

Vanessa M. Torti · Peter O. Dunn

Variable effects of climate change on six species of North American birds

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Abstract Many recent studies have shown that birds are advancing their laying date in response to long-term increases in spring temperatures. These studies have been conducted primarily in Europe and at local scales. If climate change is a large-scale phenomenon, then we should see responses at larger scales and in other regions. We examined the effects of long-term temperature change on the laying dates and clutch sizes of six ecologically diverse species of North American birds using 50 years of nest record data. As predicted, laying dates for most (four of six) species were earlier when spring temperatures were warmer. Over the long-term, laying dates advanced over time for two species (red-winged blackbirds, *Agelaius phoeniceus* and eastern bluebirds, *Sialia sialis*). Laying date of song sparrows (*Melospiza melodia*) also advanced with increasing temperature when the analysis was restricted to eastern populations. Neither laying date nor clutch sizes changed significantly over time in the remaining species (American coot, *Fulica americana*, killdeer, *Charadrius vociferous*, and American robin, *Turdus migratorius*), an unsurprising result given the lack of increase in temperatures over time at nest locations of these species. This study indicates that the relationship between climate change and breeding in birds is variable within and among species. In large-scale analyses of North American birds, four of seven species have shown advances in laying dates with increasing temperature (including song sparrows in the east). These variable responses within and among species highlight the need for more detailed studies across large spatial scales.

Keywords Climate change · Clutch size · Laying date · Temperature · Timing of breeding

Introduction

Air temperatures at ground surface have increased over the past 100 years by a global average of 0.6°C and are expected to continue to increase at a faster rate over the next 100 years (IPCC 2001). Many species of plants and animals have responded to the increase in air temperatures by advancing the time of spring events, such as flowering and egg-laying (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). The evidence for these phenological responses comes mainly from studies that have been conducted at small spatial scales, where temperature changes may actually be much less (or greater) than the global average. Such regional heterogeneity in temperature change may explain some of the variation among studies. Indeed, a review of 109 species found that phenological shifts were stronger north of 50°, where temperatures have warmed more than at lower latitudes over the past 50 years (Root et al. 2003). Furthermore, most evidence of phenological shifts in animals has come from local studies in western Europe, where there have been some of the largest increases in temperature (Walther et al. 2002; Parmesan and Yohe 2003). If climate change is a widespread phenomenon, then we should expect to see its influence on phenology at larger scales and in other regions with warming temperatures. To date, however, there have been relatively few large-scale studies of the effects of climate change on breeding phenology (e.g., Dunn and Winkler 1999; Schwartz and Reiter 2000; Visser et al. 2003).

Birds provide an excellent opportunity to study large-scale effects of climate change on breeding phenology because volunteers have contributed thousands of nesting records to collections in Europe and North America. In an analysis of over 92,000 nesting records from 36 species in the UK, Crick and Sparks (1999) found that

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V. M. Torti · P. O. Dunn (✉)
Department of Biological Sciences,
University of Wisconsin—Milwaukee,
P.O. Box 413, Milwaukee,
WI, 53201 USA

72% of species laid eggs earlier during warmer springs and 58% of these species also showed a long-term advance in laying date. Thus, it appears that most species respond to temperature change, but some species appear to be less responsive to such effects. Some of these differential responses among species may be related to differences in regional temperature change or the ecology or life history of particular species.

Regional differences in climate change may explain some of the differences in the response of plants and animals to climate change. For example, in great (*Parus major*) and blue tits (*Parus caeruleus*) there has been no long-term change in spring temperature at study sites in Russia and Finland and, not surprisingly, these populations have not shown a shift in timing of laying (Visser et al. 2003). In contrast, spring temperatures have increased and tits are laying earlier in populations in Oxford, England (McCleery and Perrins 1998). These regional differences appear to explain only part of the variation in response to climate change.

Differences in ecological and life history traits between species may explain some of the remaining variation. For example, over a 20-year period, the change in laying date within each of ten great tit populations in western Europe was not related to their local change in spring temperature (Visser et al. 2003). However, there was evidence of an effect of life history differences. Populations that showed a stronger advancement in laying date over time also showed less change over time in the proportion of second broods. Visser et al. (2003) suggest that populations with single broods will be more likely to track changes in the peak of food abundance and shifts toward earlier peaks of food abundance will reduce the reproductive value of second broods in other populations. As a consequence, those populations with a greater proportion of single broods will advance laying more and have a smaller change in the proportion of second broods.

Differences in response to climate change could also be related to ecological traits such as diet (Crick and Sparks 1999), habitat requirements (Zalakevicius and Zalakeviciute 2001; Travis 2003), body mass (Crick and Sparks 1999; Stevenson and Bryant 2000), and breeding density (Dunn and Winkler 1999). For example, species with generalist diets may show less of a response to climate change than those with more specialized diets, since the ability to feed on a greater variety of prey items increases the chance that some types of food will be available during the nestling period (reviewed by Daan et al. 1988; Rotenberry and Wiens 1991). Large body mass may also decrease sensitivity to climate change. In their analysis of the laying dates of 36 species, Crick and Sparks (1999) found that species with larger body mass showed little or no change in response to warmer spring temperatures. The response to climate change could also be influenced by breeding density. For example, if climate change reduces breeding density there may be less competition for resources and, consequently, an advancement in the time of breeding.

Most studies that have examined the effects of climate change on birds have covered either a small geographic area (McCleery and Perrins 1998; Brown et al. 1999; Przybylo et al. 2000) or a limited range of species (Forchhammer et al. 1998; Dunn and Winkler 1999; Sanz 2002). In this study, we examined the effects of climate change on laying date and clutch size of six ecologically and taxonomically diverse species with breeding ranges encompassing most of the continental USA and southern Canada. Study species included American coot (*Fulica americana*), killdeer (*Charadrius vociferous*), American robin (*Turdus migratorius*), eastern bluebird (*Sialia sialis*), red-winged blackbird (*Agelaius phoeniceus*), and song sparrow (*Melospiza melodia*). The study species represent a variety of ecological niches and span three avian orders and five families. The data set is both long-term (50 years) and large-scale, covering most of the species' ranges. The intent of this study was to test the hypothesis that birds are laying earlier and clutch sizes are increasing in relation to warming temperatures across large spatial scales.

Materials and methods

We analyzed laying dates and clutch sizes in relation to spring temperatures within 1° blocks of latitude and longitude (latilong blocks). Laying date and clutch size were obtained from over 50,000 nest records submitted by volunteers to the four largest and most comprehensive collections in North America: North American Nest Record Card Program (Cornell Laboratory of Ornithology), Ontario Nest Records Scheme (Royal Ontario Museum), Prairie Nest Records Scheme (Manitoba Museum of Man and Nature), and Quebec Nest Records Scheme (Canadian Museum of Nature). Records cover most of the North American breeding range of each bird, excluding Mexico and the northern territories of Canada.

A nest record card typically contains the date, condition of the nest, number of eggs, and number of young during each nest check. To ensure accurate estimation of reproductive parameters, only nest records with at least two observer visits to the nest were included and at least one of these must have been during the egg-laying period. Visits during egg-laying were identified by an increase in the number of eggs on subsequent visits. Laying date was estimated by back-dating one egg per day from the date of the first record of eggs in the nest. Records were excluded if they appeared to be from nests that were abandoned or re-nests (based on a drop and rise in consecutive daily egg counts in the nest). Nest records were generally excluded if clutch size could not be estimated accurately, except in American coot and song sparrow, for which low sample sizes existed for nests with both laying date and clutch size. To reduce the potential effects of outliers and to ensure consistency with Dunn and Winkler (1999), we excluded years with fewer than five nesting records for a species. The range

Table 1 Laying date and clutch sizes of six species of birds. For laying date, 1 = 1 April for all species

	<i>n</i> Records examined	Years	Records per year			Laying date			Clutch size		
			\bar{X} (mean)	SD	<i>n</i>	\bar{X} (mean)	SD	<i>n</i>	\bar{X} (mean)	SD	<i>n</i>
American coot	1,178	1956–1983	18.0	24.5	12	46.8	20.5	216	8.7	2.1	205
Killdeer	1,490	1961–1997	14.0	8.7	29	42.5	24.7	405	3.9	0.4	380
American robin	4,978	1951–2000	58.6	54.9	46	45.2	21.3	2,695	3.7	0.5	2,598
Eastern bluebird	28,625	1950–2000	291.4	271.6	51	54.9	30.4	14,862	4.6	0.8	2,605
Red-winged blackbird	14,810	1956–2000	96.7	114.1	40	58.6	16.0	3,868	3.5	0.7	3,758
Song sparrow	2,871	1962–1993	23.7	13.0	31	66.2	28.4	736	4.1	0.9	716

of years included in the analysis of each species began with the first year after 1949 in which over five records per year were available and ended with the last year prior to 2001 with over five records (see Table 1).

Mean monthly air temperature was obtained from the Global Historical Climatology Network (GHCN), version 2 (Peterson and Vose 1997). Monthly temperatures during 1950–2000 from all weather stations within a latilong block were averaged and used for analysis. Thus, references to temperatures at nest locations are for the surrounding latilong block in a particular year. To investigate how temperatures in the spring affected breeding we had to choose a biologically relevant measure of temperature for analysis. The species studied here had laying dates from mid-May to early June (Table 1), so we performed six regression analyses to determine the best set of monthly air temperatures (using March, April, May, and June, individually, and averages of March to May and April and May) that predicted laying date (as determined by highest R^2). The resulting “spring temperature” was then used in all subsequent analyses. The strongest correlate of laying date for all but one species was the average of April and May monthly temperatures; for eastern bluebirds, the best predictor of laying date was the average of the March, April, and May monthly temperatures.

We examined regional patterns in the timing of laying because some areas of North America are warming faster than others. In particular, northern ($>40^\circ\text{N}$) and western (-110°W) regions of North America have shown the greatest increases in spring temperatures over the last 50 years (e.g., Easterling et al. 1997). Our initial analyses examined geographic trends using the interactions between temperature and both latitude and longitude, similar to Dunn and Winkler (1999). To determine the location of regional differences, we divided the data into approximately northern (latitude $>40^\circ\text{N}$) and southern ($<40^\circ\text{N}$) halves of the data range, and then repeated the analysis for each half. Similarly, we divided the data into western (longitude $>110^\circ\text{W}$) and eastern ($<110^\circ\text{W}$) halves, and repeated the analyses for each half.

Estimates of abundance for each species (“density”) were obtained from the Breeding Bird Survey of the US Fish and Wildlife Service, a continent-wide program for monitoring populations of breeding birds (USGS 2001). Each survey consists of point counts (3 min each) of all birds seen or heard at 50 stops along a 25-mile section of

highway. These density estimates were available from 1964 to 2000. In some species density data were incomplete and in the case of American coots, could not be used in the analysis due to low sample size. Density estimates were averaged from multiple surveys for each year and latilong block.

Data collected by volunteers are unlikely to be independent because nests may come from the same area or year. We controlled for these spatial and temporal effects by using mixed models in JMP 4.0.2 (JMP 2002; see Dunn and Winkler 1999 for more details). Our models included both the random and fixed effects of year and location. Random temporal and spatial effects, caused by differences between years and locations in the number of nest records, were accounted for by including year and latilong block as categorical random variables. Fixed predictor variables included year (continuous in this case), latitude, longitude, spring temperature, elevation, and density. To test for curvilinear relationships, latitude and longitude were squared and included in the models.

We first examined the temperature data to determine if temperatures actually increased in the areas (latilong blocks) where nests were sampled (Table 2). Although temperatures have increased globally, such changes may not be evident at the latilong blocks where our nest records were collected. Then nest records were examined to determine if laying date has changed over the years, while controlling for geographic variables (Fig. 1; latitude, longitude, and elevation). Next, an analysis of temperature and all other predictors was conducted to determine which ones best explained laying date (Table 3). Each of the analyses in Tables 3 and 4 began with a full model and proceeded with backward stepwise elimination until all variables with $P > 0.15$ (default in JMP) were excluded. A similar analysis was conducted to determine the best predictors of clutch size; in this analysis, laying date and laying date² were also included as predictors (Table 4). Records with known clutch size were fewer than those with known laying date, resulting in lower sample sizes for some analyses (see Table 1).

Results

Many of the data sets began in the early 1900s, but there were no consistent records for all species until after 1950.

Table 2 Mixed model analyses of change in spring temperature for six species of bird

Fixed effects	American coot		Killdeer		American robin		Eastern bluebird		Red-winged blackbird		Song sparrow	
	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>
Year	-0.92	< 0.001	0.04	0.043			0.02	0.026	0.08	0.006		
Year ²	0.03	< 0.001					< 0.01	0.045				
Latitude	-0.50	< 0.001	-0.78	< 0.001	-0.73	< 0.001	-0.32	< 0.001	-0.74	< 0.001	-0.66	< 0.001
Longitude	0.08	0.113	0.05	< 0.001	0.09	< 0.001	0.09	< 0.001	0.05	< 0.001	0.05	< 0.001
Elevation	< -0.01	0.037	< -0.01	< 0.001	< -0.01	< 0.001			< -0.01	< 0.001	< -0.01	0.140
Lat. × long.			0.01	< 0.001			-0.04	< 0.001			0.01	0.005
<i>R</i> ²		0.979		0.973		0.950		0.981		0.974		0.964
<i>N</i>		121		405		2,695		14,862		3,868		736

Spring temperature was the average of the monthly mean temperatures for March, April, and May (bluebirds) or April and May (all other species). Each model included latilong and year as random (categorical) effects to account for the spatial and temporal

non-independence of the data. Estimates shown are after stepwise elimination of effects with $P > 0.15$. Non-significant effects are not shown.

The range of years for each species varied from the full 50-year period (eastern bluebird, 1950–2000) to fewer than 30 years (American coot, 1956–1983; Table 1).

Temperature

A mixed model analysis of the average of April and May monthly temperatures revealed that temperature patterns differed among species ($F_{4, 22,136} = 17$, $P < 0.001$). Spring temperature increased over the sampled years and latilong blocks for killdeer, eastern bluebird and red-winged blackbird (Table 2). Temperatures showed no trend over time at latilong blocks containing nests of American robins and song sparrows, and temperatures declined over time at latilong blocks with nests of American coots (Table 2). Both American coots and eastern bluebirds experienced a period of lower temperature in the 1960s, as indicated by the significant year² term in the models. Note that even though ranges of some species overlap, there are differences in temperature patterns because temperature data were only examined for the years and locations (latilong blocks) where we had nest records.

Laying date

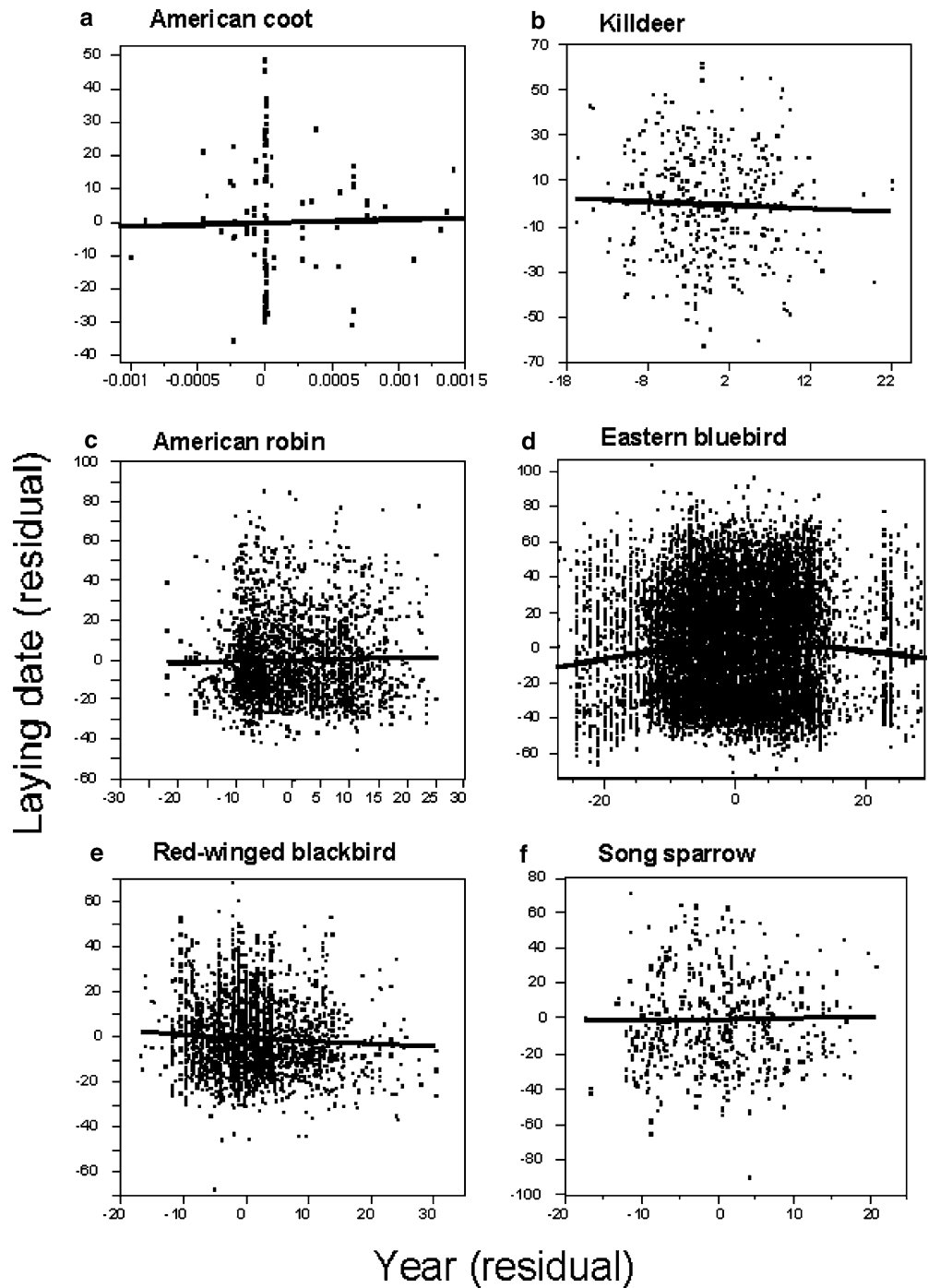
A mixed model analysis of laying date that included all species revealed a significant effect of species ($F_{5, 22,287} = 121.5$, $P < 0.001$) and a significant interaction between year and species ($F_{5, 22,2287} = 4.5$, $P = 0.0004$), which indicates that the laying date of species has been changing differently between species over time. Other predictors in the model included year ($P = 0.07$), latitude ($P < 0.001$), longitude ($P < 0.001$), latitude² ($P < 0.001$), and longitude² ($P < 0.001$). Because of the significant effects of species and the species and year interaction, we conducted all subsequent analyses separately for each species.

Two of the six species showed a long-term advancement in laying date, after controlling for latitude, longitude, and elevation (Fig. 1). Date of laying ad-

vanced by 7.5 days in red-winged blackbirds over the 50-year study period (Fig. 1). In eastern bluebirds, laying dates showed a curvilinear relationship with years, advancing by 4 days during 1976–2000. None of the other species showed a significant advancement in laying date (Fig. 1). Eastern bluebirds and red-winged blackbirds experienced an increase in spring temperature over time (Table 2) and laying date was related negatively to temperature (Table 3), suggesting that the advancement in laying in these two species was related to warmer spring temperatures. In contrast, the mean laying date of American robins has shifted later in the season in more recent years ($b = 0.13$ days/year, $n = 2,695$, $P = 0.04$; Fig. 1), even though there has been no change in temperature over the years in the latilong blocks where nests were sampled (Table 2).

To determine how temperature and other variables were influencing laying date, we conducted a mixed model analysis that started with ten predictors (Table 3). One of the most consistent predictors of laying date was spring temperature (Table 3). Laying was earlier when spring temperatures were higher in every species except American coot and song sparrow, which also had some of the smallest sample sizes (Table 2). A number of other factors also influenced laying dates. Killdeer and American robins laid eggs later at higher latitude, but this trend was not significant in the other species (Table 3), unless temperature was removed as a predictor. Laying dates of American coots exhibited a curvilinear relationship with latitude: laying was the earliest at middle latitudes (45°N) and later at higher latitudes. In killdeer, American robins, and eastern bluebirds there was also a negative interaction between latitude and temperature (Table 3), which indicated that the negative relationship between laying date and temperature was steeper at higher latitudes in these species. Killdeer and American robins also showed a positive interaction between longitude and temperature, which indicates that the negative relationship between laying date and temperature was changing more slowly at greater (more western) longitudes (Table 3). Elevation affected only American robins and red-winged blackbirds, which laid

Fig. 1 Partial regression plots of laying date in relation to year for six bird species: (a) American coot, (b) killdeer, (c) American robin, (d) eastern bluebird, (e) red-winged blackbird, and (f) song sparrow. Graphs are based on multiple regressions of laying date on year, year², latitude, longitude, and elevation. Residuals from the regression indicate the relationship between laying date and year while controlling for latitude, longitude, and elevation. Lines are from regressions, which showed recent advances in laying dates for eastern bluebird (year², $P = 0.01$) and red-winged blackbird ($P = 0.03$). American coot ($P = 0.35$), killdeer ($P = 0.69$), and song sparrow ($P = 0.17$) showed no long-term change in laying date, while the laying date of American robins ($P = 0.04$) has shifted later. Lines are from linear regressions in all species except eastern bluebird because there was no significant effect of year² in the other species



later at higher elevation. Greater breeding density was associated with earlier laying in killdeer and eastern bluebirds (Table 3).

Regional patterns

We performed another set of analyses at a larger scale to see if laying date has changed at different rates in different regions. In this case, we compared the northern and southern halves of our data set (north and south of 40°N) and the eastern and western halves of our data set

(east and west of 110°W) using two dummy variables (one for east or west, another for north or south). Song sparrows showed the only regional differences. Over the years, laying date showed an advancement in the west (interaction between region and year: $F_{1, 589} = 10.5$, $P = 0.001$). There was no difference between northern and southern regions (interaction between region and year: $F_{1, 589} < 0.01$, $P = 0.97$). Temperatures in the west have not shown any long-term change, so the cause of the change in laying is not clear. Analysis of song sparrow records from eastern North America, where most of the records were found (453 of 736 total), indicated that

Table 3 Mixed model analyses of laying date, examining effects of all variables

Fixed effects	American coot		Killdeer		American robin		Eastern blue-	blue-	Red-winged blackbird		Song sparrow	
	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	bird	bird	Estimate	<i>P</i>	Estimate	<i>P</i>
Year					0.14	0.025			-0.10	0.135		
Latitude	-1.29	0.015	1.79	0.025	1.88	< 0.001	0.57	0.126			0.91	0.139
Longitude	-0.59	0.006	0.60	0.009	-0.41	< 0.001					-0.65	< 0.001
Spring temperature			-1.83	0.038	-0.71	0.036	-0.62	0.075	-1.02	< 0.001		
Elevation					0.02	< 0.001			0.01	0.009		
Density			-0.25	0.041			-0.14	0.064				
Latitude ²	0.35	< 0.001					-0.27	0.003				
Longitude ²			-0.03	< 0.001	0.01	0.004						
Lat. × temp.			-0.16	0.011	-0.08	0.036	-0.26	0.009				
Long. × temp.			0.11	0.002	0.07	< 0.001						
<i>R</i> ²		0.398		0.305		0.165		0.041		0.277		0.411
<i>n</i>		216		319		2,695		9,494		3,868		736

Estimates shown are the best set of variables that predicts laying date after stepwise elimination of variables with $P > 0.15$ (unless they were part of an interaction). Spring temperature was the average of March, April, and May temperatures for eastern bluebird, and the average of April and May temperatures for all other

species. The model includes latilong and year as random (categorical) effects to account for the spatial and temporal non-independence of the data. Estimates shown are after stepwise elimination of effects with $P > 0.15$. Non-significant effects are not shown.

Table 4 Mixed model analyses of clutch size

Fixed effects	American coot		Killdeer		American robin		Eastern blue-	blue-	Red-winged blackbird		Song sparrow	
	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	bird	bird	Estimate	<i>P</i>	Estimate	<i>P</i>
Year									< 0.01	0.159		
Latitude	0.14	0.015			0.02	0.002	0.05	0.011	0.03	0.001	-0.05	0.121
Longitude	-0.05	0.042	< 0.01	0.917	< 0.01	0.111			< 0.01	0.738		
Spring temperature			-0.01	0.030			0.05	0.019	-0.01	0.378	-0.07	0.037
Elevation							< 0.01	0.108				
Density			< -0.01	0.039	< -0.01	0.010	0.01	0.134			-0.01	0.001
Laying date	-0.03	< 0.001			< -0.01	0.002	< -0.01	0.059	-0.01	< 0.001	-0.01	< 0.001
Latitude ²	-0.01	0.138							< 0.01	0.137		
Longitude ²					< -0.01	0.003			< -0.01	0.007		
Laying date ²					< -0.01	0.001	< -0.01	0.039			< -0.01	< 0.001
Lat. × temp.									0.01	0.125		
Long. × temp.			< 0.01	0.028					< 0.01	0.001		
<i>R</i> ²		0.273		0.073		0.055		0.047		0.108		0.413
<i>n</i>		205		299		1,914		1,405		3,758		546

Estimates shown are the best set of variables that predicts clutch size after stepwise elimination of variables with $P > 0.15$ (unless they were part of an interaction). Spring temperature was the average of March, April, and May temperatures for eastern bluebird, and the average of April and May temperatures for all other

species. The model includes latilong and year as random (categorical) effects to account for the spatial and temporal non-independence of the data. Estimates shown are after stepwise elimination of effects with $P > 0.15$. Non-significant effects are not shown.

temperatures increased over time ($F_{1, 365} = 9.1$, $P = 0.003$) and laying dates advanced with warmer temperatures ($F_{1, 365} = 4.0$, $P = 0.045$), although no advance was seen over time ($F_{1, 365} = 1.2$, $P = 0.27$).

Double broods

Three of the species (American robins, eastern bluebirds, and song sparrows) are consistently double-brooded and may produce three broods (Ehrlich et al. 1988), while killdeer, American coots, and red-winged blackbirds occasionally have two broods per season (Ehrlich et al. 1988; Gough et al. 1998). It was not possible to determine whether records were from first or second broods. This

could cause trends toward earlier laying to be underestimated in species that raise multiple broods. In bluebirds, the only species in which laying date was distinctly bimodal, removing records after 10 May (when there was a dip in the distribution of laying dates) did not produce any qualitative change in the results. Thus, although the analysis here does not control for second broods, the effect of later broods appears to be negligible.

Clutch size

As in other studies, the most consistent correlates of clutch size were laying date and latitude. All species except killdeer showed a negative relationship with lay-

ing date and all species except killdeer and song sparrow showed a positive relationship with latitude (Table 4). Clutch size did not show a consistent relationship with temperature (Table 4). Eastern bluebirds laid larger clutches when spring temperatures were warmer, but clutch sizes of song sparrow and killdeer were smaller during warmer springs (Table 4). If temperatures are increasing over time (Table 2), laying dates are related negatively to temperature (Table 3) and clutch size is related negatively to laying date (Table 4), then we might expect clutch size to increase over time. Eastern bluebirds and red-winged blackbirds showed all three of these relationships, yet neither species showed a temporal increase in clutch size (Table 4). In fact, no species showed a temporal change in clutch size. The random effect of categorical year could have explained some of the fixed effects of year, so the analyses were repeated without categorical year as a random factor. Similarly, temperature and laying date may have explained some of the variation associated with year, so analyses were repeated without temperature and laying date. However, there was still no temporal change in clutch size.

Discussion

Over the past 50 years, spring temperatures have increased for three of the six species we examined (killdeer, eastern bluebird, and red-winged blackbird). The laying dates of two of these species, red-winged blackbird, and eastern bluebird, also showed advances in laying. Warming trends are consistent with global increases (IPCC 2001), but the lack of change in temperature for two species and the significant cooling trend for American coots illustrates that temperature change is not always consistent at the scale of a latilong block. Although just two species examined here have advanced laying across their breeding range, five species laid earlier in years with warmer springs. In the future, some of these species may show an advance in laying if spring temperatures continue to increase, as predicted (IPCC 2001). In many bird species, individuals that lay earlier have larger clutches, and, thus, we might expect the five species that laid earlier in years with warmer spring temperatures to also lay larger clutches. However, only eastern bluebirds showed a positive relationship between spring temperature and clutch size. For those species that did change laying date or clutch size, the response depended not only on temperature, but also on geography (latitude, longitude, and elevation) and breeding density. Thus, variations in responses appear to be due to both geographic and ecological differences among species.

Laying date

The advances in laying dates over time in eastern bluebird and red-winged blackbird are similar to those seen previously in other species (Crick et al. 1997; Brown

et al. 1999; Dunn and Winkler 1999). These two species had the most comprehensive data sets in our study (Table 1). In the remaining species, there was no evidence of advances in laying over time, although most of the species studied here laid earlier when spring temperatures were warmer. A negative relationship between laying date and temperature has been found in almost 80% of bird species (reviewed by Dunn 2004), including three of the species we studied: American robins, eastern bluebirds, and song sparrows (James and Shugart 1974; Gowaty and Plissner 1998; Arcese et al. 2002). Our results are consistent with these findings across the species range for American robins and eastern bluebirds (Fig. 1) and in the analysis of song sparrows in the east.

Some of the relationships found here were not consistent with previous research. For example, laying date was not related to temperature in American coots in this study, but higher temperatures were correlated with earlier laying in a previous smaller-scale study (Perdeck and Cave 1989). Additionally, although American robins laid earlier with warmer temperatures, they appear to have delayed their laying in more recent years (Fig. 1). James and Shugart (1974) found a significant relationship between timing of laying and temperature in American robins; however, laying date also varied with other environmental factors such as geographic location and altitude.

The species examined in this study display a diversity of ecological traits, so we expected a variety of responses. For those that laid earlier with temperature, the advance varied from 0.7 to 1.8 days per degree Celsius of spring temperature increase (Table 3). The species that adjusted laying dates to temperatures at a slower rate (i.e., American robins and eastern bluebirds) and those that showed no response (i.e., American coots) may be less sensitive to environmental fluctuations. The mixed model analysis controlled for variation in the number of nesting records in each latilong block and year, as well as variation due to the fixed effects of latitude and longitude, although some regional differences did appear when regional subsets of the data were analyzed separately.

Previous studies have shown that birds tend to lay later in the breeding season at greater latitudes (Orell and Ojanen 1983; Sanz 1998). This includes some of the species studied here: American robins (James and Shugart 1974), red-winged blackbirds (Orians 1973; Yakusawa and Searcy 1995), and song sparrows (Johnston 1954). In this study only American robins and killdeer laid later at greater latitudes after controlling for temperature (Table 3), but most species showed this relationship when temperature was not included in the analysis. Additionally, in some species the relationship between temperature and laying date varied with latitude and longitude (changing faster at greater latitudes in killdeer, American robins, and eastern bluebirds and more slowly at greater longitudes in killdeer and American robins), suggesting that geographic location is affecting responses to temperature. Elevation also influenced the timing of breeding. American robins and

red-winged blackbirds laid later at higher elevations, even after accounting for temperature in the model (Table 3). Thus, some factor related to elevation, such as habitat or precipitation, is likely affecting the timing of breeding independent of temperature.

Higher breeding density was associated with earlier laying in killdeer and eastern bluebirds. Dunn and Winkler (1999) found a similar relationship in tree swallows, and they suggested that birds may be congregating in areas with greater food availability, which may allow for earlier laying. Greater breeding density could also lead to greater competition for resources and later breeding (Kokko 1999). For example, song sparrows on Mandarte Island in British Columbia laid their clutches later when breeding density was greater (Arcese and Smith 1988). Although laying date of song sparrows was not related to breeding density in our study (Table 3), clutch sizes of song sparrows were smaller when breeding density was greater (Table 4; see also Arcese and Smith 1988).

Clutch size

Laying date and latitude were the strongest predictors of clutch size; earlier laying dates and higher latitude were correlated to larger clutch sizes in American coots, American robins, eastern bluebirds, and red-winged blackbirds (Table 4). As in many shorebirds, killdeer typically lay four eggs (80% of clutches had four eggs, range = 3–5; also see Jackson and Jackson 2000), which may have led to the lack of a relationship in this species.

Only eastern bluebirds exhibited the predicted relationship between clutch size and temperature, but the rate of increase was small (Table 4). American robins and red-winged blackbirds showed no relationship between clutch size and temperature, although these species laid earlier with warmer temperatures and increased clutch sizes with earlier laying dates. Winkler et al. (2002) found a similar lack of relationship in tree swallows and suggested that constraints on laying earlier may act to prevent an increase in clutch size beyond the fitness optimum. One important constraint on laying earlier is the risk of hypothermia or starvation among adults early in the spring when temperatures are still relatively cold (e.g., Brown and Brown 2000). For

migratory species, earlier laying may also be constrained by their time of arrival on the breeding grounds, which is often regulated by photoperiod rather than temperature (Both and Visser 2001) and by the time and energy required to establish a territory and find a mate (Crick et al. 1993). If such constraints acted on the species studied here, they did not affect all species uniformly.

Species differences in breeding response to temperature

As responses to climate change in both laying date and clutch size varied greatly among species, we consider what other factors are acting on them. The six species examined here are not only widespread but also fairly abundant, which may be in part due to their adaptability to a range of conditions. All of the species studied here feed on a variety of plant and animal foods and, therefore, should be able to adjust their diet to available prey items. Of the six species, song sparrows appear to consume the smallest proportion of animal matter during breeding. An examination of stomach contents of song sparrows during breeding found 42% animal matter (Arcese et al. 2002); the other species typically consume greater proportions (Yakusawa and Searcy 1995; Gowaty and Plissner 1998; Sallabanks and James 1999; Jackson and Jackson 2000; Brisbin et al. 2002). If song sparrows are less dependent on arthropods, then this may have led to their apparently lower sensitivity to temperature. The responses of the six species may also be related to body mass. The species with the largest body mass, American coot, was the only species to show no relationship between laying date and temperature (Table 3). This is consistent with Crick and Sparks (1999), who found laying date responses to temperature among many smaller-bodied species but no response in coots.

It appears that different aspects of reproduction are responding to climate change with varying levels of sensitivity, even within the small sample of species studied here (Table 5). Other studies that have examined climate effects on breeding have typically examined a single species over time at one relatively small study area (but see Visser et al. 2003). Such “longitudinal studies” can allow researchers to examine the evolutionary aspects of breeding behavior and how birds change these

Table 5 Summary of statistical analyses in Table 2, 3, and 4

Relationship	American coot	Killdeer	American robin	Eastern bluebird	Red-winged blackbird	Song sparrow
Temperature vs year	–	+	0	+	+	0
Laying date vs year	0	0	+	–	–	0
Laying date vs temp.	0	–	–	(–)	–	0
Clutch size vs laying date	–	0	–	–	–	–
Clutch size vs temp.	0	–	0	+	0	–
Clutch size vs year	0	0	0	0	0	0

“+” Represents a positive relationship, “–” a negative relationship, and “0” represents no significant relationship. Parentheses around the direction of an effect (–) represents a near-significant effect ($P < 0.08$). Non-significant effects are not shown.

behaviors in response to environmental variables (e.g., Przybylo et al. 2000; Sheldon et al. 2003). However, they do not allow analysis over large geographical areas, as do cross-sectional studies such as this one. Both types of study provide insight into the changing breeding responses of birds to temperature and can complement one another. To date, most longitudinal studies suggest that the response of birds to climate change has been a behavioral rather than evolutionary change (i.e., phenotypic plasticity; Przybylo et al. 2000), although this may change with continued increases in temperature.

As two of the species examined in this study advanced their laying dates and most laid earlier at higher temperatures, we expect more species to advance their laying dates, if temperatures continue to increase as predicted (IPCC 2001). Because clutch sizes generally did not increase with temperature or time, the long-term impact of climate change remains unclear. Recent studies have determined that birds can make strategic adjustments to temperature by adjusting laying date, clutch size, and incubation periods to maximize fitness (Przybylo et al. 2000; Cresswell and McCleery 2003). If species compensate for effects of earlier laying by adjusting their clutch size or length of incubation, then effects of climate change on populations may be limited. However, some species may not respond quickly enough, leading to a mismatch between the timing of breeding and peaks in resource availability (Inouye et al. 2000; Stenseth and Mysterud 2002). For example, great tits in the Netherlands have not advanced their date of laying to match changes in the peak of food abundance for nestlings (Visser et al. 1998). As a consequence, females that are laying later are producing fewer surviving young (see also Merila et al. 2001; Sanz et al. 2003). Furthermore, regional differences in responses to temperature changes are becoming apparent within species, as described here and in a comparison of European studies on great and blue tits (Visser et al. 2003). Thus, the response of breeding birds to changes in temperature and food supply appears to vary among species in complex ways that will require further studies at both local and range-wide scales.

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References

- Arcese P, Smith JNM (1988) Effects of population density and supplemental food on reproduction in song sparrows. *J Anim Ecol* 57:119–136
- Arcese P, Sogge MK, Marr AB, Patten MA (2002) Song sparrow (*Melospiza melodia*). In: Poole A, Gill F (eds) *The birds of North America*, no. 704. The Birds of North America, Philadelphia
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298
- Brisbin IL Jr, Pratt HD, Mowbray TB (2002) American coot (*Fulica atra*) and Hawaiian coot (*Fulica alai*). In: Poole A, Gill F (eds) *The birds of North America*, no. 697. The Birds of North America, Philadelphia
- Brown CR, Brown MB (2000) Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behav Ecol Sociobiol* 47:339–345
- Brown JL, Li SH, Bhagabati N (1999) Long-term trend toward earlier breeding in an American bird: A response to global warming? *Proc Natl Acad Sci USA* 96:5565–5569
- Cresswell W, McCleery R (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J Anim Ecol* 72:356–366
- Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. *Nature* 399:423
- Crick HQP, Gibbons DW, Magrath RD (1993) Seasonal changes in clutch size in British birds. *J Anim Ecol* 63:263–273
- Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. *Nature* 388:526
- Daan S, Dijkstra C, Drent R, Meijer T (1988) Food supply and the annual timing of avian reproduction. In: *Acta XIX Congressus Internationalis Ornithologici*, vol 19, Ottawa, pp 392–407
- Dunn PO (2004) Breeding dates and reproductive performance. In: Møller AP, Fiedler W, Berthold P (eds) *Birds and climate change*. *Advances in ecological research*, vol 35. Elsevier, San Diego, CA, pp67–85
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proc R Soc Lond B* 266:2487–2490
- Easterling DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P, Folland CK (1997) Maximum and minimum temperature trends for the globe. *Science* 277:364–367
- Ehrlich PR, Dobkin DS, Wheye D (1988) *The birder's handbook*. Fireside, New York
- Forchhammer MC, Post E, Stenseth NC (1998) Breeding phenology and climate. *Nature* 391:29–30
- Gough GA, Sauer JR, Iliff M (1998) Patuxent bird identification infocenter. Version 97.1. Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/Infocenter/infocenter.html>
- Gowaty PA, Plissner JH (1998) Eastern bluebird (*Sialia sialis*). In: Poole A, Gill F (eds) *The birds of North America*, no. 381. The Birds of North America, Philadelphia
- Huppopp O, Huppopp K (2003) North Atlantic oscillations and timing of spring migration in birds. *Proc R Soc Lond B* 270:233–240
- Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. *Proc Natl Acad Sci USA* 97:1630–1633
- Intergovernmental Panel on Climate Change (IPCC) (2001) *Climate change 2001. Third assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge
- Jackson BJS, Jackson JA (2000) Killdeer (*Charadrius vociferus*). In: Poole A, Gill F (eds) *The birds of North America*, no. 517. The Birds of North America, Philadelphia
- James FC, Shugart HH Jr (1974) The phenology of the nesting season of the American robin (*Turdus migratorius*) in the United States. *Condor* 76:159–168
- Johnston RF (1954) Variation in breeding season and clutch size in song sparrows of the Pacific coast. *Condor* 56:268–273
- Lack D (1968) *Ecological adaptations for breeding in birds*. Methuen, London
- McCleery RH, Perrins CM (1998) Temperature and egg-laying trends. *Nature* 391:30–31

- Merila J, Kruuk LEB, Sheldon BC (2001) Cryptic evolution in a wild bird population. *Nature* 412:76–79
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Orell M, Ojanen M (1983) Timing and length of the breeding season of the great tit *Parus major* and the willow tit *P. montanus* near Oulu, northern Finland. *Ardea* 71:183–198
- Orians G (1973) The red-winged blackbird in tropical marshes. *Condor* 75:28–42
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–40
- Perdeck AC, Cave AJ (1989) Influence of temperature on the laying date of the coot *Fulica atra* between-pairs and within-individuals relationships. *Ardea* 77:99–106
- Peterson TC, Vose RS (1997) An overview of the Global Historical Climatology Network temperature data base. *Bull Am Meteorol Soc* 78:2837–2849
- Price T, Liou L (1989) Selection on clutch size in birds. *Am Nat* 134:950–959
- Przybylo R, Sheldon BC, Merila J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J Anim Ecol* 69:395–303
- Root TR, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Rotenberry JT, Wiens JA (1991) Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* 72:1325–1335
- Saether BE, Tufto J, Engen S, Jerstad K, Røstad OW, Skåtán JE (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science* 287:854–856
- Sallabanks R, James FC (1999) American robin (*Turdus migratorius*). In: Poole A, Gill F (eds) *The birds of North America*, no. 462. *The Birds of North America*, Philadelphia
- Sanz JJ (1998) Effects of geographic location and habitat on breeding parameters of great tits. *Auk* 115:1034–1051
- Sanz JJ (2002) Climate change and breeding parameters of great and blue tits throughout the western Palearctic. *Glob Change Biol* 8:409–422
- Sanz JJ, Potti J, Moreno J, Merino S, Frias O (2003) Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Glob Change Biol* 9:461–472
- SAS Institute Inc (2002) JMP statistics and graphics guide, vers. 4. SAS Institute Inc., Cary, NC
- Schwartz MD, Reiter BE (2000) Changes in North American spring. *Int J Climatol* 20:929–932
- Sheldon BC, Kruuk LE, Merila J (2003) Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* 57:406–420
- Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042
- Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. *Proc Natl Acad Sci USA* 99:13379–13381
- Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. *Nature* 406:366–367
- Travis JM (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc R Soc Lond B* 270:467–473
- USGS Patuxent Wildlife Research Center (2001) North American Breeding Bird Survey ftp data set, version 2001.0 (ftp://pwrctpr.er.usgs.gov/mp/bbs/datafiles/)
- Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc Lond B* 265:1867–1870
- Visser ME, Adriansen F, van Balen JH, Blondel J, Dhondt AA, van Dongen S, du Feu C, Ivankina EV, Kerimov AB, de Laet J, Matthysen E, McCleery R, Orell M, Thomson DL (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proc R Soc Lond B* 270:367–372
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Warren M, Hill J, Thomas J, Asher J, Fox R, Huntley B, Roy D, Telfer M, Jeffcoate S, Harding P (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–68
- Winkler DW, Allen PE (1996) The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology* 77:922–932
- Winkler DW, Dunn PO, McCulloch CE (2002) Predicting the effects of climate change on avian life-history traits. *Proc Natl Acad Sci USA* 99:13595–13599
- Yakusawa K, Searcy WA (1995) Red-winged blackbird (*Agelaius phoeniceus*). In: Poole A, Gill F (eds) *The birds of North America*, no. 184. *The Birds of North America*, Philadelphia
- Zalakevicius M, Zalakeviciute R (2001) Global climate change impact on birds: a review of research in Lithuania. *Folia Zool* 50:1–17