



Climate variability and the timing of spring raptor migration in eastern North America

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Many birds have advanced their spring migration and breeding phenology in response to climate change, yet some long-distance migrants appear constrained in their adjustments. In addition, bird species with long generation times and those in higher trophic positions may also be less able to track climate-induced shifts in food availability. Migratory birds of prey may therefore be particularly vulnerable to climate change because: 1) most are long-lived and have relatively low reproductive capacity, 2) many feed predominately on insectivorous passerines, and 3) several undertake annual migrations totaling tens of thousands of kilometers. Using multi-decadal datasets for 14 raptor species observed at six sites across the Great Lakes region of North America, we detected phenological shifts in spring migration consistent with decadal climatic oscillations and global climate change. While the North Atlantic and El Niño Southern Oscillations exerted heterogeneous effects on the phenology of a few species, arrival dates more generally advanced by 1.18 d per decade, a pattern consistent with the effects of global climate change. After accounting for heterogeneity across observation sites, five of the 10 most abundant species advanced the bulk of their spring migration phenology. Contrary to expectations, we found that long-distance migrants and birds with longer generation times tended to make the greatest advancements to their spring migration. Such results may indicate that phenotypic plasticity can facilitate climatic responses among these long-lived predators.

Long-term monitoring of seasonal events have revealed marked changes in species distributions and in the timing of phenological events for many animals and plants, which mirror the expected impacts of climate change (Both et al. 2004, Parmesan 2006, Knudsen et al. 2011). Such time series have produced some of the strongest evidence that climate change is altering biological phenomena (Parmesan 2006). Compared to many other organisms, the seasonal movements of migratory birds are exceptionally well-monitored throughout much of Europe and North America. The movements of many soaring raptors, such as hawks and eagles, are particularly easy to observe because they are almost exclusively diurnal migrants and utilize large topographic features to aid flight and navigation during migration. As a result, tens of thousands of individuals are funneled over relatively narrow belts of land during the spring and fall, particularly in a few locations in North America (Goodrich and Smith 2008).

Migration is a mechanism for avoiding periodic declines in local resource availability (Berthold 2001), but habitats occupied during different parts of the annual cycle are often spatially disjunct, ecologically disparate, and seasonally unstable. Despite inherent risks, migration should be favored if the benefit to survival and reproduction outweighs the costs (Greenberg and Marra 2005). Consequently, successful

migratory strategies require considerable spatial and temporal precision to reduce individual energetics and/or increase survival and reproduction (Berthold 2001). In the last decade, numerous studies have documented advancements in the timing of bird migration consistent with a compensatory response to global warming (Butler 2003, Both et al. 2004, Lehtikoinen et al. 2004, Jonzén et al. 2006, Rubolini et al. 2007, Van Buskirk et al. 2009, Knudsen et al. 2011). Such changes in phenology may be in response to climate-induced changes in the timing of peak resource availability (Both et al. 2009).

Other climatic phenomena such as the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) can drive annual to decadal fluctuations in resource availability (Glynn 1988, Oschlies 2001) and have profound consequences for the survival (Lamanna et al. 2012, García-Pérez et al. 2014), recruitment (Sillert et al. 2000), and migration (Hüppop and Hüppop 2003, Vähätalo et al. 2004, Gienapp et al. 2007, Van Buskirk et al. 2009) of many birds. Climatic variation caused by decadal patterns may also confound inferences of phenological change driven by long-term climate change. For example, long-term positive trends in the NAO can cause long periods of anomalously warm weather not directly related to anthropogenic climate change (Trouet et al. 2009).

Certain life history attributes appear to constrain climatic responsiveness, which may lead to asynchrony in phenological events across trophic levels and cause population declines (Visser et al. 2004, Both et al. 2006, Møller et al. 2008, Ter-raube et al. 2015). Mismatches between reproductive timing and food availability are expected to become more severe with increasing trophic level (Both et al. 2009, Visser et al. 2004), as for example, from granivorous sparrows to car-nivorous hawks. In addition, for K-selected top predators, changes in key demographic traits represent a greater threat than they would for r-selected bird species that have greater annual reproductive potential (MacArthur 1958). Organ-isms with low reproductive output are also expected to be constrained in their microevolutionary responses to climatic changes, as they are less able to recover from high selection intensity (Chevin et al. 2010). Finally, population declines in long-distance migrants have been attributed their weak phenological adjustments, which can lead to thermal and trophic mismatches (Both and Visser 2001, Butler 2003, Lehtikoinen et al. 2004, Marra et al. 2005, Both et al. 2006, 2010, Rubolini et al. 2007, Møller et al. 2008, Saino et al. 2011, but see Jonzén et al. 2006, Knudsen et al. 2011). This pattern is expected if wintering conditions are not correlated with conditions on the breeding ground (Møller et al. 2008). Although many birds of prey share a host of attributes asso-ciated with vulnerability to climate change, phenological changes in the spring migration of raptors and other avian predators, particularly in North America, have until recently received less attention from researchers (Van Buskirk 2012).

To investigate whether the spring timing of migratory raptors has changed over the last several decades, we used six long-term datasets collected by observatories across the Great Lakes region of North America. Together, these six sites have monitored over 100 000 migrating birds of prey each year – densities not seen elsewhere in the temperate region – for at least the last two decades (Goodrich and Smith 2008). We used these datasets to answer the following questions: 1) have raptors advanced their annual migration over the last several decades? 2) Do trends in the NAO and ENSO explain changes in spring migration arrival dates? 3) Which species traits, if any, are correlated with phenological

advancement? 4) Is the strength of phenotypic responses, expressed in haldanes, to climate change more congruent with genetic adaptation or plasticity?

Methods

Study sites and data acquisition

We identified all raptor monitoring sites with more than 20 yr of spring arrival data in Great Lakes region using the Hawk Count database (< www.hawkcount.org >) provided by the Hawk Migration Association of North America (< www.hmana.org >; Table 1). All count sites followed standardized protocols that include a professional or expert volunteer stationed at a designated count area for a pre-determined period each day. Seasonal observation periods vary among sites in order to capture the majority of the spring migration period but sites consistently monitor the same time window each year (Table 1). In total, we analyzed 11 203 d of count data for 14 species, each of which was monitored by at least four of the six sites (Table 2).

Analysis of phenological change

We used a two-step framework to characterize changes in spring migration timing. First, we used ordinary least squares (OLS) regression to estimate the $d\ yr^{-1}$ slope of the 25th, 50th and 75th percentile of cumulative arriv-als for each species at each count site. For species gen-erally present in low numbers (> 5 but $< 20\ yr^{-1}$), we constructed OLS models for only median arriv-als (Table 2). In addition to long-term climate change, arrival dates may also vary systematically with interannual climatic trends and temporal autocorrelation. To account for these potential sources of non-random error, OLS residuals were assessed for significant correlation ($\alpha = 0.05$ for all tests) with normalized indices of the NAO (December–March, Hurrell 1995) and the atmo-spheric component of the ENSO (December–February, Trenberth 1984).

Table 1. Characteristics of the six analyzed hawk observatory sites in the Great Lakes region of North America.

Site	Location	Coordinates	Years analyzed [‡]	Observation period [‡]	Average count ¹
Braddock Bay Raptor Research Count	Greece, New York	43°19'0"N, –77°43'0"W	1979–2011 (1993, 1998, 2006)	1 March–17 May (60–137)	42 723 ¹
Derby Hill Bird Observatory	Mexico, New York	43°31'4"N, –76°14'2"W	1980–2011 (1996, 2001–2002)	1 March–20 May (60–140)	31 609 ¹
Port Huron Hawk Count	Port Huron, Michigan	43°6'0"N, –82°30'0"W	1990–2011 (2008–2009)	10 March–27 May (69–147)	3993 ¹
Niagara Peninsula Hawk Watch	Grimsby, Ontario	43°11'2"N, –79°34'2"W	1991–2011	1 March–15 May (60–135)	13 381 ¹
Thunder Cape Bird Observatory	Thunder Bay, Ontario	48°18'8"N, –88°56'2"W	1992–2012 (1998)	1 March–15 May (60–135)	408
Whitefish Point Bird Observatory	Paradise, Michigan	46°46'2"N, –84°57'2"W	1984–2011 (1996)	15 March–31 May (74–151)	17 000 ¹

[‡]– Years in parenthesis were excluded due to truncated observation periods.

[‡]– Calendar dates given for non-leap years. Analyses were performed with ordinal dates, in parenthesis.

¹– Goodrich and Smith 2008.

Table 2. Species and migration distribution percentiles analyzed at each hawk count site. Numerals indicate the 1st, 2nd, and 3rd quartiles, respectively.

Species/Site	Braddock Bay	Derby Hill	Niagara Peninsula	Port Huron	Thunder Cape	Whitefish Point
American kestrel <i>Falco sparverius</i>	1, 2, 3	1, 2, 3	1, 2, 3	2	2	1, 2, 3
Bald eagle <i>Haliaeetus leucocephalus</i>	2	2	2	–	–	2
Broad-winged hawk <i>Buteo platypterus</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3
Cooper's hawk <i>Accipiter cooperii</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3
Golden eagle <i>Aquila chrysaetos</i>	2	2	2	–	–	2
Merlin <i>Falco columbarius</i>	2	2	2	–	2	2
Northern goshawk <i>Accipiter gentilis</i>	2	2	2	–	–	2
Northern harrier <i>Circus cyaneus</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3
Osprey <i>Pandion haliaetus</i>	1, 2, 3	1, 2, 3	1, 2, 3	–	–	1, 2, 3
Rough-legged hawk <i>Buteo lagopus</i>	1, 2, 3	1, 2, 3	1, 2, 3	2	–	1, 2, 3
Red-shouldered hawk <i>Buteo lineatus</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3
Red-tailed hawk <i>Buteo jamaicensis</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3
Sharp-shinned hawk <i>Accipiter striatus</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3
Turkey vulture <i>Cathartes aura</i>	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	–	1, 2, 3

Time series are commonly autocorrelated; if this is not addressed, regression models may underestimate standard errors and generate spurious results (von Storch 1999). We assessed the presence of first-order autocorrelation (ρ) by means of the Durbin–Watson test as contained in the car package (Fox and Weisberg 2010) in R ver. 3.0.0 (R Core Team). When significant evidence for autocorrelation was found, we transformed the data by prewhitening:

$$\tilde{Y}_{t-1} = Y_t - \hat{\rho}Y_{t-1}$$

where Y are arrival times, t equals time, and $\hat{\rho}$ is the estimate of first-order autocorrelation (von Storch 1999). In all cases, models were refit and reexamined after removal of any significant trends.

In the second step of the analysis, we estimated marginal means for each species to account for geographic and intraspecific variability in phenological adjustments with linear mixed models. The OLS slope (Δ d yr^{−1}) of each species by site was included as the response variable while latitude, longitude, initial year of observation, and their squared terms were included as fixed effects (Rubolini et al. 2007). Site was considered as a random effect to capture unmeasured variability associated with e.g. local weather conditions, disturbance, and land use changes. Models were constructed using the lme4 package (Bates et al. 2013) in R and optimized according to the maximum likelihood criterion. Parsimonious models were selected according to the small sample adjusted Akaike information criterion (AIC_c) using an exhaustive search implemented in the R package MuMin (Barton 2013). Separate models were constructed for each of the 25th, 50th, and 75th arrival percentiles. Final models including the fixed effects identified in the model selection procedure were fitted with the restricted maximum likelihood algorithm.

Species life-history trait analysis

We investigated the relationship between species life history attributes and their responses to climate change by means of linear mixed models for the 10 migratory raptor species abundant in the Great Lakes. Broadly, a phenological response can

be facilitated by plasticity and/or evolutionary adaptation, but we note that the emergent demographic properties of a population may also be important (Gill et al. 2014). In the first category, we initially considered trophic position (Both et al. 2009, Thackeray et al. 2010), migratory strategy (partial vs complete), flight mode (Bohrer et al. 2012, flapping vs soaring), migration distance (Butler 2003, Rubolini et al. 2007, Møller et al. 2008, Both et al. 2010, Végvári et al. 2010) and habitat specialization (Crick 2004, Jiguet et al. 2007, Végvári et al. 2010) as predictors of a species' likelihood to respond to climate change. We extracted data on diet during the breeding season for each species from the Birds of North America monographs (BNA; Poole 2005). Trophic level was coded as a binary value according to whether the primary prey were herbivores (e.g. small mammals) or insectivores (e.g. songbirds). Migratory strategy and flight strategy were also summarized from BNA species monographs. Similarly, migration distances were inferred from BNA species range maps: species were considered 'long' distance migrants if breeding and winter habitats were disjunct in eastern North America and 'short' if the ranges were conterminous. The number of habitat types used during the breeding season, as a proxy for habitat specialization, was extracted from Birdlife factsheets (Birdlife International 2013).

The rate at which a species may respond to climate change through genetic adaptation can be partially predicted by generation time and population size. Shorter generation times can allow a more rapid response to weak selection, while large populations may harbor more adaptive genetic variation and can better sustain the demographic consequences of stronger selection (Chevin et al. 2010). North American population size was obtained from the Partners in Flight database (Partners in Flight Science Committee 2012) and population trends were described categorically as 'decreasing', 'increasing', or 'stable' according to the North American Breeding Bird Survey (Sauer et al. 2012). Generation time, defined as the inverse of mean annual mortality plus the age at first breeding, i.e. the average age of parents in the population, was included as a numeric variable and obtained from the Birdlife factsheets (Birdlife International 2013).

Species trait mixed-effects models were only constructed for the median arrival dates of the 10 most abundant spe-

cies. The phenological response of each species at each site, represented by the OLS Δ d yr⁻¹ slope, was included as the dependent variable (Møller et al. 2008) and site was included as a random effect. Values of the trait attributes considered as explanatory variables are provided in Supplementary material Appendix 1, Table A1. Model development and selection followed the procedure outlined above. Variance inflation factors (VIF) were used to identify multicollinearity. Coefficients were removed according to the severity of their multicollinearity until all remaining variables had a VIF less than five.

Rates of phenotypic change

We quantified the tempo of per-generation advances in migration timing using the haldane, measure of change in a trait expressed in terms of standard deviations per generation:

$$h = \frac{\Delta X}{\frac{s_p}{g}}$$

where h is the change in haldanes, ΔX is the median change in arrival dates in days over the time series, s_p is the pooled standard deviation, and g is the number of generations (Gienapp et al. 2007, Van Buskirk et al. 2012. See Supplementary material Appendix 1, Table A1 for generation times). We calculated haldane values for the change in median arrival dates for the five most climatically responsive species (see Results below). As a standardized measure, haldanes allow comparison of the rates of migration advancement for birds of prey with those previously reported for passerines (Gienapp et al. 2007, Van Buskirk et al. 2012).

Analysis of climatic oscillations

We constructed OLS regression models for each species at each site to estimate the correlation between arrival dates and the NAO and ENSO indices. For significant correlations, the effects of the oscillation may be exerted on any part of the species' annual range, including at the hawk count site itself. If the relationship between an oscillation and migratory phenology is predominately driven by local or regional conditions near the hawk count sites, then a larger proportion of species should be influenced at sites where local weather is more strongly correlated to NAO or ENSO. To illustrate the relationship between NAO/ENSO on meteorological conditions on Great Lakes and arrival dates at the hawk count sites, we generated maps of the correlation coefficient between temperature and precipitation (Willmott and Matsuura 1995) and the NAO index (Hurrell 1995) and Southern Oscillation Index as a proxy for ENSO (Trenberth 1984) from 1941 to 2011 (Earth System Research Laboratory 2008; < www.esrl.noaa.gov/psd/data/correlation/ >).

Results

We analyzed a total of 165 time-series (Table 2) and residual analysis indicated systematic bias in 14 models. Linear

trends in residuals explained by the NAO or ENSO indices were removed from 8 (4.8%) models. The Durbin–Watson test found evidence for significant autocorrelation ($p < 0.05$) in 6 (3.6%) time-series.

Phenological changes across arrival percentiles

Arrival dates in the 25th percentile of the migration distribution advanced by an average of 1.55 (SE 0.03) days per decade (0.155 d yr⁻¹) when averaged across all species and sites (Fig. 1). Median and 75th percentile arrival dates advanced somewhat less: 0.90 (SE 0.04) and 1.09 (SE 0.26) days per decade, respectively (Fig. 1). Median arrival dates advanced less than 75th percentile dates due to the bald eagles at the Derby Hill Bird Observatory on the southern shore of Lake Ontario, who delayed their arrival an average of 10 d per decade over the last 30 yr (Supplementary material Appendix 1, Table A2). Overall, 32% (52) of the time-series demonstrated a significant ($p < 0.05$) phenological response, which is more than expected by chance at the $\alpha = 0.05$ level (two-tailed binomial test, $p < 0.001$). For significant models, the Δ d yr⁻¹ relationship explained an average of 25% of the variability in arrival dates ($r^2 = 0.25$, SE = 0.02).

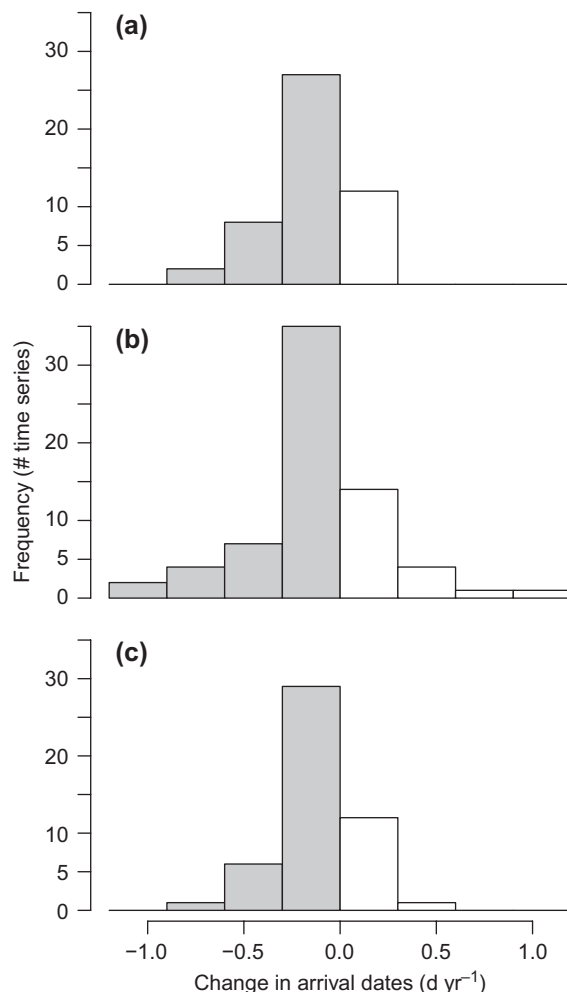


Figure 1. Distribution of changes in spring arrival dates (Δ d yr⁻¹) in the (a) 25th, (b) 50th, and (c) 75th arrival percentiles of 14 raptor species migrating across six monitoring sites across the Great Lakes region of North America.

Interspecific consistency and geographic variability

The mixed-effects model analysis indicated small but significant non-linear longitudinal patterns in each of the 25th, 50th, and 75th migration percentiles. In each segment of the migration distribution, birds at mid-longitude sites showed the greatest advance in arrival dates (Supplementary material Appendix 1, Fig. A1a). All three also varied positively with latitude, suggesting a tendency for larger arrival advancements at more southern latitudes (Supplementary material Appendix 1, Fig. A1b), even within the relatively narrow latitudinal belt included in this study. Seventy percent (7/10) of species significantly advanced their earliest arrival dates across all six hawk watch sites (Fig. 2, Supplementary material Appendix 1, Table A3). Large standard errors in marginal means from the 50th and 75th percentiles reflect intraspecific variability in responses across the six observation sites (Supplementary material Appendix 1, Table A3). Despite this, 43 and 50% of species made significant phenological advancements to their median and last (75th migration percentile) arrival dates, respectively (Fig. 2, Supplementary material Appendix 1, Table A3).

Of the 14 raptor species, 10 were abundant enough (> 20 individuals in all years) to enable analysis of phenological trends at all three arrival percentiles. Seven of the 10 species made a significant phenological advancement in at least one segment of their migration distribution over the entire Great Lakes region. The American kestrel, red-shouldered hawk, and red-tailed hawk showed no consistent change in migratory timing (Fig. 2, Supplementary material Appendix 1, Table A3). Red-shouldered hawks did not significantly advance their migration at any of the six sites but American kestrel and red-tailed hawk did significantly advance their arrivals at some sites (Supplementary material Appendix 1,

Table A2). The broad-winged hawk, rough-legged hawk, osprey, sharp-shinned hawk and turkey vulture were the most climatically responsive species and significantly advanced their 25th–75th arrival percentiles across the Great Lakes corridor, even after correcting for heterogeneity in responses across sites (Fig. 2, 3, Supplementary material Appendix 1, Table A3).

For rare species (≥ 5 but < 20 individuals in one or more years), phenological trends were only analyzed for median arrival dates. While three of the four species are naturally rare migrants in the Great Lakes, the bald eagle was only rare during the initial decades of the time series. Of these rare migrants, only the merlin significantly advanced its median migration date (Fig. 2, Supplementary material Appendix 1, Table A3).

Changes in the timing of migration in relation to life history traits

Migration distance and migration strategy were completely collinear among the species studied here (Supplementary material Appendix 1, Table A1). Population trend was strongly collinear with the remaining predictors ($VIF = 59$) and was significantly correlated with generation time and population size, where species longer generation times and smaller populations were more likely to be stable or increasing ($p < 0.001$ for both). After removing migration strategy and population trend, the remaining predictors – generation time, population size, trophic level, flight mode, niche breadth, and migration distance – were not strongly collinear ($VIF \leq 3.23$).

Longer generation times, longer migration distances, and higher trophic level positions were all associated with larger advancements in spring arrival dates (Table 3) in

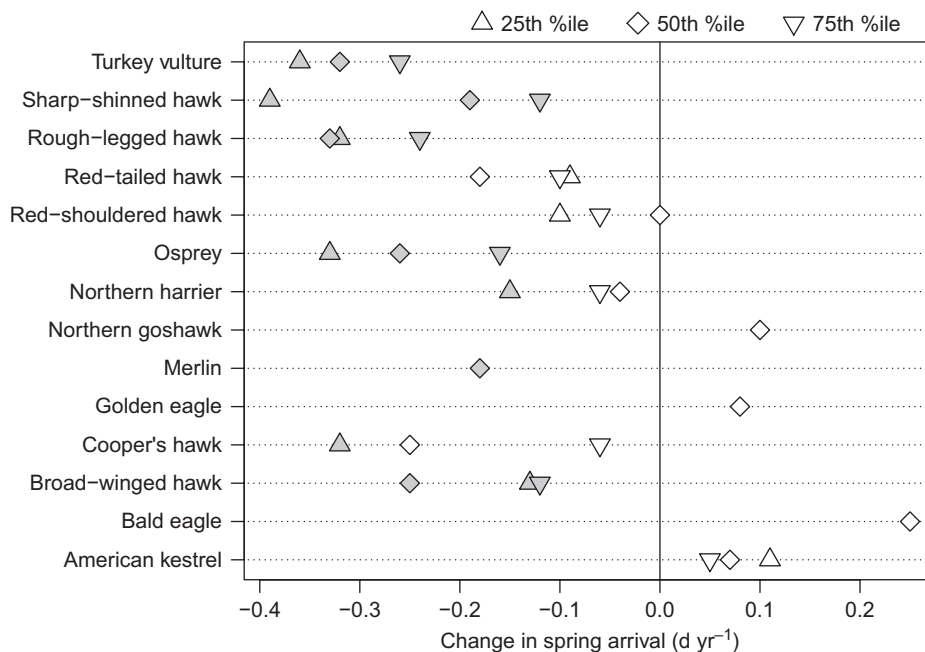


Figure 2. Marginal mean changes in spring arrival dates (Δ d yr⁻¹) after accounting for interspecific variability, geography, and random effects by means of mixed models. Changes in each migration percentile (25th, 50th, and 75th) are presented for abundant species (> 20 in all years), while changes in median arrival dates are presented for rare species. Shaded symbols denote a mean slope significantly different from zero. Standard errors for slopes are given in Supplementary material Appendix 1, Table A3.

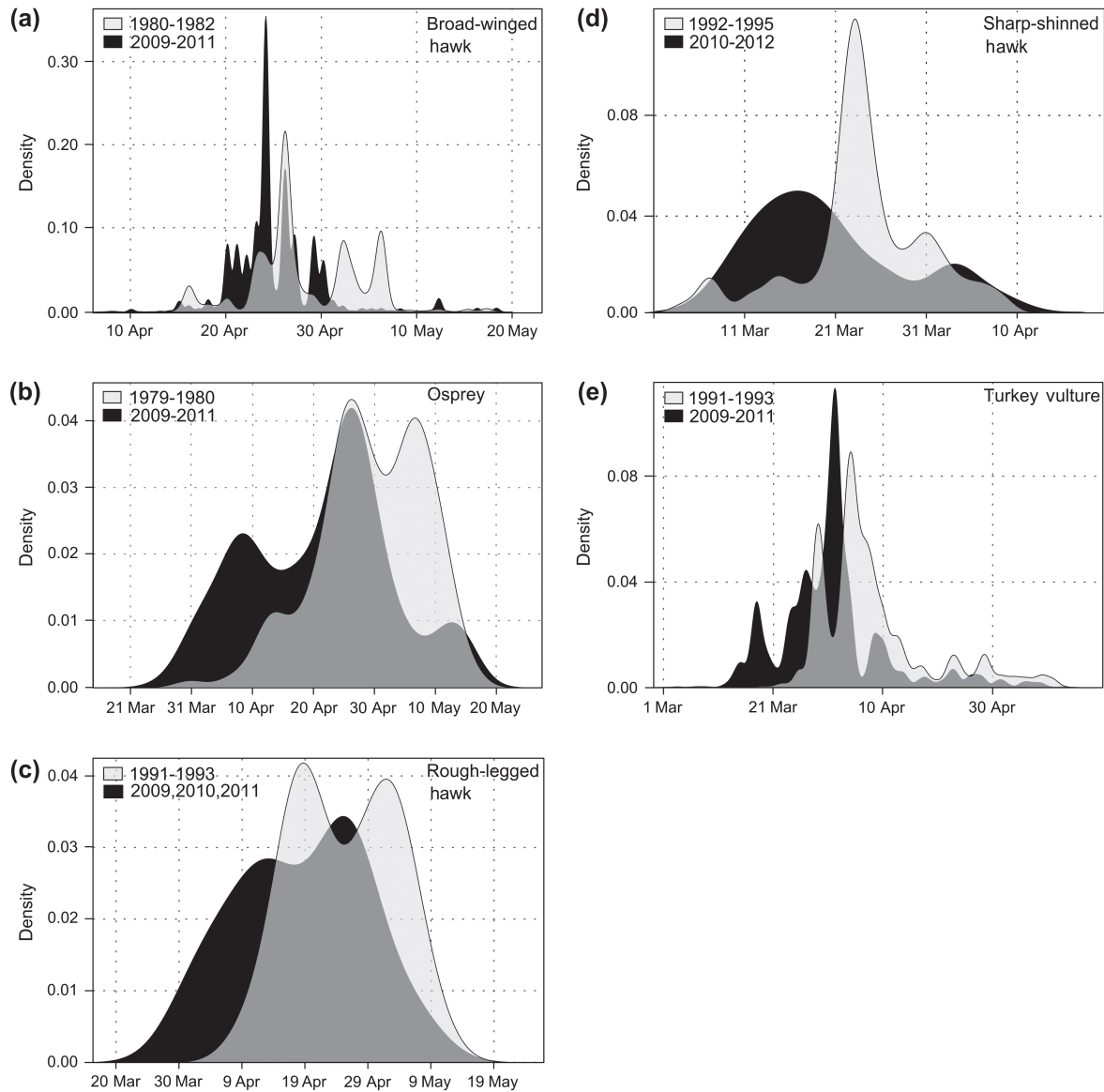


Figure 3. Kernel density estimates of spring migration timing for species in which at least half the of individuals (i.e. 25th–75th percentiles) advanced their migration across the entire Great Lakes region in recent years. For ease of display, the first and last three years of a time series at a representative site are shown for each species: (a) broad-wing hawks at Derby Hill, (b) ospreys, Braddock Bay, (c) rough-legged hawks, Port Huron, (d) sharp-shinned hawks, Thunder Cape, (e) turkey vultures, Niagara Peninsula.

the six models ranked higher than the null model. The top-ranked model indicated that species with longer generation times have tended towards greater phenological advancements (Table 3). Spring migration advanced by 0.39 d/decade per each year of generation time, a result consistent with the relatively strong advancements of the long-lived osprey, turkey vulture, and rough-legged hawk (Table 3). The second-ranked model ($\Delta AIC_c = 0.05$) indicated that the median arrival dates of long-distance migrants advanced 1.37 d/decade more than short-distance migrants, while the third-ranked model included trophic level and generation time (Table 3). The top model was only about twice as likely as the null model (Burnham et al. 2011; $\Delta AIC_c = 1.78$; Table 3), but these results indicate a weak tendency for species that are long-distance migrants, long-lived, and avivorous to make the largest migratory adjustments. We present

the top seven models, including the null, because they optimize the trade-off between model complexity and fit nearly as well.

Tempo of phenotypic change

Advancement in spring median arrival dates in haldanes (i.e. the rate of phenotypic change expressed in terms of standard deviations per generation) ranged from an average of 0.16 to 0.33 for the five most climatically responsive species (Table 4). That is, the average rate of phenotypic change per generation for all five species exceeded 15% of the pooled standard deviation per generation, which suggests a rapid rate of evolution. Nevertheless, haldane values varied within species and among sites, which reflects geographic variability in the magnitude of phenotypic change (Table 4).

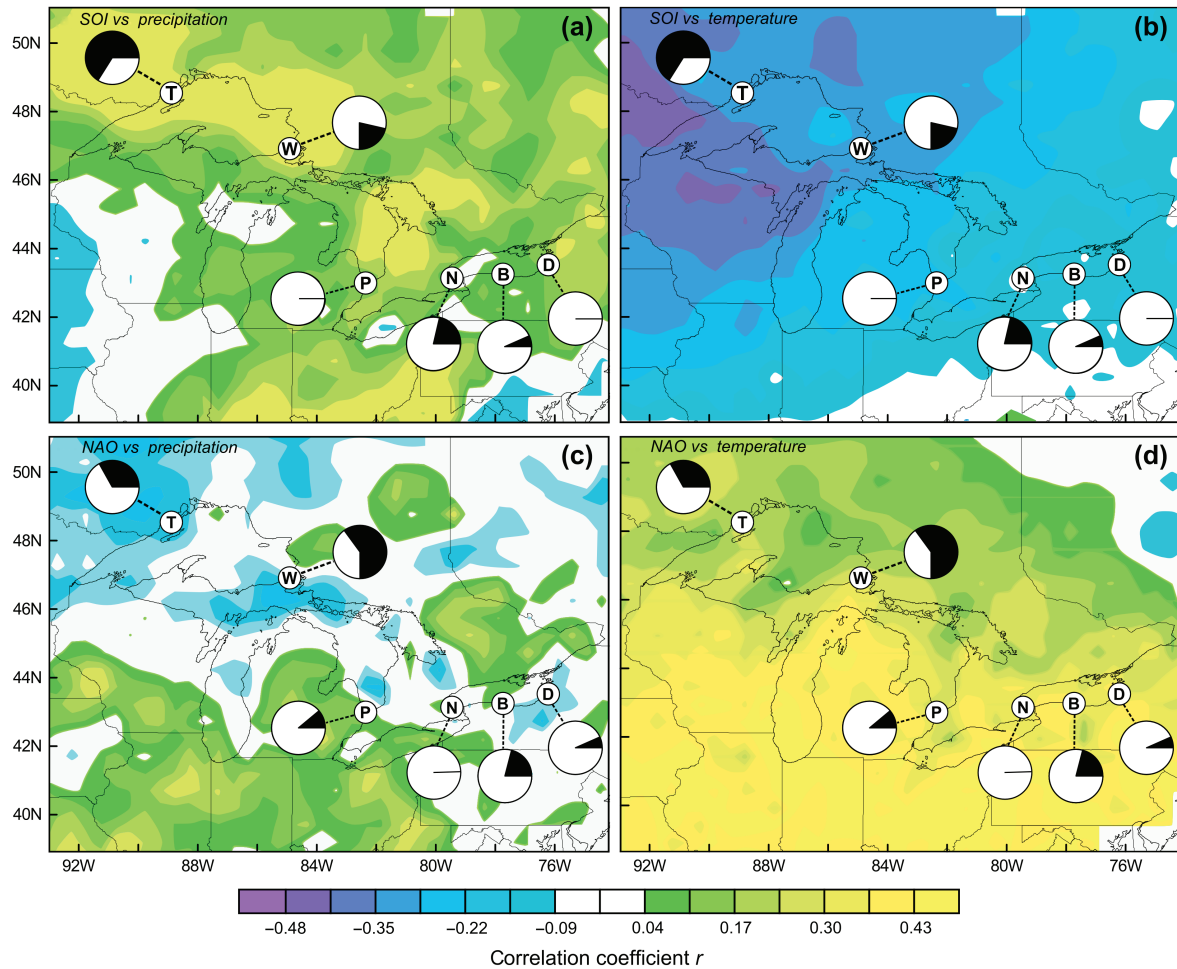


Figure 4. Correlations between winter surface precipitation and air temperature and the North Atlantic and Southern Oscillation indices. Absolute values of correlation coefficients > 0.254 are significant at the $\alpha = 0.05$ level. Pie charts indicate the percentage of migration time series at each hawk count site that can be significantly explained by each index. Hawk count sites are abbreviated by the first letter of their name (Table 1).

Influence of climatic oscillations on bird migration

Variation in arrival dates could be explained by either the NAO or ENSO indices in a total of 29 time series: 18 (10.9%) and 11 (6.7%), respectively. The winter NAO index is positively and significantly correlated with precipitation through much of the Great Lakes Region, while the SOI demonstrates the opposite trend (Fig. 4). Arrival dates tended to be positively

correlated with the NAO and negatively correlated with ENSO (Supplementary material Appendix 1, Table A4, A5). Because our data are coded in ordinal calendar dates, a positive correlation indicates an arrival later in the year. Hence, both indices paradoxically indicate earlier spring arrivals during phases of the NAO and ENSO that are associated with cooler and wetter weather in the Great Lakes (Fig. 4).

Winter precipitation patterns over Lake Superior are more strongly correlated with the NAO and ENSO than in

Table 3. Species trait predictors of changes in median arrival dates (Δ d/decade) in the 10 abundant raptor species according to mixed model analysis. Observation sites were included as random intercepts and best models selected accord to the small-sample corrected Akaike information criterion (AIC_c). We present the top five models, as the top-model is not conclusively superior to the null model ($\Delta AIC_c = -1.76$).

Rank	Fixed effects (Δ d/decade; SE)	Random effects (%variance)	Residual variance	ΔAIC_c
1	Generation time (-0.39 ; 0.20)	52.94	0.52	0
2	Migration distance: long (-1.37 ; 0.70)	51.98	0.52	0.05
3	Generation time (-0.50 ; 0.22) + trophic level: avivore (-1.05 ; 0.85)	53.44	0.51	0.43
4	Migration distance: long (-1.60 ; 0.74) + trophic level: avivore (-0.79 ; 0.82)	51.81	0.52	1.09
5	Migration distance: long (-0.82 ; 0.91) + generation time (-0.24 ; 0.26)	52.73	0.52	1.14
6	Migration distance: long (-0.91 ; 0.90) + generation time (-0.35 ; 0.27) + trophic level: avivore (-1.11 ; 0.85)	53.34	0.51	1.35
7	null			1.76

Table 4. Per-generation advances in migration timing measured in haldanes (h ; SD units per generation) for the five species that made significant adjustments to their 25th–75th arrival percentiles.

Species	Braddock Bay	Derby Hill	Niagara Point	Port Huron	Whitefish Point	Thunder Cape	Species $\hat{h}$
Osprey	0.23	0.03	0.27	–	0.15	–	0.17
Broad-winged hawk	0.44	0.27	0.28	0.23	0.24	–	0.29
Turkey vulture	0.51	0.12	0.16	0.56	0.30	–	0.33
Rough-legged hawk	0.08	0.09	0.16	0.46	0.35	–	0.23
Sharp-shinned hawk	0.16	0.04	0.10	0.27	0.13	0.26	0.16
$\hat{h}$ by site	0.28	0.11	0.19	0.38	0.23	0.26	0.17

the southern Great Lakes (Fig. 4a, c). Variation in the arrival dates of 64% of species observed at Whitefish Point and 33% at Thunder Cape Bird Observatory could be explained by the NAO index (Fig. 4c), although the number of species observed during the spring migration at the latter is small. Similarly, arrival dates of more species at these two Lake Superior hawk counts were also correlated with the SOI, a proxy for ENSO activity, than at the count sites on the southern Lakes (Fig. 4a). Despite our small sample size and low power, NAO-associated local precipitation anomalies were significantly correlated to the proportion of species at each site whose arrival dates were affected by NAO (Pearson's $r = 0.84$, $p < 0.05$). Any possible relationship between the NAO/ENSO-related temperature fluctuations and arrival dates was less clear, as regional temperatures at all the hawk count sites are all similarly influenced by these oscillations (Fig. 4b, d).

Finally, we note that for significant correlations, the NAOI and SOI explain on average 20% of the variance in arrival dates (mean $r^2 = 0.20$, $SE = 0.05$). Therefore, decadal climatic trends explain significantly less variation in arrival dates than the apparent response to global warming (two-tailed t-test, $p < 0.02$).

Discussion

We found strong evidence that many North American raptors species have advanced their spring migration in a pattern consistent with climate change on a continental scale, even after accounting for the potentially confounding effects of climatic oscillations and temporal autocorrelation. Consistent with prior studies of passerines, we observed intraspecific consistency of phenological responses but also geographic heterogeneity (Rubolini et al. 2007, Knudsen et al. 2011). Over half (8/14) of the raptors consistently advanced some portion of their spring migration phenology, while five of the 10 most abundant species advanced nearly their entire arrival distribution across the Great Lakes. The magnitude of significant responses ranged from 1.2 to 3.9 d per decade, similar to those reported for passerines and other non-predatory birds (Lehikoinen et al. 2004, Rubolini et al. 2007, Knudsen et al. 2011), especially in North America (Van Buskirk et al. 2009). Given the long generation time of raptors, however, this shift represents a much faster per-generation response compared to many passerines (mean h for raptors = 0.23, $SD = 0.14$, passerines = 0.05, $SD = 0.04$; Gienapp et al. 2007, Van Buskirk et al. 2012) but is similar

to the rate of change observed the breeding times of other birds ($h = 0.19$, Gienapp et al. 2007).

Such changes in mean arrival time may appear modest, yet the importance of phenological synchrony between predator and prey have been shown for some bird taxa (Strode 2003, Visser et al. 2004). We focus on spring arrivals, but multiple studies in North America and Europe have found that migratory birds of prey delay their fall departures in a manner consistent with climate change (Rosenfield et al. 2011, Van Buskirk 2012, Jaffré et al. 2013) and may also be undergoing adaptive changes in nesting dates and migration distances (Heath et al. 2012). Lacking evidence that these behavioral responses are sufficient to maintain productivity, survivorship and competitive relationships, we believe such shifts are a cause for concern and a call for detailed studies such as ours in other parts of the world (Knudsen et al. 2011).

Species trait predictors of phenological response

Climate-induced asynchrony with resource availability is expected to increase with trophic level (Both et al. 2006, 2009), and many raptors are avivores who feed on insectivorous passerine birds. In addition, the slow, K-selected life history strategy of many birds of prey may render them sensitive to demographic declines (MacArthur 1958) and limit their potential for rapid evolutionary adaptation (Chevin et al. 2010). While we did not find strong evidence for an association between any trait and migratory adjustment, long-distance migrants (and thus also complete migrants), avivores, and species with long generation times tended to make the largest migration advancements among the raptors studied here. This association, albeit weak, between longer generation times, longer migration distances, and higher trophic levels and larger climatic adjustments contrasts markedly with many other studies, which suggest these traits may constrain phenological responses in other birds (Both and Visser 2001, Butler 2003, Lehikoinen et al. 2004, Visser et al. 2004, Marra et al. 2005, Both et al. 2006, 2010, Rubolini et al. 2007, Møller et al. 2008, Thackeray et al. 2010, Végvári et al. 2010, Saino et al. 2011).

Long-lived birds in our analysis advanced their spring arrival dates at least as much as shorter-lived birds and tended to arrive 0.39 d earlier per decade for each year of generation time (Table 3; 9-yr gap between the shortest and longest generation times). Long generation times and high annual survival can constrain genetic adaptation (Gienapp et al. 2007, Chevin et al. 2010) and demographic mechanisms for advancing key phenological events (Gill

et al. 2014) Indeed, haldane values for advancement timing reported here are large and, assuming migration timing has a heritability of approximately 0.54 (Møller 2001) would require a selection intensity of 42% of the standard phenotypic deviation to be explained solely by genetic adaptation, an unrealistic and demographically unsustainable scenario (Gienapp et al. 2008).

Phenotypic plasticity could be important in facilitating responses to climate change in long-lived birds if individuals can learn from previous seasons and alter their migratory behavior in response. The short-lived blue tit *Parus caeruleus* has been shown experimentally to learn from past reproductive failure and change the timing of their nesting phenology (Grieco et al. 2002), but individual learning in populations comprised mostly of inexperienced birds is unlikely to drive a population-level response (Visser et al. 2004). Whether individual learning can explain the advances in migration timing of phenologically-responsive raptors is unknown, but multiyear satellite tracking of osprey has revealed that individuals modulate both their departure from their winter habitat and arrival to the breeding ground by 1–17 d (Martell et al. 2014). While further research is required to tease apart the mechanisms driving phenological change, the climatic responsiveness of this long-lived group of birds is congruent with evidence underlining the importance and prevalence of migratory plasticity (Gienapp et al. 2007, 2008, Charman-tier et al. 2008, Chevin et al. 2010, Knudsen et al. 2011, Vedder et al. 2013).

NAO/ENSO-mediated phenological responses

Decadal climatic oscillations had a pronounced effect on arrival dates in approximately 17% of the analyzed time series but explained changes in phenology less well than the annual signal of climate change overall. Part of this correlation is evidently explained by local weather at the hawk count sites; sites whose precipitation is more tightly linked to either the NAO or ENSO had a greater proportion of birds whose migrations were affected by these climatic oscillations. Unexpectedly, OLS slopes indicate earlier arrivals following winters likely to be colder and wetter than average. In fact, the bald eagle, which may overwinter near many of our analyzed sites, was the only species to arrive earlier in the generally warmer and drier El Niño or NAO-positive years.

Given reluctance of many species to fly in snow or rain and the reduced visibility in such conditions, it seems unlikely that colder and wetter weather actually causes earlier arrivals, although we did not directly model the relationship between local weather and migratory timing. Instead, the recent negative trend of the NAO and associated long, cold winters in the Great Lakes may have contributed to the smaller phenological adjustments made by short-distance migrants, whereas long-distance migrants would be naïve to these conditions prior to migration. Accordingly, we hypothesize that differences in hawk count catchment area, coupled with heterogeneous global effects of these oscillations (Crick 2004), may explain the observed pattern. In addition to being more strongly affected by the NAO and ENSO, the two western most hawk count sites are also more likely to include migrants from Mexico or Central America (Goodrich and Smith 2008). Birds may increase stop-over

durations from these sites in favorable, NAO-positive years, leading to later arrivals dates (Courter et al. 2013), or high productivity of tropical wintering grounds in NAO-negative years may improve body condition and facilitate early departures (Marra et al. 1998, Sillett et al. 2000, Studds and Marra 2007, McKellar et al. 2012). While both NAO- and ENSO-induced events appear important to the annual cycle of some species, further research will require more detailed knowledge of migratory connectivity (McKellar et al. 2012, López-López et al. 2014). Continued improvements in satellite telemetry should enable detailed assessment of the importance of weather and other cues across a bird's annual range in driving migration (López-López et al. 2014).

In general, we found that many birds of prey in the Great Lakes region have advanced their migration in an inter-annual pattern consistent with climate change and may modulate their migration in response to decadal climatic patterns. Species traits associated with phenological adjustments may not be broadly generalizable across taxa or functional groups. Instead, whether a particular trait, such as long generation times, constrains or promotes a response will likely depend on other life-history attributes and ecological context. We expect that the international network of bird observatories and the long-term monitoring they provide will serve as early barometers of the capacity of raptors to adjust and persist in the coming decades. Moreover, continuing satellite telemetry efforts will enable direct testing of the importance of individual (Charman-tier et al. 2008) and population (Gill et al. 2014) responses to climate change in the future.

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References

- Bárton, K. 2013. MuMIn: multi-model inference. – R package ver. 1.9.13, <<http://CRAN.R-project.org/package=MuMIn>>.
- Bates, D., Maechler, M. and Bolker, B. 2013. lme4: linear mixed-effects models using Eigen and Eigen. – R package ver. 1.0-5, <<http://CRAN.R-project.org/package=lme4>>.
- Berthold, P. 2001. Bird migration: a general survey. – Oxford Univ. Press.
- Birdlife International 2013. IUCN Red List for birds. – <www.birdlife.org>.
- Bohrer, G., Brandes, D., Mandel, J. T., Bildstein, K. L., Miller, T. A., Lanzone, M., Katzner, T., Maisonneuve, C. and Tremblay, J. A. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. – Ecol. Lett. 15: 96–103.

- Both, C. and 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., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Järvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Sanz, J. J., Silverin, B., Slater, F. M., Skolov, L. V., Török, J., Winkel, W., Wright, J., Zang, H. and Visser, M. E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. – *Proc. R. Soc. B* 271: 1657–1662.
- Both, C., Bouwhuis, S., Lessells, C. and 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. and Visser, M. E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? – *J. Anim. Ecol.* 78: 73–83.
- Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. and Foppen, R. P. B. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. – *Proc. R. Soc. B* 277: 1259–1266.
- Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. – *Behav. Ecol. Sociobiol.* 65: 23–35.
- Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. – *Ibis* 145: 484–495.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. and Sheldon, B. C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – *Science* 320: 800–803.
- Chevin, L.-M., Lande, R. and Mace, G. M. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. – *PLoS Biol.* 8: e1000357.
- Courter, J. R., Johnson, R. J., Bridges, W. C. and Hubbard, K. G. 2013. Assessing migration of ruby-throated hummingbirds (*Archilochus colubris*) at broad spatial and temporal scales. – *Auk* 130: 107–117.
- Crick, H. Q. P. 2004. The impact of climate change on birds. – *Ibis* 146: 48–56.
- Earth System Research Laboratory 2008. Linear correlations in atmospheric seasonal/monthly averages. – NOAA, Boulder, CO, <www.cdc.noaa.gov/Correlation/>.
- Fox, J. and Weisberg, S. 2010. An R companion to applied regression. – Sage.
- García-Pérez, B., Hobson, K. A., Albrecht, G., Cadman, M. D. and Salvadori, A. 2014. Influence of climate on annual survival of barn swallows (*Hirundo rustica*) breeding in North America. – *Auk* 131: 351–362.
- Gienapp, P., Leimu, R. and Merilä, J. 2007. Responses to climate change in avian migration time: microevolution versus phenotypic plasticity. – *Clim. Res.* 35: 25–35.
- Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. and Merilä, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. – *Mol. Ecol.* 17: 167–178.
- Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M. and Gunnarsson, T. G. 2014. Why is timing of bird migration advancing when individuals are not? – *Proc. R. Soc. B* 281: 20132161.
- Glynn, P. W. 1988. El Niño-Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. – *Annu. Rev. Ecol. Syst.* 19: 309–346.
- Goodrich, L. J. and Smith, J. P. 2008. Raptor migration in North America. – In: Bildstein, K. L., Smith, J. P., Inzuna, E. R. and Veit, R. R. (eds), State of North America's birds of prey. Nuttall Ornithological Club and American Ornithologists Union, pp. 37–150.
- Greenberg, R. and Marra, P. P. 2005. Birds of two worlds: the ecology and evolution of migration. – JHU Press.
- Grieco, F., Van Noordwijk, A. J. and Visser, M. E. 2002. Evidence for the effect of learning on timing of reproduction in blue tits. – *Science* 296: 136–138.
- Heath, J. A., Steenhof, K. and Foster, M. A. 2012. Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. – *J. Avian Biol.* 43: 376–384.
- Hüppop, O. and Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. – *Proc. R. Soc. B* 270: 233–240.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Jaffré, M., Beaugrand, G., Goberville, E., Jiguet, F., Kjellén, N., Troost, G., Dubois, P. J., Lepêtre, A. and Luczak, C. 2013. Long-term phenological shifts in raptor migration and climate. – *PLoS One* 8: e79112.
- Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S. E. and Couvet, D. 2007. Climate envelope, life history traits and the resilience of birds facing global change. – *Global Change Biol.* 13: 1672–1684.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. and Stenseth, N. C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. – *Science* 312: 1959–1961.
- Knudsen, E., Linden, 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., Hedenstrom, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Peron, G., Ranta, E., Rubolini, D., Sparks, T. H., Spina, F., Studds, C. E., Sæther, S. A., Tryjanowski, P. and Stenseth, N. C. 2011. Challenging claims in the study of migratory birds and climate change. – *Biol. Rev.* 86: 928–946.
- Lamanna, J. A., George, T. L., Saracco, J. F., Nott, M. P. and DeSante, D. F. 2012. El Niño-Southern Oscillation influences annual survival of a migratory songbird at a regional scale. – *Auk* 129: 734–743.
- Lehikoinen, E., Sparks, T. and Zolakevicius, M. 2004. Arrival and departure dates. – *Adv. Ecol. Res.* 35: 1–31.
- López-López, P., García-Ripollés, C. and Urios, V. 2014. Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. – *Curr. Zool.* 60: 642–652.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. – *Ecology* 39: 599–619.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Marra, P. P., Francis, C. M., Mulvihill, R. S. and Moore, F. R. 2005. The influence of climate on the timing and rate of spring bird migration. – *Oecologia* 142: 307–315.
- Martell, M. S., Bierregaard Jr, R. O., Washburn, B. E., Elliott, J. E., Henny, C. J., Kennedy, R. S. and MacLeod, I. 2014. The spring migration of adult North American ospreys. – *J. Raptor Res.* 48: 309–324.
- McKellar, A. E., Marra, P. P., Hannon, S. J., Studds, C. E. and Ratcliffe, L. M. 2012. Winter rainfall predicts phenology in widely separated populations of a migrant songbird. – *Oecologia* 172: 1–11.
- Møller, A. P. 2001. Heritability of arrival date in a migratory bird. – *Proc. R. Soc. B* 268: 203–206.

- Møller, A. P., Rubolini, D. and Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. – *Proc. Natl Acad. Sci. USA* 105: 16195–16200.
- Oschlies, A. 2001. NAO-induced long-term changes in nutrient supply to the surface waters of the North Atlantic. – *Geophys. Res. Lett.* 28: 1751–1754.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Partners in Flight Science Committee 2012. Species assessment database, version 2012. – <<http://rmbo.org/pifassessment>>.
- Poole, A. 2005. The birds of North America online. – Cornell Laboratory of Ornithology.
- Rosenfield, R. N., Lamers, D., Evans, D. L, Evans, M. and Cava, J. A. 2011. Shift to later timing by autumnal migrating sharp-shinned hawks. – *Wilson J. Ornithol.* 123: 154–158.
- Rubolini, D., Møller, A., Rainio, K. and Lehikoinen, E. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. – *Clim. Res.* 35: 135–146.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M. and Sokolov, L. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. – *Proc. R. Soc. B* 278: 835–842.
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski Jr, D. J. and Link, W. A. 2012. The North American Breeding Bird Survey, results and analysis 1966–2011, version 07.03.2013. – USGS Patuxent Wildlife Research Center, Laurel, MD, <www.mbr-pwrc.usgs.gov/bbs/bbs.html>.
- Sillett, T. S., Holmes, R. T. and Sherry, T. W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. – *Science* 288: 2040–2042.
- Strode, P. K. 2003. Implications of climate change for North American wood warblers (Parulidae). – *Global Change Biol.* 9: 1137–1144.
- Studds, C. E. and Marra, P. P. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. – *Clim. Res.* 35: 115.
- Terraube, J., Villers, A., Ruffina, L., Iso-Livari, L., Henttonen, H., Oksanen, T. and Korpimäki, E. 2015. Coping with fast climate change in northern ecosystems: mechanisms underlying the population-level response of a specialist avian predator. – *Ecography* 38: 690–699.
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., Roy, D. B., Scott, W. A., Smith, M., Smithers, R. J., Winfield, I. J. and Wanless, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. – *Global Change Biol.* 16: 3304–3313.
- Trenberth, K. E. 1984. Signal versus noise in the Southern Oscillation. – *Mon. Weather Rev.* 112: 326–332.
- Trouet, V., Esper, J., Graham, N. E., Baker, A., Scourse, J. D. and Frank, D. C. 2009. Persistent positive North Atlantic Oscillation mode dominated the medieval climate anomaly. – *Science* 324: 78–80.
- Vähätalo, A., Rainio, K., Lehikoinen, A. and Lehikoinen, E. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. – *J. Avian Biol.* 35: 210–221.
- Van Buskirk, J. 2012. Changes in the annual cycle of North American raptors associated with recent shifts in migration timing. – *Auk* 129: 691–698.
- Van Buskirk, J., Mulvihill, R. S. and Leberman, R. C. 2009. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. – *Global Change Biol.* 15: 760–771.
- Van Buskirk, J., Mulvihill, R. S. and Leberman, R. C. 2012. Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. – *Ecol. Evol.* 2: 2430–2437.
- Vedder, O., Bouwhuis, S. and Sheldon, B. C. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. – *PLoS Biol.* 11: e1001605.
- Végvári, Z., Bokony, V., Barta, Z. and Kovacs, G. 2010. Life history predicts advancement of avian spring migration in response to climate change. – *Global Change Biol.* 16: 1–11.
- Visser, M. E., Both, C. and Lambrechts, M. M. 2004. Global climate change leads to mistimed avian reproduction. – *Adv. Ecol. Res.* 35: 89–110.
- von Storch, H. 1999. Misuses of statistical analysis in climate research. – In: von Storch, H. and Navarra, A. (eds), *Analysis of climate variability*. Springer, pp. 11–26.
- Willmott, C. J. and Matsuura, K. 1995. Smart interpolation of annually averaged air temperature in the United States. – *J. Appl. Meteorol.* 34: 2577–2586.

Supplementary material (Appendix JAV-00692 at <www.avianbiology.org/readers/appendix>). Appendix 1.