of zero and standard deviation of 1 in all analyses.

2.4 | Relationship between phenological and morphological shifts

We tested whether shifts in migration phenology predict shifts in relative wing and tarsus length over time. For each species, we calculated rates of change in spring and fall migration phenology as the rates of change in spring and fall passage dates during 1978–2016 using linear mixed-effects models. In these models, Julian day was modelled as a function of year (transformed to start at zero), sex and age as fixed effects and random intercepts and slopes for year for each species. Spring and fall were modelled separately. The resulting random slopes represent species-specific rates of spring or fall passage date change over the past four decades in days per year.

Data on rates of change in morphology were obtained following Weeks et al. (2020a), who quantified species-specific values of rates of change in tarsus and relative wing lengths in percent per year using the same dataset. The logarithm of wing length and tarsus length was each modelled as a function of year (transformed to start at zero), sex and age as fixed effects and random intercepts and slopes for year were estimated for each species using linear mixed-effects models. Because both wing and tarsus lengths were log-transformed prior the analyses, the resulting random slopes represent species-specific rates of percent change in tarsus or wing length per year, a measure that is directly comparable between differently sized species. The model estimating rates of change in the logarithm of wing length also included the logarithm of tarsus length as a fixed effect, which is equivalent to using relative wing length (the logarithm of wing length/tarsus length), as the dependent variable.

We then tested for associations between the species-specific rates of phenological and morphological changes using phylogenetic generalized least squares (PGLS) models in the `ape` package (Paradis et al., 2004; Pinheiro et al., 2013). To test whether phenological shifts imposed selection on wing morphology to increase migration speed, we modelled species' rates of change in relative wing length as a function of their rates of change in phenology. Next, to test whether advancing spring phenology mitigated the effects of warming on body size declines, we modelled species' rates

of change in tarsus length as a function of their rates of change in phenology. In these models, we also included migration distance (scaled) and breeding range latitude (scaled) as covariates to examine their effect on rates of change in morphology. To account for non-independence of observations caused by phylogenetic relatedness, we incorporated the same phylogenetic variance covariance matrix as described above. All PGLS models were fit using a Brownian motion model of evolution with simultaneous estimation of Pagel's λ (Pagel, 1999).

2.5 | Comparison of estimated migration phenology with eBird data

To assess whether our collision dataset is a reliable reflection of migration phenology within and across years, we compared it to citizen science observations from eBird (Sullivan et al., 2009; www.ebird.org, 'basic' dataset, accessed 1 May 2020). We downloaded observations for the 52 species for Cook County, IL, where Chicago is located, during the spring and fall migration periods (1 March–31 May, 1 August–30 October). We only used observations from the last 10 years (2007–2016), owing to the low sampling effort in earlier years. Using these data, we calculated the 5th, 50th and 95th passage dates for each species for each year (i.e. the same statistics we calculated for our collision dataset).

To test whether the collision data reflect annual migration phenology for each year, we modelled each collision-based passage date (collision passage date) as a function of its equivalent eBird-based passage date (eBird passage date) using linear models. Second, to assess whether the collision data collection was consistent over time (i.e. did not bias our estimates of phenological shifts), we modelled the residuals derived from regressing the collision passage dates on eBird passage dates as a function of year using linear models. We run separate models for each phenology date (i.e. 5th, 50th and 95th passage date) and season.

3 | RESULTS

3.1 | Relationship between wing length and within-year migration phenology

We found a strong association between relative wing length and spring migration phenology, but no relationship between relative wing length and fall migration phenology (Table 1). After controlling for phylogeny and species identity, individuals with longer wings relative to their body size migrated through Chicago earlier in the spring (-10.242 , 95% CI $[-13.197, -7.0498]$, $p < 0.001$; Table 1). Phylogenetic signal was strong in spring and fall with $\lambda = 0.950$ and $\lambda = 0.913$, respectively (Table 1). The effects of relative wing length on intra-annual migration phenology were similar when we used tarsus length and wing length as separate predictors instead of relative wing length (Table S6).

TABLE 1 Increased relative wing length is associated with earlier migration in the spring but not the fall. We modelled the effects of relative wing length on spring and fall mean passage date of 52 North American migratory bird species during the period 1978–2016, while controlling for year, sex, age and phylogeny. SexM denotes males and AgeHY denotes hatch year birds

Coefficient	Estimate	Lower CI	Upper CI	MCMC p-value	Pagel's λ (95% CI)
Spring					
Intercept	131.362	91.732	172.018	<0.001	0.950 (0.932, 0.969)
Year	−0.0415	−0.0524	−0.0291	<0.001	
SexM	−6.801	−7.0624	−6.553	<0.001	
Relative wing	−10.242	−13.197	−7.0498	<0.001	
Fall					
Intercept	274.493	236.919	315.387	<0.001	0.913 (0.879, 0.941)
Year	−0.0338	−0.0461	−0.0202	<0.001	
SexM	2.350	2.0924	2.600	<0.001	
AgeHY	−1.740	−2.0443	−1.450	<0.001	
Relative wing	−1.199	−4.792	1.868	0.458	

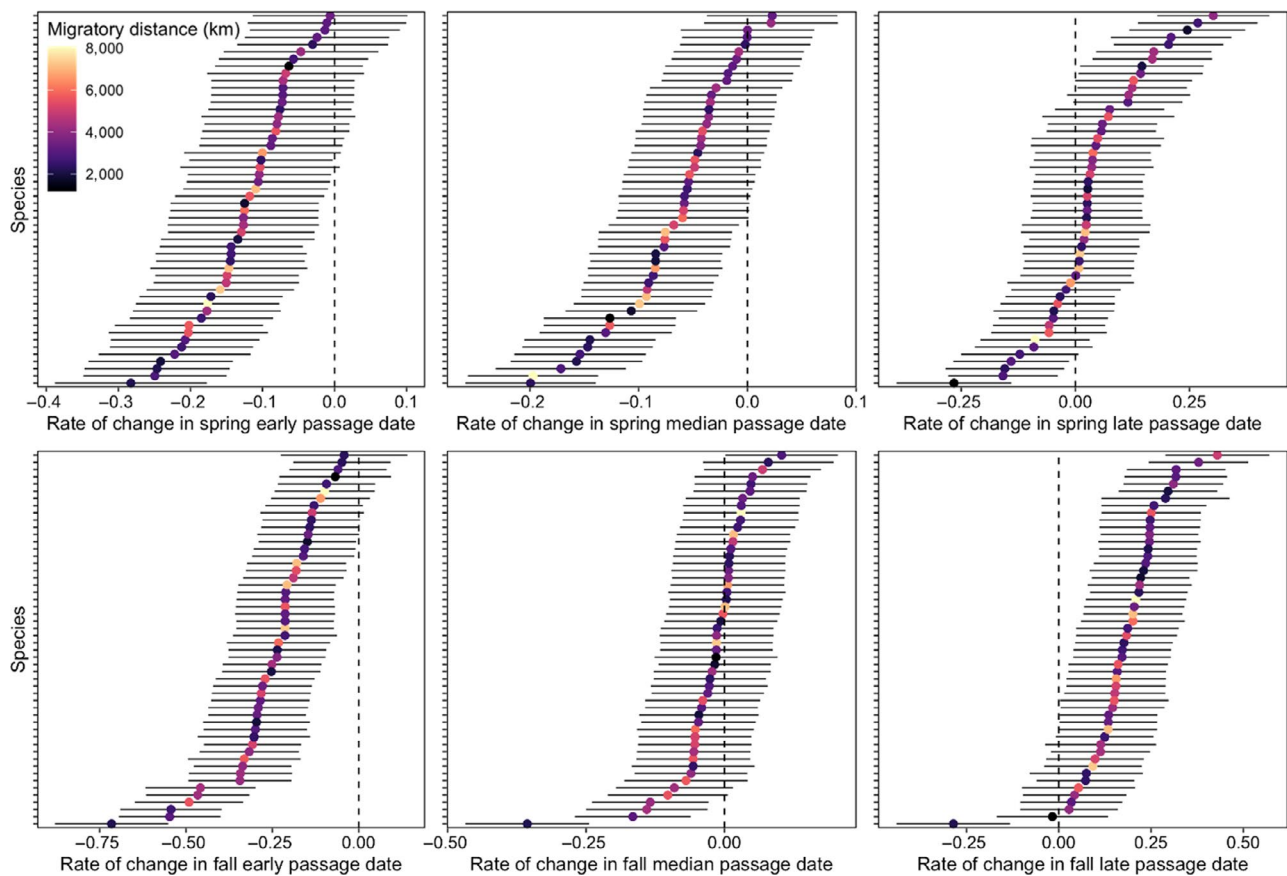


FIGURE 2 Shifts in migration phenology in 52 North American migratory birds from 1978 to 2016. Points represent species-specific rates of change in each spring (top row) and fall (bottom row) passage date through Chicago in days per year, with the bars showing their respective standard errors (Table S9), derived from the linear mixed-effects models. Spring early and median passage dates have advanced, but late passage dates have not. In the fall, the median date did not change, but the early date advanced and the late passage date got later. Migratory distance, indicated by the color scale, impacted the degree of spring advancement in the median and potentially in the early passage dates, although its effects were weak

3.2 | Shifts in migration phenology across years

In the spring, on average, the early (=5th sample percentile) (-0.123 ± 0.0252 days/year, $p < 0.001$, Table S7, Figure 2) and median (-0.0686 ± 0.0201 , $p < 0.01$, Table S7, Figure 2) passage dates

advanced, but late passage date (=95th sample percentile) remained the same (0.0339 ± 0.0300 days/year, $p = 0.263$, Table S7, Figure 2). In the fall, the median date did not change (-0.0230 ± 0.0255 days/year, $p = 0.376$, Table S8, Figure 2), but the overall passage duration increased: the early date advanced (-0.249 ± 0.0354 days/

year, $p < 0.001$, Table S8, Figure 2) and the late passage date got later (0.176 ± 0.0324 days/year, $p < 0.001$, Table S8, Figure 2). Migratory distance impacted the degree of advancement in the spring, with shorter-distance migrants having advanced their median (0.0482 ± 0.0168 , $p < 0.01$, Table S7, Figure 2), and potentially early (0.0384 ± 0.0209 , $p = 0.0739$, Table S7, Figure 2) passage dates, more than long-distance migrants. No effects were detected for the spring late passage date or for any of the fall passage dates (all p values > 0.1 , Tables S7 and S8). Mean breeding range latitude had no effect of phenological shift in either season (all p values > 0.1 , Tables S7 and S8).

3.3 | Relationship between phenological and morphological shifts

Rate of change in spring or fall migration phenology was not related to the rates of change in relative wing length or tarsus length (all p values > 0.05 , Table 2, Figure 3). Additionally, we found no evidence that differences in migratory distance or breeding range latitude are associated with different rates of change in either morphological trait (all p values > 0.05 , Table 2). We found strong phylogenetic signal in all models (all $\lambda > 0.8$, Table 2).

3.4 | Comparison of estimated migration phenology with eBird data

The phenology dates estimated based on our collision data and eBird were similar within and across years. The eBird passage dates were relevant predictors of the collision passage dates for all dates and seasons

(all R^2 value ranged between 0.56 and 0.84 except for 5th passage date in the fall = 0.26; all p values < 0.001 , Figure S1). Such a strong relationship between the collision- and eBird-based passage dates indicates that our collision dataset provides a reliable data for annual timing of migration through Chicago. Furthermore, year was not a relevant predictor of the residuals resulting from regressing collision passage dates on eBird passage dates for any passage date or season (all p values > 0.1), suggesting a lack of temporal trend in differences between collision data and eBird.

4 | DISCUSSION

As warming temperatures lead to shifts in morphology, phenology and range, it is important to understand the extent to which interactions among these axes of adaptation facilitate or inhibit adaptive responses to climate change. Using over 70,000 specimens from 52 species of North American migratory birds, we document widespread changes in both spring and fall migration phenology but find that these phenological changes do not explain the concurrent widespread shifts in morphology. Furthermore, we found no evidence that species' migratory distances or differential rates of warming at the breeding grounds—as indexed by breeding range latitude—influence the rates of morphological changes.

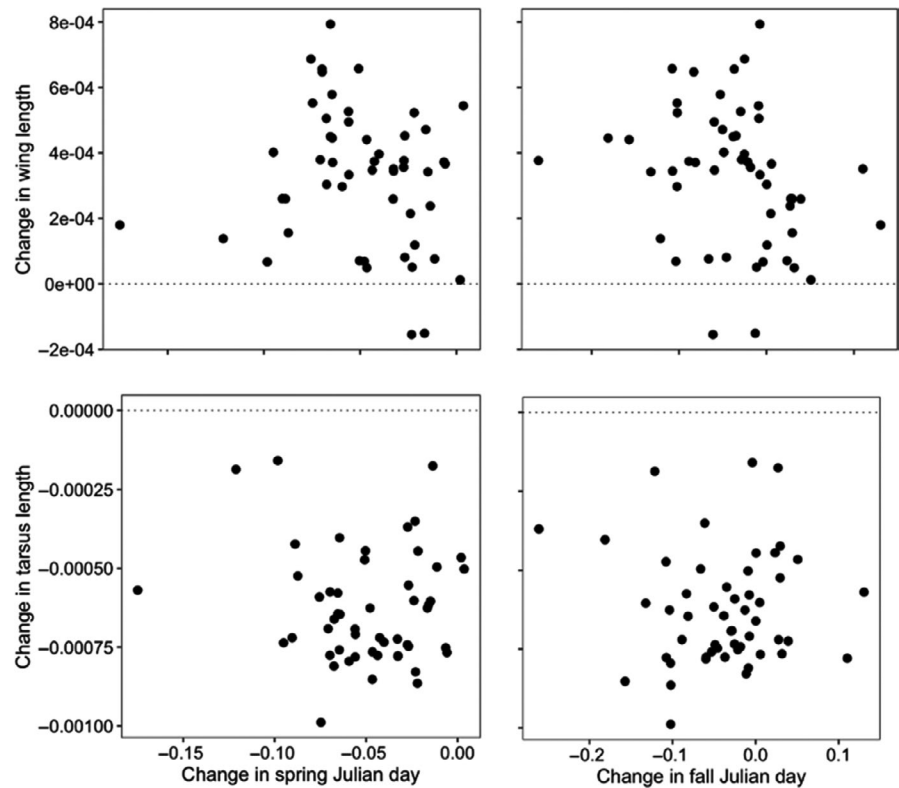
4.1 | Individuals with longer wings migrate earlier each spring

We found that individuals with longer wings relative to their body size pass through Chicago earlier in the spring (Table 1), suggesting

TABLE 2 No effects of rate of change in spring and fall migration phenology, migratory distance and breeding latitude on the rate of change in relative wing length and tarsus length for 52 North American migratory bird species during the period 1978–2016. Migratory distance and breeding latitude were centred and standardized to have a mean of 0 and a standard deviation of 1

	Coefficient	Estimate	SE	t value	$p(> t)$	Pagel's λ
Relative wing length Spring	Intercept	2.74E-04	1.59E-04	1.724	0.0911	0.820 (0.569, 1.0710)
	Spring rate	1.28E-03	7.56E-04	1.698	0.0959	
	Migratory distance	-5.69E-05	3.21E-05	-1.769	0.0832	
	Breeding latitude	4.06E-06	2.55E-05	0.159	0.874	
Relative wing length Fall	Intercept	2.33E-04	1.64E-04	1.422	0.162	0.830 (0.557, 1.103)
	Fall rate	-3.03E-04	3.54E-04	-0.858	0.395	
	Migratory distance	-3.50E-05	3.18E-05	-1.101	0.276	
	Breeding latitude	5.13E-06	2.60E-05	0.198	0.844	
Tarsus length Spring	Intercept	-4.75E-04	1.45E-04	-3.277	0.002	0.980 (0.923, 1.0368)
	Spring rate	-7.70E-04	4.61E-04	-1.671	0.101	
	Migratory distance	1.90E-05	1.92E-05	0.991	0.327	
	Breeding latitude	1.29E-05	1.33E-05	0.964	0.340	
Tarsus length Fall	Intercept	-4.54E-04	1.53E-04	-2.964	0.0047	0.988 (0.944, 1.0322)
	Fall rate	-8.56E-05	1.95E-04	-0.438	0.663	
	Migratory distance	1.26E-05	1.90E-05	0.664	0.510	
	Breeding latitude	7.99E-06	1.28E-05	0.622	0.537	

FIGURE 3 There is no relationship between phenological shifts and the rate of change in wing length or body size. Points represent species-specific rates of change, dotted lines through 0 indicate no change in morphological traits



a link between morphology and timing of migration. Similar strong effects of individual wing length and shape on spring migration phenology have been described in previous studies that focused on single species (Bowlin, 2007; Cooper et al., 2011; Hahn et al., 2016; Potti, 1998), and these relationships have been attributed to the influence of wing morphology on flight efficiency and speed (Yong & Moore, 1994). However, this relationship could be complicated by breeding geography, if early migrant individuals breed further north and have longer relative wing lengths. In contrast to the spring, no effects of wing length were detected on annual fall passage dates (Table 1). The lack of connection between fall migration phenology and morphology may be due to weaker selection for increased migration speed during fall migration (Karlsson et al., 2012; Nilsson et al., 2013).

4.2 | Advancing spring passage dates and extended fall passage duration

Using comparisons with eBird data, we find that our window collision data represent a reliable proxy for migration phenology, both within and across years, suggesting they can be used to detect trends through time (Figure S1). Our finding that spring migration has advanced is consistent with widespread evidence of earlier spring migration in birds across the globe (Bitterlin & Van Buskirk, 2014; Chambers et al., 2014; Gordo & Sanz, 2006; Lehikoinen et al., 2004; Miller-Rushing et al., 2008; Mills, 2005; Oliver et al., 2020; Usui et al., 2017; Van Buskirk et al., 2009). According to recent multi-species studies, migratory birds have advanced their mean spring

migration phenology by on average 2.1–2.2 days per decade globally (Cohen et al., 2018; Usui et al., 2017), and 0.4–1.0 days per decade in North America (Dorian et al., 2020; Horton, La Sorte, et al., 2019; Mayor et al., 2017). This is similar to what we find, with the early, and median passage dates through Chicago occurring 1.2 and 0.7, respectively, days per decade earlier on average across species (Figure 2, Table S7). Our results indicate that, after controlling for differences among species, the earliest migrants have advanced their phenology twice as fast as the population median. Similar findings were reported for other species (Bitterlin & Van Buskirk, 2014) in response to stronger warming earlier than later in the spring (Ahola et al., 2004).

Albeit considerably less studied than spring migration (Gallinat et al., 2015; Haest et al., 2019), changes in fall migration phenology tend to be more variable across taxa and continents (Barton & Sandercock, 2018; Chambers et al., 2014; Jenni & Kéry, 2003; Lehikoinen et al., 2004; Mills, 2005). Consistent with previous studies (Bitterlin & Van Buskirk, 2014; Van Buskirk et al., 2009), we find no shifts in median fall migration date across species (Figure 2, Table S8). However, there has been increasing variation in the timing of fall migration, with the first migrants advancing their migration (2.4 days per decade) and late migrants migrating later (1.7 days per decade; Figure 2, Table S8). This is similar to other studies that documented increasing fall passage duration (Covino et al., 2020; Dorian et al., 2020; Miles et al., 2017). The earlier departure from the breeding grounds may result from earlier breeding and/or earlier moult completion as documented in multiple species (Mitchell et al., 2012; Saino et al., 2017; Stutchbury et al., 2011; van Wijk et al., 2017, but see Tomotani et al., 2019). On the other hand, the protraction of fall migration, especially in combination with the advancement of spring,

may be the result of longer breeding seasons selecting for double brooding and/or re-nesting after failed breeding attempts (Halupka & Halupka, 2017; Jenni & Kéry, 2003; Møller et al., 2010; Townsend et al., 2013; Végvári et al., 2010); but see Hällfors et al., 2020).

Our study is consistent with previous studies (Bitterlin & Van Buskirk, 2014; Knudsen et al., 2011; Végvári et al., 2010) in finding that short-distance migratory species advanced spring migration phenology more than long-distance migrants (Table S7); the latter may be more reliant on photoperiodic cues and less able to respond to local weather conditions at the breeding grounds (Åkesson et al., 2017; Both & Visser, 2001; Butler, 2003; Dawson et al., 2001; Gwinner, 2003; Lehikoinen et al., 2004; Miller-Rushing et al., 2008; Rubolini et al., 2007; Usui et al., 2017). However, we found no evidence that migratory distance affected phenological shifts in the fall (Table S8), in contrast to studies that have suggested that short-distance migrants tend to delay their departure while long-distance migrants tend to advance fall migration (Jenni & Kéry, 2003; Van Buskirk et al., 2009). Finally, we found no effect of breeding latitude on phenological shifts in either season, corroborating previous findings in migratory birds (Rubolini et al., 2007; Usui et al., 2017), but see Horton, La Sorte, et al., (2019). Although global meta-analyses showed greater phenological shifts in animals and plants occupying higher latitudes (Parmesan, 2007; Post et al., 2018), the relationships between latitude and phenological responsiveness are likely complex (Chmura et al., 2019).

4.3 | Phenological shifts have been independent of morphological change

We find clear evidence that migratory phenology has shifted concurrently with consistent increases in wing length in the same set of species (Weeks et al., 2020a). Given that we find longer wing length is associated with earlier migration within years (Table 1), the advancing date of spring migration over time could select for, and be accomplished by, increased wing length. However, we found no evidence that species that are advancing their phenology faster are also experiencing faster increases in wing length (Table 2, Figure 3). Furthermore, we found no evidence that species with longer migratory distance or those breeding at higher latitudes showed faster increases in wing length (Table 2). Together, these findings suggest that, while the phenology of migration has changed, it has not driven the observed increase in wing length.

The lack of association between phenological responses and increasing wing length suggests that spring advancements are accomplished through means other than morphological adaptation for more efficient flight. Previous studies have shown that variables reflecting fuel deposition (e.g. stopover duration, foraging rate) have a stronger impact on migration speed than those related to flight speed (Houston, 2000; Nilsson et al., 2013). Similarly, studies tracking individuals throughout migration showed that annual advancements in spring migration phenology were achieved via adjustments in stopover frequency and duration (Haest et al., 2020; Lameris

et al., 2018; Oliver et al., 2020). Future research will benefit from studies that link morphological differences, flight speed and individual migration phenology by tracking individuals along their entire migration routes (McKinnon & Love, 2018).

In addition to being decoupled from increases in wing length, we found no evidence that advancing spring phenology mitigated the nearly universal declines in body size in response to warming temperatures documented across species in this study (Table 2; Weeks et al., 2020a). In early developmental stages, altricial birds have little ability to thermoregulate endogenously and are effectively poikilothermic (Andreasson et al., 2016; Dunn, 1975; Pereyra & Morton, 2001). Therefore, shifts in ambient temperatures can affect growth and body size, with heat-stressed nestlings reaching smaller body size (Andrew et al., 2017; Cunningham et al., 2013; Rodríguez et al., 2016; Wada et al., 2015). If advanced spring phenology resulted in earlier breeding, developing nestlings might experience less drastic increases in ambient temperature and as a result would be predicted to show smaller declines in body size. It is possible that we did not find a relationship between advancing phenology and rates of body size decline because advanced arrival on the breeding grounds has not led to proportionate advancements in reproduction. While earlier arrival on the breeding grounds is generally associated with earlier initiation of reproduction (Moore et al., 2005; Visser et al., 2015; Woodworth et al., 2016), some studies have shown that species that recently advanced migration phenology did not advance breeding (Ahola et al., 2004; Lameris et al., 2018; Valtonen et al., 2017). Finally, it is possible that the error associated with our single-point estimates of rates of change prevented us from detecting relationships between phenological shifts and changes in morphology.

5 | CONCLUSIONS

While interactions among shifts in phenology, morphology and range are expected to influence species responses to climate change, our understanding of these interactions is limited. We find that across a diverse group of 52 North American migratory bird species, spring migration phenology has advanced over the past 40 years, concurrent with widespread shifts in morphology. Our analysis of a dataset with more than 70,000 individual observations spanning a 40-year period indicates that these phenological and morphological changes are decoupled. This lack of association between shifts in phenology and morphology is compelling given the consistent and near-universal nature of the changes in both of those dimensions, and the strong empirical and theoretical connections between wing morphology and migration phenology. Our results suggest that biotic responses to climate change are multidimensional, and that the connections between these axes of adaptation are complex.

ACKNOWLEDGEMENTS

We thank the staff, curators and volunteers of the Field Museum, and the Chicago Bird Collision Monitors, for their assistance in salvaging

birds. We thank Mary Hennen for assistance with data preparation. This work was supported by the Institute for Global Change Biology at the University of Michigan. We have no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.Z., B.M.W. and B.C.W. designed the research; D.E.W. collected the data; M.Z. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data are publicly available in the Dryad Digital Repository <https://datadryad.org/stash/dataset/doi:10.5061/dryad.8pk0p2nhw> (Weeks et al., 2020b).

ORCID

Marketa Zimova  <https://orcid.org/0000-0002-8264-9879>

Benjamin M. Winger  <https://orcid.org/0000-0002-2095-2020>

Brian C. Weeks  <https://orcid.org/0000-0003-2967-2970>

REFERENCES

- Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., & Lehikoinen, E. (2004). Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology*, 10(9), 1610–1617. <https://doi.org/10.1111/j.1365-2486.2004.00823.x>
- Åkesson, S., Ilieva, M., Karagicheva, J., Rakhimberdiev, E., Tomotani, B., & Helm, B. (2017). Timing avian long-distance migration: From internal clock mechanisms to global flights. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160252. <https://doi.org/10.1098/rstb.2016.0252>
- Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology*, 152, 5–23. <https://doi.org/10.1007/s10336-011-0694-1>
- Andreasson, F., Nord, A., & Nilsson, J. Å. (2016). Brood size constrains the development of endothermy in blue tits. *Journal of Experimental Biology*, 219(14), 2212–2219. <https://doi.org/10.1242/jeb.135350>
- Andrew, S. C., Hurley, L. L., Mariette, M. M., & Griffith, S. C. (2017). Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. *Journal of Evolutionary Biology*, 30(12), 2156–2164. <https://doi.org/10.1111/jeb.13181>
- Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., Payne, N., & Blanchard, J. L. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution*, 4, 809–814. <https://doi.org/10.1038/s41559-020-1171-0>
- Barton, G. G., & Sandercock, B. K. (2018). Long-term changes in the seasonal timing of landbird migration on the Pacific Flyway. *The Condor*, 120(1), 30–46. <https://doi.org/10.1650/condor-17-88.1>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 48. <https://doi.org/10.18637/jss.v067.i01>
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4), 1023–1031. <https://doi.org/10.1111/gcb.12514>
- Bennett, N. L., Severns, P. M., Parmesan, C., & Singer, M. C. (2015). Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos*, 124(1), 41–53. <https://doi.org/10.1111/oik.01490>
- Bergmann, C. (1847). Über die verhältnisse der warmekonomie der thiere zu ihrer grosse. *Göttinger Studien*, 1, 595–708.
- BirdLife International. (2015). *IUCN red list for birds*. Retrieved from <http://www.birdlife.org>
- Bitterlin, L. R., & Van Buskirk, J. (2014). Ecological and life history correlates of changes in avian migration timing in response to climate change. *Climate Research*, 61(2), 109–121. <https://doi.org/10.3354/cr01238>
- Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411(6835), 296–298. <https://doi.org/10.1038/35077063>
- Bowlin, M. S. (2007). Sex, wingtip shape, and wing-loading predict arrival date at a stopover site in the Swainson's Thrush (*Catharus ustulatus*). *The Auk*, 124(4), 1388–1396. <https://doi.org/10.1093/auk/124.4.1388>
- Bowlin, M. S., & Wikelski, M. (2008). Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PLoS ONE*, 3(5), e2154. <https://doi.org/10.1371/journal.pone.0002154>
- Burns, J. G. (2003). Relationship of calidris sandpiper wing shape with relative fuel load and total migration distance. *The Auk*, 120(3), 827–835. <https://doi.org/10.2307/4090113>
- Butler, C. J. (2003). The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis*, 145(3), 484–495. <https://doi.org/10.1046/j.1474-919X.2003.00193.x>
- Chambers, L. E., Beaumont, L. J., & Hudson, I. L. (2014). Continental scale analysis of bird migration timing: Influences of climate and life history traits – A generalized mixture model clustering and discriminant approach. *International Journal of Biometeorology*, 58(6), 1147–1162. <https://doi.org/10.1007/s00484-013-0707-2>
- Chmura, H. E., Kharouba, H. M., Ashander, J., Ehman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, 89(1), e01337. <https://doi.org/10.1002/ecm.1337>
- Claramunt, S., Derryberry, E. P., Remsen, J. V., & Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 279(1733), 1567–1574. <https://doi.org/10.1098/rspb.2011.1922>
- Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), 224–228. <https://doi.org/10.1038/s41558-018-0067-3>
- Cooper, N. W., Murphy, M. T., Redmond, L. J., & Dolan, A. C. (2011). Reproductive correlates of spring arrival date in the Eastern Kingbird *Tyrannus tyrannus*. *Journal of Ornithology*, 152(1), 143–152. <https://doi.org/10.1007/s10336-010-0559-z>
- Corman, A. M., Bairlein, F., & Schmaljohann, H. (2014). The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. *Behavioral Ecology and Sociobiology*, 68(3), 391–402. <https://doi.org/10.1007/s00265-013-1653-z>
- Covino, K. M., Horton, K. G., & Morris, S. R. (2020). Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler. *The Auk*, 137(2). <https://doi.org/10.1093/auk/ukz080>
- Cunningham, S. J., Martin, R. O., Hojem, C. L., & Hockey, P. A. R. (2013). Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: A study of common fiscals. *PLoS ONE*, 8(9), e74613. <https://doi.org/10.1371/journal.pone.0074613>
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(31), 12788–12793. <https://doi.org/10.1073/pnas.0902080106>
- Dawson, A., King, V. M., Bentley, G. E., & Ball, G. F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms*, 16(4), 365–380. <https://doi.org/10.1177/074873001129002079>

- Desrochers, A. (2010). Morphological response of songbirds to 100 years of landscape change in North America. *Ecology*, 91(6), 1577–1582. <https://doi.org/10.1890/09-2202.1>
- Dorian, N. N., Lloyd-Evans, T. L., & Reed, J. M. (2020). Non-parallel changes in songbird migration timing are not explained by changes in stopover duration. *PeerJ*, 8, e8975. <https://doi.org/10.7717/peerj.8975>
- Dunn, E. H. (1975). The timing of endothermy in the development of altricial birds. *The Condor*, 77(3), 288–293. <https://doi.org/10.2307/1366224>
- Eastman, L. M., Morelli, T. L., Rowe, K. C., Conroy, C. J., & Moritz, C. (2012). Size increase in high elevation ground squirrels over the last century. *Global Change Biology*, 18(5), 1499–1508. <https://doi.org/10.1111/j.1365-2486.2012.02644.x>
- Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, 109(47), 19310–19314. <https://doi.org/10.1073/pnas.1210460109>
- Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30(3), 169–176. <https://doi.org/10.1016/j.tree.2015.01.004>
- Gardner, J. L., Amano, T., Mackey, B. G., Sutherland, W. J., Clayton, M., & Peters, A. (2014). Dynamic size responses to climate change: Prevailing effects of rising temperature drive long-term body size increases in a semi-arid passerine. *Global Change Biology*, 20(7), 2062–2075. <https://doi.org/10.1111/gcb.12507>
- Gardner, J. L., Amano, T., Peters, A., Sutherland, W. J., Mackey, B., Joseph, L., Stein, J., Ikin, K., Little, R., Smith, J., & Symonds, M. R. E. (2019). Australian songbird body size tracks climate variation: 82 species over 50 years. *Proceedings of the Royal Society B: Biological Sciences*, 286(1916), 20192258. <https://doi.org/10.1098/rspb.2019.2258>
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>
- Giery, S. T., & Layman, C. A. (2019). Ecological consequences of sexually selected traits: An eco-evolutionary perspective. *Quarterly Review of Biology*, 94(1), 29–74. <https://doi.org/10.1086/702341>
- Gordo, O., & Sanz, J. J. (2006). Climate change and bird phenology: A long-term study in the Iberian Peninsula. *Global Change Biology*, 12(10), 1993–2004. <https://doi.org/10.1111/j.1365-2486.2006.01178.x>
- Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology*, 13(6), 770–778. <https://doi.org/10.1016/j.conb.2003.10.010>
- Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Andrew Cox, W., Han, K.-L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320(5884), 1763–1768. <https://doi.org/10.1126/science.1157704>
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22. <https://doi.org/10.18637/jss.v033.i02>
- Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23(3), 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>
- Haest, B., Hüppop, O., & Bairlein, F. (2020). Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. *Proceedings of the National Academy of Sciences of the United States of America*, 117(29), 17056–17062. <https://doi.org/10.1073/pnas.1920448117>
- Haest, B., Hüppop, O., van de Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology: A potpourri of wind, precipitation, and temperature effects. *Global Change Biology*, 25(12), 4064–4080. <https://doi.org/10.1111/gcb.14746>
- Hahn, S., Korner-Nievergelt, F., Emmenegger, T., Amrhein, V., Csörgő, T., Gursoy, A., Ilieva, M., Kverek, P., Pérez-Tris, J., Pirrello, S., Zehntindjiev, P., & Salewski, V. (2016). Longer wings for faster springs – Wing length relates to spring phenology in a long-distance migrant across its range. *Ecology and Evolution*, 6(1), 68–77. <https://doi.org/10.1002/ece3.1862>
- Hällfors, M. H., Antão, L. H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., & Saastamoinen, M. (2020). Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Proceedings of the National Academy of Sciences of the United States of America*, 117(31), 18557–18565. <https://doi.org/10.1073/pnas.1913579117>
- Halupka, L., & Halupka, K. (2017). The effect of climate change on the duration of avian breeding seasons: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, 284(1867), 20171710. <https://doi.org/10.1098/rspb.2017.1710>
- Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2019). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change*, 10, 63–68. <https://doi.org/10.1038/s41558-019-0648-9>
- Horton, K. G., Nilsson, C., Van Doren, B. M., La Sorte, F. A., Dokter, A. M., & Farnsworth, A. (2019). Bright lights in the big cities: Migratory birds' exposure to artificial light. *Frontiers in Ecology and the Environment*, 17(4), 209–214. <https://doi.org/10.1002/fee.2029>
- Horton, K. G., Van Doren, B. M., La Sorte, F. A., Cohen, E. B., Clipp, H. L., Buler, J. J., Fink, D., Kelly, J. F., & Farnsworth, A. (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Global Change Biology*, 25(3), 1106–1118. <https://doi.org/10.1111/gcb.14540>
- Houston, A. I. (2000). The strength of selection in the context of migration speed. *Proceedings of the Royal Society B: Biological Sciences*, 267(1460), 2393–2395. <https://doi.org/10.1098/rspb.2000.1296>
- Housworth, E. A., Martins, E. P., & Lynch, M. (2004). The phylogenetic mixed model. *The American Naturalist*, 163(1), 84–96. <https://doi.org/10.1086/380570>
- IPCC. (2013). *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley Eds.). Cambridge University Press. <https://doi.org/10.1017/CBO9781107415324>
- Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, 270(1523), 1467–1471. <https://doi.org/10.1098/rspb.2003.2394>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Karlsson, H., Nilsson, C., Bäckman, J., & Ålerstam, T. (2012). Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis. *Animal Behaviour*, 83(1), 87–93. <https://doi.org/10.1016/j.anbehav.2011.10.009>
- Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., & Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), 5211–5216. <https://doi.org/10.1073/pnas.1714511115>
- Kipp, F. A. (1958). Der Handflügel-Index als flugbiologisches Maß. *Vogelwarte*, 20, 77–86.

- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehtikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86(4), 928–946. <https://doi.org/10.1111/j.1469-185X.2011.00179.x>
- Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68(5), 940–950. <https://doi.org/10.1046/j.1365-2656.1999.00343.x>
- Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, 28(15), 2467–2473.e4. <https://doi.org/10.1016/j.cub.2018.05.077>
- Lank, D. B., Xu, C., Harrington, B. A., Morrison, R. I. G., Gratto-Trevor, C. L., Hicklin, P. W., Sandercock, B. K., Smith, P. A., Kwon, E., Rausch, J., Pirie Dominix, L. D., Hamilton, D. J., Paquet, J., Bliss, S. E., Neima, S. G., Friis, C., Flemming, S. A., Anderson, A. M., & Ydenberg, R. C. (2017). Long-term continental changes in wing length, but not bill length, of a long-distance migratory shorebird. *Ecology and Evolution*, 7(9), 3243–3256. <https://doi.org/10.1002/ece3.2898>
- Lehtikoinen, E., Sparks, T. H., & Zalakevicius, M. (2004). Arrival and departure dates. *Advances in Ecological Research*, 35, 1–31. [https://doi.org/10.1016/S0065-2504\(04\)35001-4](https://doi.org/10.1016/S0065-2504(04)35001-4)
- Martin, A. E., Desrochers, A., & Fahrig, L. (2017). Homogenization of dispersal ability across bird species in response to landscape change. *Oikos*, 126(7), 996–1003. <https://doi.org/10.1111/oik.03859>
- Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, 7, 1902. <https://doi.org/10.1038/s41598-017-02045-z>
- Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, 10(1), 105–108. <https://doi.org/10.2307/2406103>
- McKinnon, E. A., & Love, O. P. (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk*, 135(4), 834–856. <https://doi.org/10.1642/AUK-17-202.1>
- Miles, W. T. S., Bolton, M., Davis, P., Dennis, R., Broad, R., Robertson, I., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., & Reid, J. M. (2017). Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Global Change Biology*, 23(4), 1400–1414. <https://doi.org/10.1111/gcb.13486>
- Miller-Rushing, A. J., Lloyd-Evans, T. L., Primack, R. B., & Satzing, P. (2008). Bird migration times, climate change, and changing population sizes. *Global Change Biology*, 14(9), 1959–1972. <https://doi.org/10.1111/j.1365-2486.2008.01619.x>
- Mills, A. M. (2005). Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis*, 147(2), 259–269. <https://doi.org/10.1111/j.1474-919X.2005.00380.x>
- Mitchell, G. W., Newman, A. E. M., Wikelski, M., & Norris, D. R. (2012). Timing of breeding carries over to influence migratory departure in a songbird: An automated radiotracking study. *Journal of Animal Ecology*, 81(5), 1024–1033. <https://doi.org/10.1111/j.1365-2656.2012.01978.x>
- Møller, A. P., Flensted-Jensen, E., Klarborg, K., Mardal, W., & Nielsen, J. T. (2010). Climate change affects the duration of the reproductive season in birds. *Journal of Animal Ecology*, 79(4), 777–784. <https://doi.org/10.1111/j.1365-2656.2010.01677.x>
- Møller, A. P., Rubolini, D., & Saino, N. (2017). Morphological constraints on changing avian migration phenology. *Journal of Evolutionary Biology*, 30(6), 1177–1184. <https://doi.org/10.1111/jeb.13086>
- Moore, F. R., Smith, R. J., & Sandberg, R. (2005). Stopover ecology of intercontinental migrants: Solutions to problems and consequences for reproductive performance. In *Birds of two worlds: The ecology and evolution of migration* (pp. 251–261). Johns Hopkins Press. Retrieved from <https://ci.nii.ac.jp/naid/10026360658/>
- Moreno-Rueda, G., & Rivas, J. M. (2007). Recent changes in allometric relationships among morphological traits in the dipper (*Cinclus cinclus*). *Journal of Ornithology*, 148(4), 489–494. <https://doi.org/10.1007/s10336-007-0184-7>
- Nilsson, C., Klaassen, R. H. G., & Alerstam, T. (2013). Differences in speed and duration of bird migration between spring and autumn. *The American Naturalist*, 181(6), 837–845. <https://doi.org/10.1086/670335>
- Oliver, R. Y., Mahoney, P. J., Gurarie, E., Krikun, N., Weeks, B. C., Hebblewhite, M., Liston, G., & Boelman, N. (2020). Behavioral responses to spring snow conditions contribute to long-term shift in migration phenology in American robins. *Environmental Research Letters*, 15(4), 045003. <https://doi.org/10.1088/1748-9326/ab71a0>
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466(7305), 482–485. <https://doi.org/10.1038/nature09210>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Parnesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13(9), 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Parnesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>
- Pennycuik, C. J. (2008). *Modelling the flying bird*. Elsevier.
- Pereyra, M. E., & Morton, M. L. (2001). Nestling growth and thermoregulatory development in subalpine dusky flycatchers. *The Auk*, 118(1), 116–136. <https://doi.org/10.1093/auk/118.1.116>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Deepayan, S. (2013). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-140.
- Post, E., Steinman, B. R., & Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports*, 8, 3927. <https://doi.org/10.1038/s41598-018-22258-0>
- Potti, J. (1998). Arrival time from spring migration in male pied flycatchers: Individual consistency and familial resemblance. *The Condor*, 100(4), 702–708. <https://doi.org/10.2307/1369752>
- Prokosch, J., Bernitz, Z., Bernitz, H., Erni, B., & Altwegg, R. (2019). Are animals shrinking due to climate change? Temperature-mediated selection on body mass in mountain wagtails. *Oecologia*, 189(3), 841–849. <https://doi.org/10.1007/s00442-019-04368-2>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Rising, J. D., & Somers, K. M. (1989). The measurement of overall body size in birds. *The Auk*, 106(October), 666–674. <https://doi.org/10.1093/auk/106.4.666>
- Rodríguez, S., Díez-Méndez, D., & Barba, E. (2016). Negative effects of high temperatures during development on immediate post-fledging survival in great tits *parus major*. *Acta Ornithologica*, 51(2), 235–244. <https://doi.org/10.3161/00016454ao2016.51.2.009>
- Root, T. L., 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(6918), 57–60. <https://doi.org/10.1038/nature01333>
- Rubolini, D., Liker, A., Garamszegi, L. Z., Møller, A. P., & Saino, N. (2015). Using the birdtree.org website to obtain robust phylogenies for avian comparative studies: A primer. *Current Zoology*, 61(6), 959–965.

- 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(1–2), 135–146. <https://doi.org/10.3354/cr00720>
- Rubolini, D., Saino, N., & Møller, A. P. (2010). Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, 42(1), 45–55. <https://doi.org/10.3354/cr00862>
- Saino, N., Ambrosini, R., Caprioli, M., Romano, A., Romano, M., Rubolini, D., Scandolara, C., & Liechti, F. (2017). Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. *Journal of Animal Ecology*, 86(2), 239–249. <https://doi.org/10.1111/1365-2656.12625>
- Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Schmaljohann, H. (2018). Proximate mechanisms affecting seasonal differences in migration speed of avian species. *Scientific Reports*, 8(1), 4106. <https://doi.org/10.1038/s41598-018-22421-7>
- Schmaljohann, H., & Both, C. (2017). The limits of modifying migration speed to adjust to climate change. *Nature Climate Change*, 7(8), 573–576. <https://doi.org/10.1038/nclimate3336>
- Senar, J. C., & Pascual, J. (1997). Keel and tarsus length may provide a good predictor of avian body size. *Ardea*, 85, 269–274.
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), 401–406. <https://doi.org/10.1038/nclimate1259>
- Socolar, J. B., Epanchin, P. N., Beissinger, S. R., & Tingley, M. W. (2017). Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 114(49), 12976–12981. <https://doi.org/10.1073/pnas.1705897114>
- Speakman, J. R., & Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: Neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, 79, 726–746. <https://doi.org/10.1111/j.1365-2656.2010.01689.x>
- Spottiswoode, C. N., Tøttrup, A. P., Coppack, T., Tottrup, A. P., & Coppack, T. (2006). Sexual selection predicts advancement of avian spring migration in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 273(1605), 3023–3029. <https://doi.org/10.1098/rspb.2006.3688>
- Stutchbury, B. J. M., Gow, E. A., Done, T., MacPherson, M., Fox, J. W., & Afanasyev, V. (2011). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), 131–137. <https://doi.org/10.1098/rspb.2010.1220>
- Sukumaran, J., & Holder, M. T. (2010). DendroPy: A Python library for phylogenetic computing. *Bioinformatics*, 26(12), 1569–1571. <https://doi.org/10.1093/bioinformatics/btq228>
- Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142(10), 2282–2292. <https://doi.org/10.1016/j.biocon.2009.05.006>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241. <https://doi.org/10.1038/nature18608>
- Tomotani, B. M., de la Hera, I., Lange, C. Y. M. J. G. M. J. G., van Lith, B., Meddle, S. L., Both, C., & Visser, M. E. (2019). Timing manipulations reveal the lack of a causal link across timing of annual-cycle stages in a long-distance migrant. *Journal of Experimental Biology*, 222(17), jeb201467. <https://doi.org/10.1242/jeb.201467>
- Townsend, A. K., Sillett, T. S., Lany, N. K., Kaiser, S. A., Rodenhouse, N. L., Webster, M. S., & Holmes, R. T. (2013). Warm springs, early lay dates, and double brooding in a North American migratory songbird, the black-throated blue warbler. *PLoS ONE*, 8(4), 59467. <https://doi.org/10.1371/journal.pone.0059467>
- Usui, T., Butchart, S. H. M., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: A phylogenetic meta-analysis. *Journal of Animal Ecology*, 86(2), 250–261. <https://doi.org/10.1111/1365-2656.12612>
- Valtonen, A., Latja, R., Leinonen, R., & Pöysä, H. (2017). Arrival and onset of breeding of three passerine birds in eastern Finland tracks climatic variation and phenology of insects. *Journal of Avian Biology*, 48(6), 785–795. <https://doi.org/10.1111/jav.01128>
- 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(3), 760–771. <https://doi.org/10.1111/j.1365-2486.2008.01751.x>
- Van Buskirk, J., Mulvihill, R. S., & Leberman, R. C. (2010). Declining body sizes in North American birds associated with climate change. *Oikos*, 119(6), 1047–1055. <https://doi.org/10.1111/j.1600-0706.2009.18349.x>
- Van Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., De Fouw, J., Rakhimberdiev, E., Soloviev, M. Y., Piersma, T., & Klaassen, M. (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science*, 352(6287), 819–821. <https://doi.org/10.1126/science.aad6351>
- van Wijk, R. E., Schaub, M., & Bauer, S. (2017). Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. *Behavioral Ecology and Sociobiology*, 71(4), 73. <https://doi.org/10.1007/s00265-017-2305-5>
- 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), 1–11. <https://doi.org/10.1111/j.1365-2486.2009.01876.x>
- Visser, M. E., Gienapp, P., Husby, A., Morrissey, M., de la Hera, I., Pulido, F., & Both, C. (2015). Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *Plos Biology*, 13(4), 1–17. <https://doi.org/10.1371/journal.pbio.1002120>
- Wada, H., Kriengwatana, B., Allen, N., Schmidt, K. L., Soma, K. K., & MacDougall-Shackleton, S. A. (2015). Transient and permanent effects of suboptimal incubation temperatures on growth, metabolic rate, immune function and adrenocortical responses in zebra finches. *Journal of Experimental Biology*, 218(18), 2847–2855. <https://doi.org/10.1242/jeb.114108>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395. <https://doi.org/10.1038/416389a>
- Weeks, B. C., Willard, D. E., Zimova, M., Ellis, A. A., Witynski, M. L., Hennen, M., & Winger, B. M. (2020a). Shared morphological consequences of global warming in North American migratory birds. *Ecology Letters*, 23(2), 316–325. <https://doi.org/10.1111/ele.13434>
- Weeks, B. C., Willard, D. E., Zimova, M., Ellis, A. A., Witynski, M. L., Hennen, M., & Winger, B. M. (2020b). Data from: Shared morphological consequences of global warming in North American migratory birds. *Dryad Digital Repository*, <https://datadryad.org/stash/dataset/10.5061/dryad.8pkOp2nhw>
- Winger, B. M., Weeks, B. C., Farnsworth, A., Jones, A. W., Hennen, M., & Willard, D. E. (2019). Nocturnal flight-calling behaviour predicts vulnerability to artificial light in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 286(1900), 20190364. <https://doi.org/10.1098/rspb.2019.0364>

- Woodworth, B. K., Newman, A. E. M., Turbek, S. P., Dossman, B. C., Hobson, K. A., Wassenaar, L. I., Mitchell, G. W., Wheelwright, N. T., & Norris, D. R. (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia*, 181(2), 413–422. <https://doi.org/10.1007/s00442-015-3527-8>
- Yom-Tov, Y., Yom-Tov, S., Wright, J., Thorne, C. J. R. R., & Du Feu, R. (2006). Recent changes in body weight and wing length among some British passerine birds. *Oikos*, 112(1), 91–101. <https://doi.org/10.1111/j.0030-1299.2006.14183.x>
- Yong, W., & Moore, F. R. (1994). Flight morphology, energetic condition, and the stopover biology of migrating thrushes. *The Auk*, 111(3), 683–692. <https://doi.org/10.1093/auk/111.3.683>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zimova, M., Willard, D. E., Winger, B. M., & Weeks, B. C. (2021). Widespread shifts in bird migration phenology are decoupled from parallel shifts in morphology. *Journal of Animal Ecology*, 90, 2348–2361. <https://doi.org/10.1111/1365-2656.13543>