

RESEARCH ARTICLE

Climate change affects bird nesting phenology: Comparing contemporary field and historical museum nesting records

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Abstract

1. Global climate change impacts species and ecosystems in potentially harmful ways. For migratory bird species, earlier spring warm-up could lead to a mismatch between nesting activities and food availability. CO₂ provides a useful proxy for temperature and an environmental indicator of climate change when temperature data are not available for an entire time series.
2. Our objectives were to (a) examine nesting phenology over time; (b) determine how nesting phenology relates to changes in atmospheric CO₂ concentration; and (c) demonstrate the usefulness of historical museum collections combined with modern observations for trend analyses.
3. We assessed changes in nesting dates of 72 bird species in the Upper Midwest of the United States by comparing contemporary lay dates with those obtained from archived, historical museum nest records over a 143-year period (1872–2015).
4. Species-specific changes in lay date per one unit change in the CO₂ residual ranged from −0.75 (95% CI: −1.57 to −0.10) to 0.45 (95% CI: −0.29 to 1.43). Overall, lay dates advanced ~10 days over the 143-year period. Resident, short-distance migrants and long-distance migrants lay dates advanced by ~15, 18 and 16 days on average respectively. Twenty-four species (33.3%) significantly advanced, one (1.4%) significantly delayed and we failed to detect an advance or delay in lay date for 47 species (65.3%). Overall mean advance in first lay date (for the species that have significantly advanced laying date) was 25.1 days (min: 10.7, max: 49.9).
5. Our study highlights the scientific importance of both data gathering and archiving through time to understand phenological change. The detailed archived information reported by egg collectors provide the early data of our study. As with studies of egg-shell thinning and pesticide exposure, our use of these data illustrates another scientific utility of egg collections that these pioneer naturalists never imagined. As museums archive historical data, these locations are also ideal candidates to store contemporary field data as it is collected. Together, such information will provide the ability to track, understand and perhaps predict responses to human-driven environmental change.

KEYWORDS

birds, climate change, CO₂, museum collections, nest records, nesting phenology

1 | INTRODUCTION

Overwhelming evidence demonstrates that global climate change drives shift in the timing of physical and biological processes (Menzel et al., 2006; Parmesan, 2007). Many phenological patterns, from ice melt (Bradley et al., 1998) to flowering (Amano et al., 2014; Bradley et al., 1998; Ellwood et al., 2013; McEwan et al., 2011; Miller-Rushing & Primack, 2008) and migration (Bradley et al., 1998; Cadahía et al., 2017; Hüppop & Hüppop, 2003; Inouye et al., 2000) are shifting to earlier dates owing to calendar advances in warming spring weather (Menzel & Fabian, 1999). Some bird species are found to nest at earlier dates (Crick et al., 1997) or change the length of their breeding season (Halupka & Halupka, 2017). How widespread the shift to earlier breeding dates is across all species and all geography is not known. Although a growing number of studies report patterns of bird nesting phenology with respect to climate change, we believe data exist for less than 5% of the world's bird species across limited geography.

In temperate zones, in particular, phenological mismatches of tree leaf-out, herbivore emergence and nesting bird species (which include species that range from rear-round residents to long-distance migrants) may lead to reproductive failure and population declines (Both et al., 2006; Ceballos et al., 2017; Dunn & Winkler, 2010; Visser et al., 1998, 2004) if food abundance no longer coincides with food demand during nesting. To date, for some well-studied species (e.g. Great Tits, *Parus major*, at Whytham Woods; Simmonds et al., 2020), anticipated population declines from such phenological mismatches have not been documented, although models suggest this may be possible in the future (Simmonds et al., 2020). For migratory birds, phenological mismatches can be compounded by the need for food to fuel migration along the migratory route. Food mismatches at wintering, migratory stopover and breeding areas could catastrophically compromise survivorship and reproductive capacity. Significant declines over the last 40 years in many species of North American birds have recently been documented (Rosenberg et al., 2019), but specific causes of these declines require much more data.

A potential limitation of some nesting phenology studies is that their short temporal span may not be of sufficient length to capture slowly developing phenomena. Crick et al. (1997), for example, found that 30.8% of 65 bird species examined over a 25-year time series from the British Trust for Ornithology nest record scheme significantly shifted to earlier nesting dates. In contrast, Townsend et al. (2013) used 25 years of long-term demographic data from the Hubbard Brook Experimental Forest in New Hampshire, USA, to demonstrate that the black-throated blue warbler *Setophaga caerulescens* nested earlier in springs with warmer weather. But this study did not find a progressive shift to earlier nesting, and there was no progressive shift to earlier, warmer springs over the 25-year period. Archived museum nest and egg records provide one way to increase the temporal extent available for comparison to contemporary field data. Natural history

collections offer data on specimens collected over the last 150 years, thus sampling a longer time span for assessing patterns of change in phenology and other phenomena (e.g. DuBay & Fuldner, 2017).

We examined nesting dates for 72 bird species using 1,550 historical museum nest and egg collection records from Northeastern Illinois with 3,038 contemporary records of bird nesting dates from the same region over a 143-year period (1872–2015). Clutch initiation dates for both museum and contemporary egg and nest records were calculated with standard protocols. For museum records, we estimated the initial lay date by subtracting the clutch size from the date of clutch collection, following methods described by McNair (1987). For contemporary nests, either the date the first egg was laid was observed directly, or we back-calculated the first egg-laying date by adjusting for stage of nest development (incubation, hatching, brooding and fledging).

Because temperature records for Northeastern Illinois are not available for the earliest years of our time series of nest records, we used concentration of atmospheric CO₂ as a proxy for proximate phenological changes associated with climate change (e.g. rising temperatures, leaf and insect emergence, etc.). Note that we neither assert nor assume that birds are capable of detecting subtle changes in atmospheric CO₂. We do, however, assume that atmospheric CO₂ concentrations correlate with proximate phenological changes (Cleland et al., 2007; Johnston & Reekie, 2008; Norby & Luo, 2004; see Supporting Information) that birds likely respond to directly.

Our objectives are to (a) examine nesting phenology over time; (b) determine how nesting phenology relates to changes in atmospheric CO₂ concentration, an environmental indicator of climate change that is highly correlated with temperature; and (c) demonstrate the usefulness of historical museum collections for trend analyses. Specifically, we test the hypotheses that (a) earlier nest initiation dates will correlate with rising concentrations of atmospheric CO₂; and (b) earlier nest initiation dates will be more pronounced among year-round resident and short-distance migrant species than long-distance migrant species. Where egg collections exist (Marini et al., 2020), similar analyses can be done elsewhere around the world comparing contemporary and historical records from museum collections. Archiving contemporary phenological data, including bird nesting records, in combination with these extended specimens (sensu Lendemer et al., 2020; Webster, 2017), is essential for long-term monitoring of these and other biological phenomena.

2 | MATERIALS AND METHODS

2.1 | Data collection

We compare nest phenology of bird species nesting in Northeastern Illinois representing dates pre- and post-atmospheric CO₂ changes. Atmospheric CO₂ levels are directly associated with global

climate change (IPCC, 2007; Norby & Luo, 2004; Zhu et al., 2016). Specifically, we used archived historical nesting and contemporary records, ranging from 1872–1963 and 1983–2015 respectively. The latter data on nest phenology were obtained principally through the comprehensive fieldwork of three of us who have recorded data on nesting birds in Northeastern Illinois for unrelated projects. Notably, all nest records used in this study were within seven adjoining counties located in Northeastern Illinois, USA: Cook, Lake, Kane, DuPage, McHenry, Kankakee and Will counties. Nesting data were collected with the approval of the University of Illinois Chicago's Institutional Animal Care and Use Committee (ACC protocol 12-061).

A total of 72 species comprising 11 orders and 32 families were included in the analysis (Table S1). We classified species into three categories: long-distance migrants (species that spend the non-breeding season primarily in the subtropics/tropics south of the United States border), short-distance migrants (species that spend the non-breeding season in southern temperate regions of the southern United States) and permanent residents (species that maintain most of their populations in the study region throughout the year).

2.2 | Lay date

2.2.1 | Historical, archived museum records

Date of first laying (lay date) was estimated based on the observation that one egg is laid per day in the majority of avian species (McNair, 1987). Therefore, we subtracted 1 day for each egg (1 egg = 1 day) in a clutch from the date the nest was collected. Scharlemann (2001) subtracted additional days from the date of collection when clutches were not noted as 'fresh'. We did not follow this procedure because (a) a majority (about 85%) of egg slips contain no or ambiguous information about clutch incubation, and (b) we reduced the influence of outliers in the dataset, which will decrease their influence on species-specific estimations of change in lay date (see model description below).

2.2.2 | Contemporary nests

For contemporary nests, we determined lay date in a variety of different ways. These include: (a) the date the first egg was laid was observed directly, (b) eggs were candled (Lokomoen & Koford, 1996) and the earliest date of laying was estimated based on the oldest egg in the clutch, (c) the day the first egg hatched was observed, and the first lay date was estimated based on known incubation periods for the focal species, (d) the date of fledging was known, and lay date was estimated based on known incubation and nestling periods for the focal species. For (d), to avoid systematically biasing the estimated lay date early or late, we chose the midpoint of the week of laying. Published species-specific life-history data, that is, median clutch size, incubation and nestling periods, were obtained from Birds of North America species accounts (Rodewald, 2015).

2.3 | Estimating overall temporal trends in bird species egg-laying dates with atmospheric change in CO₂

We developed our statistical model to better capture how climate change could influence bird egg-laying dates as well as correct for the structure of the data we collected. For example, climate change not only increases the mean temperature of a region, but also the likelihood of extreme temperature events (Stocker et al., 2013). Thus, to estimate temporal trends in a bird species egg laying dates, it is important to consider that both the mean and the variance of egg-laying dates may be affected by climate change. Further, as our own data have been collected through time by multiple observers and methods, the propensity for outliers is high. Finally, the total number of records among species in this dataset substantially varies wherein some species have fewer than 10 nest records and others have hundreds. To address these issues, our Bayesian multilevel linear model (a) allows the estimated mean and variance associated with lay dates to change through time, (b) reduces the influence of outliers in the data on the resulting model coefficients and (c) aids in the estimation of species-level coefficients for all species by sharing information (i.e. by treating species as a random effect within the model). Therefore, for s in $1, \dots, S$ species, i in $1, \dots, n$ data points and $K = 3$ species-level covariates (including the constant term in the regression), a robust varying-intercept, varying-slope model parameterized by the lay dates, y , is

$$y_i \sim t(x_i \beta_{s[i]} \nu \sigma_{y[i]}^2, \omega) \text{ for } i \text{ in } 1, \dots, n. \quad (1)$$

Here, β is an $S \times K$ matrix of species-level regression coefficients that are estimated from the data. The nested indexing present in $\beta_{s(i)}$ represents the $s(i)$ th row of the β matrix. Thus, $\beta_{s(i)}$ is the intercept and slope terms of the species that is associated with the i th data point. Continuing with Equation 1, x_i represents a vector of length K from the i th row of \mathbf{X} , which is an $n \times K$ matrix of species-level covariates associated with the n data points and y_i is the ordinal date of the egg laid for the i th data point.

To represent the constant term in the regression, the first column of \mathbf{X} is denoted as a column of 1s. The second and third columns of \mathbf{X} are respectively the number of years that have passed since the first year of data were collected (1872) for data point y_i and the CO₂ residual associated with the year y_i was collected. This CO₂ residual was used in place of the atmospheric CO₂ levels (ppmv) because atmospheric CO₂ was highly correlated with year (Pearson's correlation = 0.91). To calculate this covariate, we first compiled atmospheric CO₂ data from published datasets (Keeling et al., 2008; Neftel et al., 1994). As CO₂ levels were not available for all years, we linearly interpolated CO₂ levels for unavailable years with the 'approx' function in R version 3.3.2 (R Core Development Team, 2016). With these CO₂ data, we fit a simple linear regression treating CO₂ levels between 1872 and 2015 as the response variable and year as the independent variable. However, as the CO₂ level was known in 1872, we manually set the intercept value in

this regression to 289.42 units. We calculated the residuals from this model by subtracting the median estimate of the model's predicted CO₂ levels for each year from the actual CO₂ levels, which was less correlated with the time (Pearson's correlation = 0.52). Bayesian methods were used to parameterize this supplementary model, and the regression coefficient associated with the independent variable was given a vague N(0, 10,000) prior. Because of the linear detrending we applied to CO₂, positive values of the CO₂ residual indicate years with higher than expected CO₂ levels and negative values indicate years with lower than expected CO₂ levels. This covariate therefore captures the nonlinear change in CO₂ that is relatively independent of year.

As stated earlier, climate change may influence the mean and variance of species egg-laying dates. While the mean structure of our model accounts for the former, we allowed the variance term in Equation 1, $\sigma_{y[i]}^2$ to vary linearly through time to account for the latter. As most Markov chain Monte Carlo (MCMC) sampling software parameterize models in terms of precision (the inverse of the variance), $\sigma_{y[i]}^2$ can be derived as:

$$\sigma_{y[i]}^2 = \exp(\tau_0 + \tau_1 m x_i)^{-1}. \quad (2)$$

Here, τ_0 represents the log-scaled average precision of y across time and τ_1 is the estimated change in precision through time (the slope). $m x_i$ is the mean-centred year that data point y_i was collected (i.e. $m x_i = x_{[i,2]} - \bar{x}_{[2]}$). τ_0 and τ_1 were given vague Uniform(-10,10) priors. As differences in laying dates among species are accounted for in the mean structure of Equation 1, the variance in Equation 2 applies to all species and can be interpreted as the average deviation of all species from their estimated mean. The final term in Equation 1, ω , is the normality parameter of the t -distribution. As ω increases in size, the t -distribution more closely approximates the normal distribution but has heavier tails when ω is small. To reduce the influence of outliers in our analysis, we estimate ω from the data and follow Kruschke (2013) by applying a vague prior to ω where $\omega = 1 + \lambda$ and $\lambda \sim \text{Expon}(29^{-1})$. This specification gives equal prior probability to distributions that are close to normal ($\omega > 30$) and those with heavier tails ($\omega < 30$; Kruschke, 2013).

To allow for species-level regression coefficients to share some information, we included random effects within the model. Instead of drawing all species coefficients from a global community average, we allowed the species-level regression coefficients in β to vary by group (i.e. migratory status). We did this because our hypothesis is that resident birds will experience changes over time in situ, whereas short-distance and long-distance migrants will not. Likewise, specifying a model this way allowed us to compare average differences among resident, short-distance and long-distance migrants. To do so, we drew the β_s values from the following multivariate normal distribution:

$$\beta_s \sim N(U_s, M \Sigma_B) \text{ for } s \text{ in } 1, \dots, S. \quad (3)$$

Here, U is a $S \times L$ matrix of group-level covariates, where $L = 3$. Similar to X , the first column of U is a column of 1s that represent the constant

term in the group-level regression. The remaining two columns of U are dummy variables that respectively take the value of 1 if species s is a short or long-distance migrant in Northeastern Illinois and is zero otherwise (<https://birdsoftheworld.org/bow/home>). M is a $L \times K$ matrix that contains the coefficients of the group-level regression in Equation 1 that were all given vague N(0, 1,000) priors. A vector of covariates for species s , U_s , is therefore multiplied by M to generate the vector β_s that is then used in Equation 1. Finally, Σ_B is a covariance matrix for the multivariate normal distribution. Following Gelman and Hill (2007), we model this using the scaled inverse Wishart distribution. Briefly, this is done by setting the degrees of freedom parameter of the inverse Wishart distribution to $K + 1$ and introducing the scale parameter ξ_k where $\Sigma_B = \text{Diag}(\xi) \mathbf{V} \text{Diag}(\xi)$.

Given this model parameterization, we assume that species-specific responses are partially informed by migratory status and not by other factors such as species phylogeny. We made this assumption for three reasons. First, the 72 species were relatively diverse and represented 31 families (mean species per family = 2.3, min = 1, max = 8). Second, because the model provided species-specific parameter estimates, it still allowed the data to speak to species relatedness, whether it be through phylogeny or some other factor. And third, the model we fitted here was created to test our specific hypotheses (e.g. that resident birds will advance their lay date faster than migratory birds).

We used a vague prior for the unscaled covariance matrix, V , which can be written as $V \sim \text{Inv-Wishart}_{K+1}(I)$, where I is a $K \times K$ identity matrix. Vague priors for the K scale parameters were specified as $\xi_k \sim \text{unif}(0,100)$. The variance terms of the covariance matrix can then be derived as $\sigma_k^2 = \xi_k^2 V_{kk}$ for k in 1, ... K while the covariance terms are $\Sigma_{kf} = \xi_k \xi_f V_{kf}$, for k, f in 1, ... K . These variance and covariance terms can then be respectively converted to the estimates of standard deviations and correlations (Gelman & Hill, 2007). Estimating these associated correlations is important, as they may help to identify biologically reasonable values that species-level regression coefficients could take. For example, a negative correlation between a species intercept and response to year would indicate that species with a more positive intercept (i.e. a species that historically nested later in 1872) are more likely to have a stronger and more negative response to year (i.e. advance their lay date over time).

To fit this model, we used JAGS (Plummer, 2003) version 4.2.0 through program R version 3.3.2 (R Core Development Team, 2016). After a 100,000 step adaptation and 100,000 step burn-in, the posterior distribution was sampled 200,000 times. MCMC chains were thinned by 20 owing to the computational intensity of tracking each parameter. To verify model convergence, we inspected the MCMC chains to ensure proper mixing and ensured that all Gelman-Rubin diagnostics for each parameter were < 1.10 (Gelman et al., 2014). To assess model fit, we calculated a posterior predictive p -value, which represents the probability that predicted quantities from the model (estimated egg-laying dates for each data point) are more extreme than the observed data itself. Bayesian p -values near 0.5 indicate adequate model fit. We assessed the significance of parameter

estimates at two levels by determining if the 95% and 90% credible intervals (CI) of a parameter's posterior did not bound zero.

3 | RESULTS

3.1 | Bayesian model fit

The Bayesian *p*-value of our model, 0.49, indicates the model adequately fits these data.

3.2 | Overall trends

Species-specific changes in lay date to year ranged from -0.35 for the American kestrel (95% CI: -0.52 to -0.17) to 0.23 for the American robin (95% CI: 0.14 – 0.31). The average change in lay date per year across species was -0.08 (95% CI: -0.11 to -0.05). Species-specific changes in lay date to a one unit change in the CO₂ residual ranged from -0.75 for the sedge wren (95% CI: -1.57 to -0.10) to 0.45 for the Canada goose (95% CI: -0.29 to 1.43). The average change in lay date per one unit change in the CO₂ residual across species was -0.07 (95% CI: -0.20 to -0.01).

Of the 72 species analysed, 18 species in five orders and 13 families significantly advanced their dates of first laying (hereafter, lay date) at the 0.05 level over the 143 years, and one species delayed its lay date, in contemporary times (Table 1). An additional six species advanced their lay date at the 0.1 level. Of 26 year-round resident species, 10 advanced their lay dates (mourning dove, American kestrel, killdeer and seven passerines in four families), and the American robin delayed its lay date. Of 14 short-distance migrant species, six species advanced their lay dates (northern harrier and five passerines in four families). Of 32 long-distance migrant species, eight advanced their lay dates (yellow-billed cuckoo, Cooper's hawk and six passerines of five families). Of the 10 year-round resident species that advanced their lay dates, year was significantly correlated with the lay date of five species, CO₂ but not year was significantly correlated with the lay date of three species and both CO₂ and year were significantly correlated with lay date of two species. Of the six short-distance migrants that advanced their lay dates, year but not CO₂ was significantly correlated with lay date of two species, and CO₂ but not year was significantly correlated with lay date of four species. Only year was significantly correlated with lay date of all eight long-distance migrants. Both CO₂ and year were significantly correlated with the American robin—the only species that delayed lay date.

Overall mean advance in first lay date (for the species that have significantly advanced laying date) was 25.1 days (min: 10.7, max: 49.9). For resident species, the mean advance was 21.7 days (min: 10.7, max: 49.9). For short-distance migrants, the mean advance was 28.5 days (min: 22.1, max: 40.32). For long-distance migrants, the mean advance was 26.5 days (min: 12.2, max: 43.4). The variance

in lay dates increased from 10.58 (95% CI: 9.91–11.26) in 1872 to 12.42 (95% CI: 11.75–13.14) in 2015. Given this change, the width of the 95% predictive interval around mean lay dates increased by roughly 10 days across the length of this study. Finally, the normality parameter of the t-distribution was estimated to be 4.51 (95% CI: 3.92–5.97), which indicates that the distribution of lay dates has tails heavier than a standard normal distribution.

3.3 | Representative species examples

Of the 15 species that significantly advanced lay date with respect to year, yellow warbler is a representative example (Figure 1a). Field sparrow illustrates species that advanced lay date significantly with respect to CO₂ (Figure 1b). Blue jay is a representative of 48 species that neither advanced nor delayed lay date over the study period (Figure 1c). American robin was the sole species that delayed lay date (Figure 1d).

3.4 | Response by migratory group

Regarding group-level estimates that partially informed species-specific shifts in lay date, resident birds, on average, had an initial ordinal lay date in 1872 of 138 (i.e. 18 May; 95% CI: 130.24–146.73). In 1872, long-distance migrants, on average, nested 20.89 days (i.e. 7 June; 95% CI: 9.98–31.74) later than resident birds. In contrast, the initial lay date of short-distance migrants did not significantly differ from that of resident species in 1872. On average, species in each of the three migratory groups advanced their laying date per year by 0.07 days (95% CI: 0.0040–0.15), or about 10 days over the 143-year study period. Lay date did not change significantly for all three groups with respect to CO₂.

3.5 | Relationship of historic initial lay date and magnitude of advance

Species-specific initial lay dates in 1872 were weakly, but significantly correlated with the magnitude of the slope parameter associated with a species change in lay date per year (correlation coefficient: -0.40 ; 95% CI: -0.03 to -0.66). This indicates that species which nested later historically have the greatest potential to advance their first lay date, relative to those that nested earlier historically. Likewise, species-specific responses to year and CO₂ were significantly and negatively correlated (correlation coefficient: -0.79 ; 95% CI: -0.45 to -0.93 , Figure 2). Thus, species are not likely to respond equally to year and CO₂ in the same direction (both will not be negative, both will not be positive). If a species advances its lay date through time, it either did so nonlinearly, which our model captures via the CO₂ residual, or linearly through time (i.e. year).

TABLE 1 Species, order, family and migratory status of the 24 bird species whose laying date advanced or retarded from historical to contemporary times. Days advance is the number of days earlier first laying date is in contemporary times compared to historical records. Species whose common names are bolded and italicized responded to increasing CO₂ but not time, those whose names are bolded and underlined responded to both CO₂ and time and the remaining responded only to time. An asterisk following the species name indicates significance at the 0.1 level

Common name	Species name	Order	Family	Migratory status	Days advance
Killdeer*	<i>Charadrius vociferus</i>	Charadriiformes	Charadriidae	Resident	30.35
American kestrel	<i>Falco sparverius</i>	Falconiformes	Falconidae	Resident	50.34
American robin	<i>Turdus migratorius</i>	Passeriformes	Turdidae	Resident	-14.02
American goldfinch*	<i>Spinus tristis</i>	Passeriformes	Fringillidae	Resident	19.27
Field sparrow	<i>Spizella pusilla</i>	Passeriformes	Emberizidae	Resident	26.52
Song sparrow	<i>Melospiza melodia</i>	Passeriformes	Emberizidae	Resident	12.77
Red-winged blackbird	<i>Agelaius phoeniceus</i>	Passeriformes	Icteridae	Resident	10.59
Brown-headed cowbird	<i>Molothrus ater</i>	Passeriformes	Icteridae	Resident	40.82
Common grackle	<i>Quiscalus quiscula</i>	Passeriformes	Icteridae	Resident	17.6
Northern cardinal	<i>Cardinalis cardinalis</i>	Passeriformes	Cardinalidae	Resident	11.01
Northern harrier	<i>Circus hudsonius</i>	Falconiformes	Accipitridae	Short	33.68
Sedge wren	<i>Cistothorus platensis</i>	Passeriformes	Troglodytidae	Short	28.64
Brown thrasher	<i>Toxostoma rufum</i>	Passeriformes	Mimidae	Short	22.58
Cedar waxwing	<i>Bombycilla cedrorum</i>	Passeriformes	Bombycillidae	Short	29.32
Chipping sparrow	<i>Spizella passerina</i>	Passeriformes	Emberizidae	Short	18.52
Swamp sparrow*	<i>Melospiza georgiana</i>	Passeriformes	Emberizidae	Short	22.73
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	Cuculiformes	Cuculidae	Long	37.49
Black tern	<i>Chlidonias niger</i>	Charadriiformes	Laridae	Long	24.61
Eastern wood-pewee*	<i>Contopus virens</i>	Passeriformes	Tyrannidae	Long	23.55
Grey catbird	<i>Dumetella carolinensis</i>	Passeriformes	Mimidae	Long	17.11
Grasshopper sparrow	<i>Ammodramus savannarum</i>	Passeriformes	Emberizidae	Long	44.67
Yellow-headed blackbird	<i>Xanthocephalus xanthocephalus</i>	Passeriformes	Icteridae	Long	30.97
Bobolink*	<i>Dolichonyx oryzivorus</i>	Passeriformes	Icteridae	Long	12.4
Yellow warbler	<i>Setophaga petechia</i>	Passeriformes	Parulidae	Long	23.25

3.6 | Effect size as a function of sample size

Using this model, we estimated the difference in species average laying date between 1872 and 2015, with negative values indicating that species have increased their lay date over time. Overall, all species but one, the American robin, shifted to earlier initial lay dates, and sample size increased precision (i.e. decreased 95% credible interval width; Figure 3). However, evidence of an earlier initial lay date was strongest for species with the largest effect sizes or sample sizes (Figure 3). See supplemental material for figures of species-specific slope estimates from the model as a function of sample size, as well as estimates for all parameters in the model.

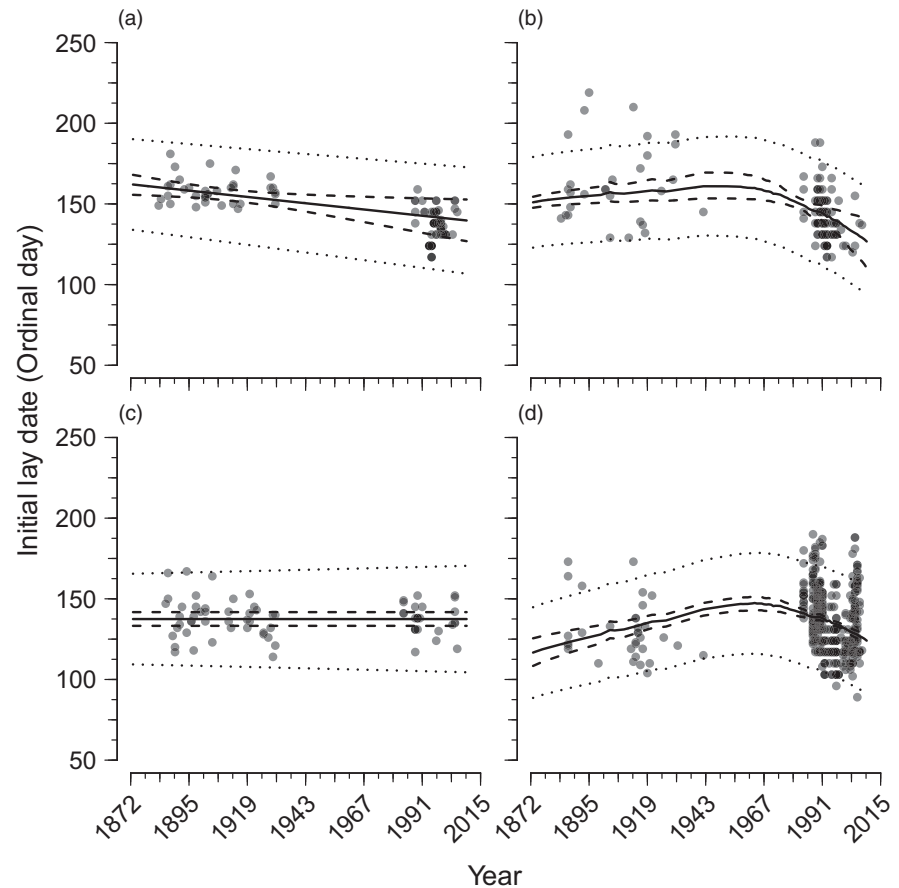
4 | DISCUSSION

4.1 | Advancement of lay dates

Our data indicate that the overall lay date advanced by approximately 25 days for those species having significantly advanced initial laying dates. Of the 72 bird species examined over the 143-year

time period, 24 (33.3%) advanced their initial lay date, one (1.4%) delayed its initial lay date and 47 (65.3%) did not change their initial lay date. Furthermore, of the 25 species that significantly changed initial lay date, the changes in lay date of some species were correlated with changes in CO₂, some were correlated with year and some were correlated with both CO₂ and year. We also identified that not every portion of the parameter space was biologically reasonable for species-level responses (Figure 2). Species which nested later in 1872, for example, were the most likely to advance their lay date, as evidenced by the negative correlation between species intercept estimates and their response to year. Likewise, we also found a negative correlation between species' response to year and CO₂. This indicates that species are far less likely to greatly advance or delay their lay dates by having responses for both year and CO₂ in the same direction (i.e. both negative or both positive). Instead, species were more likely to change lay dates either linearly or non-linearly, depending on whether their lay date through time was more correlated with year or CO₂ respectively. Because our analysis includes species from diverse taxonomic groups, it indicates the variability of responses we observed is widespread taxonomically.

FIGURE 1 Four bird species illustrate the different responses we observed in initial lay dates through time. Species either showed a linear decrease through time (a; yellow warbler), a nonlinear decrease that was correlated with global CO₂ levels (b; field sparrow) or no change through time (c; blue jay). One species, the American robin (d), increased its lay date. Solid lines in each figure represent median estimates of a species initial lay date through time, dashed lines are 95% credible intervals and dotted lines are 95% predictive intervals



4.2 | Lay date and migratory classification

When we looked at shifts in initial lay date by migratory classification, all three classes shifted their initial lay date by 0.07 days per year—about 10 days over the 143-year period. That the resident group exhibited a shift to earlier lay dates makes intuitive sense. Species present year-round in the nesting area experience earlier phenological changes in situ. The long and short-distance migratory groups also exhibited this shift in lay date, even though many of these migratory species may be constrained in the timing of departure dates from wintering areas by relative hours of day length, and other factors related to physiological condition, which may be related to habitat quality of the wintering area (Jonzén et al., 2006; Marra et al., 2005; Norris et al., 2004). Despite these group-level results, we found considerable variability among species within each migratory group. For each migratory group, we found some species exhibited an advance in initial lay date, while most species did not. This variability must reflect considerable intrinsic variation in ability to respond flexibly to changing phenology and climate (Crick et al., 1997; Halupka & Halupka, 2017; Travers et al., 2015). Some of this variability is due to species which nested later historically have greater opportunity to shift to earlier lay dates than those that nested earlier historically. Some species also were more difficult to classify as whether regional populations are truly resident or migratory. The shift to later initial lay dates of the American robin, the only species found to delay initial lay date in contemporary records,

warrants more study; we had much greater sample sizes of first-egg dates in the modern period than in the historical period. Rosenberg et al. (2019) found this species to be one of few North American passerines that was increasing in population size which suggests American robins have traits that allow them to cope with changing climates and/or landscapes more effectively.

While egg collecting and nest monitoring are different motivations for the temporal datasets that we studied, we find no reason that these different approaches would result in different estimates of first-egg dates across time. In both approaches, the common goal is to characterize the nesting period with respect to egg production, and estimated dates of first eggs are similar under either scenario (nest collectors were essentially ‘monitoring’ the nests they collected to collect complete clutches whenever possible). In the literature, data from early egg collectors have been considered biased towards sampling earlier lay dates; however, other research has argued this is not the case (McNair, 1985, 1987). If our historic estimates are biased, the historic initial lay dates used in our analyses are biased towards earlier dates. This would make it harder to identify significant shifts to earlier initial lay dates through time. However, even with this possible bias, we estimated 25 of 72 species shifted towards earlier initial lay dates over the period studied. Thus, our results show that many species, and perhaps even more than our analysis indicates, are shifting initial lay dates in response to earlier phenology and increases in temperature through time, while others are not.

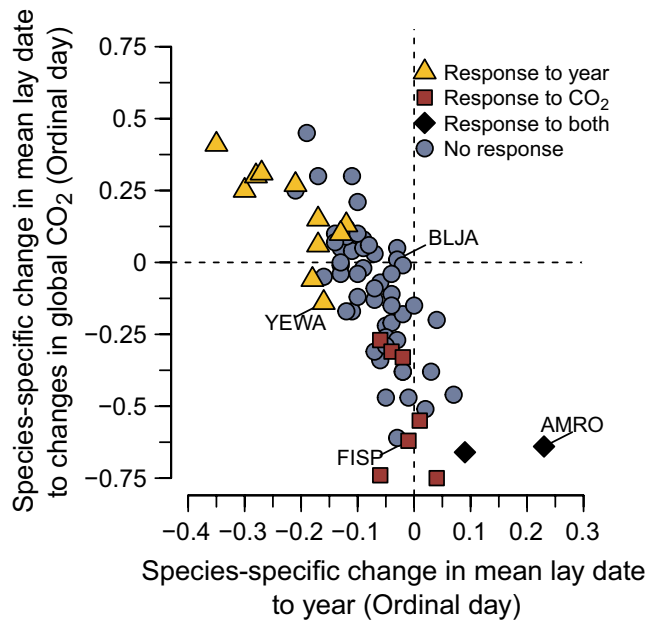


FIGURE 2 Species-specific changes in lay date in response to changes in atmospheric CO₂ with respect to species-specific change in lay date over time. How the average lay date of a species changes across years is negatively correlated with how the average lay date of a species changes in response to global CO₂ levels. Species which respond significantly to only year are in the upper left portion of the parameter space while those that respond significantly to CO₂ are typically in the bottom right. Response to CO₂, year, both or neither is based on significance at the 0.10 level. Labeled species are BLJA: blue jay, YEWA: yellow warbler, FISP: field sparrow, and AMRO: American robin

Given that global temperature increases accelerated in the 1980s (IPCC, 2015, Figure S1), the timing of studies on bird nesting phenology may influence estimates of how rapidly species shift their lay date. From our 143-year analysis, we estimated that birds throughout Northeastern Illinois advanced their lay date by -0.7 days per decade. These findings are close to those estimated by Socolar et al. (2017), who analysed avian lay dates over a 100-year period in California. While they were not able to provide species-specific estimates as we did, the lay date of their bird communities advanced by roughly 0.9 days per decade. In contrast, Bradley et al. (1998) reported that eight of 18 bird species nesting in Wisconsin advanced their spring arrival dates about 2.2 days per decade between 1936 and 1998. Similarly, Both et al. (2009) analysed lay dates in four bird species between 1988 and 2005, and estimated advances between 3.6–5 days per decade. The greater rates of phenological change per decade in these two studies, conducted over more recent decades than ours, likely reflect the acceleration of climate change over time. Socolar et al. (2017) hypothesized that their study species shifted to an earlier lay date to maintain their thermal niche. Given the similarity of our findings to theirs, maintaining a thermal niche also may hold for the species we found shifting to earlier lay dates in Illinois.

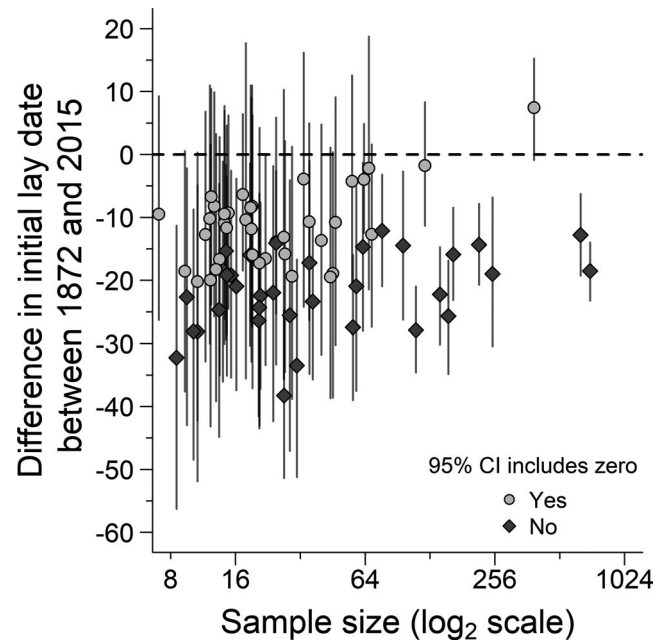


FIGURE 3 Estimated species-specific differences in initial lay date (ordinal date) between 1872 and 2015 as a function of sample size. Dots and diamonds are median estimates for each species while vertical lines represent 95% credible intervals. Median estimates for all species but one (the American robin) were negative, which indicates an overall earlier initial lay date for this bird community. Sample size is on the log₂ scale

4.3 | Prospectus

The approach of using museum nest-egg records adopted in our study could be expanded to explore and establish phenological means, inter-annual variances and asynchrony in phenological phenomena among interacting species. These data would be particularly useful for geographical regions where few (or no) phenological studies exist. Furthermore, similar analyses using techniques like stable isotope analysis of tissues and feathers (e.g. Bowen et al., 2005; Hobson, 1999) could permit tracking changes in species characteristics like diet, migratory pathways and geographic range shifts that may be driven by climate change or other human modifications of natural habitats. As indicated below, Marini et al. (2020) wrote extensively on the underuse of the world's museum egg-set collections, and interested readers would benefit from consulting this valuable publication.

5 | CONCLUSIONS

Our study highlights the scientific importance of both data gathering and archiving through time. The detailed archived information reported by egg collectors provide the early data of our study. As with studies of egg-shell thinning and pesticide exposure (Hickey & Anderson, 1968), our use of these data illustrates another scientific utility of egg collections that these pioneer naturalists likely never

imagined (Marini et al., 2020). From an ornithological perspective, these egg sets, because of the additional data associated with them, constitute the earliest extended specimens (Webster, 2017) in ornithology. It may also be possible to combine such analyses from museum data on plants and prey (e.g. insects and small mammals) to assess broader community patterns. Years of effort to monitor nests by three of us in recent decades provided most of the current data, a period where egg collecting has not happened. As essential as we feel egg collections can be for multiple types of research questions (Marini et al., 2020), we emphasize this modern detailed field data should be archived in retrievable ways for such patterns to be studied with new data in the future. Museums hold the historical data; they may be the most logical repository for current and future field data as well. The variation in response we find across species illustrates there is much to learn about how biodiversity responds to changes in global climate driven by human activities. Scientific collections in museums around the world, together with contemporary field data that we believe should be archived in these museums as well, will provide the ability to track, understand and perhaps even predict responses to present and future human-driven environmental change.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

J.M.B. had the original idea for the manuscript and compiled the historical nesting records; B.M.S., C.J.W. and K.A.S. collected the contemporary nesting data; M.F. analysed the data and made the figures; J.M.B., B.M.S., C.J.W. and M.F. wrote the first draft of the manuscript, and all co-authors substantially contributed to revisions of the original draft. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data and code are available on github at https://github.com/mfidino/bates_phenology and archived on zenodo at <https://doi.org/10.5281/zenodo.6025222> (Fidino, 2022).

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