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ASSESSING MIGRATION OF RUBY-THROATED HUMMINGBIRDS (*ARCHILOCHUS COLUBRIS*) AT BROAD SPATIAL AND TEMPORAL SCALES

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Abstract.—Phenological patterns in birds appear to be temperature-dependent in part, and global temperatures are undergoing change. Many studies of bird phenology are conducted at broad temporal but local spatial scales, making it difficult to assess how temperature affects bird migration across landscapes. Recently, networks of "citizen science" volunteers have emerged whose collective efforts may improve phenology studies as biases associated with such efforts are recognized and addressed. We compared mean Ruby-throated Hummingbird (*Archilochus colubris*) first arrival dates from Journey North (2001–2010) with data from the North American Bird Phenology Program (1880–1969). Ruby-throated Hummingbirds arrived earlier in the more recent period throughout the eastern United States; these advances, however, varied by latitude from 11.4 to 18.2 days, with less pronounced changes above 41°N. Warmer winter and spring temperatures in North American breeding grounds were correlated with earlier arrivals at lower latitudes in our recent period. Surprisingly, Ruby-throated Hummingbirds arrived later at high latitudes (42–43°N) during warmer winters and later at both mid- and high latitudes (38–39, 41–44°N) during warmer springs, which perhaps indicates extended migratory stopovers below 40°N during these years. Overall, weather variables predicted arrival dates better in the recent than in the historical period. Our results document spatial variability in how warming temperatures affect hummingbird arrivals and add credence to the hypothesis that spatial differences in arrival patterns at high versus low latitudes could exacerbate asynchrony between some birds and their food resources and modify associated ecosystem services such as pollination and insect pest suppression. *Received 28 March 2012, accepted 19 October 2012.*

Key words: *Archilochus colubris*, arrival, bird phenology, citizen science, climate change, ecosystem services, Ruby-throated Hummingbird, spatial trend.

Evaluación de la Migración de *Archilochus colubris* a Escalas Amplias de Tiempo y Espacio

Resumen.—Los patrones fenológicos de las aves parecen ser en parte dependientes de la temperatura y las temperaturas globales están cambiando. Muchos estudios de fenología de aves son hechos a lo largo de escalas temporales amplias pero a escalas espaciales locales, lo que hace difícil evaluar cómo los cambios de temperatura afectan la migración de las aves a través de diferentes paisajes. Recientemente, han aparecido redes de "científicos ciudadanos" voluntarios, cuyos esfuerzos colectivos podrían mejorar los estudios de fenología en la medida en que los sesgos asociados con dichos esfuerzos sean reconocidos y abordados. Comparamos las fechas medias de llegada de *Archilochus colubris* de Journey North (2001-2010) con datos del North American Bird Phenology Program (1880-1969). El arribo de *A. colubris* fue más temprano en periodos m) duanitudes medias y altas (38-39, 1-44tro periodo reciente. 18.2 diada con los parentales se correlacionaron con los ial en eás recientes a través del este de Estados Unidos; sin embargo, estos avances variaron con la latitud entre 11.4 y 18.2 días, con cambios menos pronunciados por encima de 41°N. Temperaturas mayores en invierno y primavera en las áreas de reproducción en Norte América estuvieron correlacionadas con llegadas más tempranas en latitudes menores en nuestro periodo reciente. Sorpresivamente, *A. colubris* llegó más tarde a latitudes altas (42-43°N) durante inviernos más cálidos, y más tarde a latitudes medias y altas (38-39, 41-44°N) durante primaveras más cálidas, lo que tal vez indicaría paradas migratorias extendidas a menos de 40°N durante esos años. En general, las variables climáticas fueron mejores predictores de las fechas de llegada en el periodo reciente que en el periodo histórico. Nuestros resultados documentan variabilidad espacial en cómo las temperaturas más cálidas afectan la llegada de los colibríes y dan credibilidad a la hipótesis de que las diferencias espaciales en los patrones de llegada en latitudes altas y bajas podrían aumentar la asincronía entre algunas aves y sus recursos alimenticios, y modificar los servicios ecosistémicos asociados como la polinización y la supresión de pestes de insectos.

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Birds are often used to assess the effects of climate change on wildlife species because they are charismatic and easy to identify, and monitoring programs have been in place for more than a century (Crick 2004; Møller et al. 2004, 2010; Wilson 2007; Newson et al. 2009; Knudsen et al. 2011). The results of recent studies suggest that many species are returning earlier than in previous periods largely because of changes in global climate (Cotton 2003, Miller-Rushing et al. 2008), such as changes in mean annual temperature (Ledneva et al. 2004), winter temperature (Cotton 2003, Swanson and Palmer 2009, Hurlbert and Liang 2012), spring temperature (Murphy-Klassen et al. 2005), and large-scale climate indices such as the North Atlantic Oscillation Index (Hüppop and Hüppop 2003, Vähätalo et al. 2004). Changing arrival dates have also been correlated to nonclimate factors, such as an increase in the popularity of backyard bird feeding (Robb et al. 2008), changing sizes of bird populations (Miller-Rushing et al. 2008), and landcover changes in wintering grounds, breeding grounds, and migratory pathways (Moore et al. 1995, Parrish 2000).

In addition to serving as sentinels of climate change, birds provide important ecosystem services to farmers and the general public (Şekercioğlu 2006, Whelan et al. 2008, Wenny et al. 2011). Birds function as insect predators (Mols and Visser 2002), pollinators (Clout and Hay 1989), scavengers (Şekercioğlu et al. 2004), seed dispersers (Levey et al. 2005), seed predators (Holmes and Froud-Williams 2005), and ecosystem engineers (Valdivia-Hoeflich et al. 2005). Recent evidence suggests that changing temperatures and other factors are disrupting important food webs by causing birds to arrive either too early or too late compared with food resources (Marra et al. 2005, Visser and Both 2005, Saino et al. 2011). Møller et al. (2008) reported that population sizes of migratory bird species that were unable to adjust their spring migrations to use peak food resources declined between 1990 and 2000 in Europe. Such asynchrony could be detrimental to bird populations and, potentially, to the biological pest suppression that birds provide, leading to increased pest outbreaks (Price 2002). Predicting where potential asynchronies may be most severe and how climate change may alter migration patterns remains difficult because of the spatial variability of changing temperatures (Stenseth et al. 2002, Stokke et al. 2005, Visser and Both 2005). The effects of climate change often vary regionally and are most pronounced in northern latitudes, especially in North America (Easterling et al. 1997, Hurrell and Trenberth 2010), providing challenges to birds that pass through multiple climate regions during migration (Strode 2003, Newton 2008).

Many studies of bird phenology have been conducted at broad temporal but narrow spatial scales (Bradley et al. 1999, Cotton 2003, Ledneva et al. 2004, Murphy-Klassen et al. 2005, Swanson and Palmer 2009). Benefits of site-based migration studies include the ability for multiple species to be compared simultaneously, observer error to be reduced, and available weather data to be collected and correlated consistently over multiple years. Inferences, however, can be limited spatially, making it difficult to assess the effects of temperature changes that vary widely across landscapes (Primack et al. 2009, Knudsen et al. 2011). Some studies have used multiple observations along migratory routes to examine how temperature influences migration (Knudsen et al. 2011). For example, Marra et al. (2005) compared the interval between banding dates of long-distance migrants at stations 2,500 km apart in the eastern United States and found that mean passage time was inversely related to temperature. Hüppop and Winkel (2006) used first arrival dates of Pied Flycatchers (*Ficedula hypoleuca*) at six sites along a migratory pathway in Europe to show that migration was strongly influenced by temperatures en route. One of the broadest-scale studies to date used observations from an extensive network of volunteer observers at >1,300 sites around Spain to predict changes in arrival dates for common migratory species from 1944 to 2004 in relation to weather variables (Gordo and Sanz 2006). In general, however, studies of this magnitude are difficult because of the enormous network of observers required to pinpoint annual "first-events" that often span thousands of kilometers.

A counterpart for assessing historical, broad-scale changes in migration in North America had been largely unavailable until a recent effort by the U.S. Geological Survey revitalized the North American Bird Phenology Program (NABPP; see Acknowledgments). From 1880 to 1970, the NABPP coordinated efforts of hundreds of naturalist volunteers to report annual first bird sightings in North America using standardized observation protocols to better understand migration patterns and bird distributions (Merriam 1885, J. Zelt pers. comm.). Efforts are currently under way to scan and digitize this largely unanalyzed (except for Droege et al. 2003, Zelt et al. 2012) database and make records available to the public through the USA National Phenology Network (see Acknowledgments; Dickinson et al. 2010). At the same time, "citizen scientists" are reporting spring events such as dates of bird arrival, insect emergence, and plant flowering dates that have enabled others to describe spring arrival in birds (Wilson 2007) and migratory pathways of Monarch Butterflies (*Danaus plexippus*; Howard and Davis 2009). Such data could improve phenology studies if biases associated with citizen data-collection techniques are recognized and addressed (Miller-Rushing et al. 2008, Dickinson et al. 2010).

Hummingbirds are charismatic, abundant Neotropical migrants that have fascinated naturalists for centuries (Robinson et al. 1996), and detailed observations of the Ruby-throated Hummingbird (*Archilochus colubris*; hereafter "ruby-throat") have been made in both recent and historical periods. Ruby-throats are easily identified and, given that they are the only regularly occurring hummingbird in eastern North America, are suitable subjects for long-term monitoring programs. Ruby-throats regularly winter in Central America between northern Panama and southern Mexico, and most migrate across the Gulf of Mexico, arriving at their breeding grounds in eastern North America between February and May (Robinson et al. 1996). During migration, ruby-throats feed primarily on nectar and small insects (Robinson et al. 1996) and occasionally on tree sap associated with wells of Yellow-bellied Sapsuckers (*Sphyrapicus varius*; Miller and Nero 1983). Recent studies have indicated that ruby-throats are arriving earlier at their breeding grounds than in previous periods in Maine (Wilson et al. 2000), Massachusetts (Butler 2003, Ledneva et al. 2004), South Dakota (Swanson and Palmer 2009), and New York (Butler 2003).

Given the recent trend of earlier ruby-throat arrivals, the extensive geographic database of observations now available, and a general understanding that climate influences bird migration at multiple scales, we assessed spatial differences in arrival dates of ruby-throats from 1880 to 2010 in eastern North America in relation to climate variables. We also examined potential mechanisms

for the observed changes in relation to their long-distance migration patterns and foraging habits, and spatial variation of climate effects from wintering grounds to their more northerly breeding areas.

METHODS

Arrival data.—Historical ruby-throat migration data (1880–1969; hereafter "historical") provided by the NABPP were transcribed from handwritten arrival cards to Microsoft Excel spreadsheets by J.R.C. and student volunteers. Each arrival record was then rechecked to ensure accuracy. Recent ruby-throat data (2001–2010; hereafter "recent"), reported by citizen science volunteers through hummingbirds.net and Journey North, were accessed from the Journey North online database (see Acknowledgments). First arrivals reported between 1 February and 31 May were double checked for accuracy and converted to day of year (e.g., 10 April = day 100), accounting for leap years. Arrivals were assigned a location (i.e., latitude, longitude, and elevation) based on the centroid of the reported arrival city and zip code using the ARCGIS, version 10, Geocoding Function (ESRI, Redlands, California) and the GPS Visualizer geocoding service (see Acknowledgments).

Arrivals from historical and recent periods were divided into 1° latitudinal bands (~111 km each; Fig. 1) from 33 to 44.99°N to encompass the northward pattern of ruby-throat migration in the eastern United States. For example, all arrival records between 35 and 35.99°N were grouped into the 35°N band. When summarizing results, we refer to bands 33–36°N as "lower" latitudes, bands 37–41°N as "middle" latitudes, and bands 42–44°N as "higher" latitudes. Arrival data north of 45°N and south of 33°N did not meet our minimum sample size requirement (≥75 observations per period) and were omitted from analyses. Longitudinally, we included arrival records east of 94°W, which is the approximate range limit for ruby-throats (Robinson et al. 1996). Outliers were removed at 3 standard deviations by period and 1° latitudinal band to remove first arrivals that were likely incorrectly reported by citizen volunteers. In sum, we analyzed 36,457 first-arrival records (n = 4,652 from historical and n = 31,805 from recent period; Fig. 1).

Weather data.—To approximate annual weather conditions in the eastern United States, we used monthly weather data (1895–2010) from the National Oceanic and Atmospheric Administration Time Bias Corrected Divisional Temperature–Precipitation–Drought Index Data Set (see Acknowledgments), reported by climate division (designations of the U.S. National Climate Data Center that group areas of similar elevation, temperature, and precipitation). Weather variables previously linked to changes in bird phenology (i.e., winter temperature, spring temperature, and spring precipitation; Gordo 2007) were joined to arrival records by year and climate division using ARCGIS, version 10 (ESRI). We used mean monthly temperatures in January and February for winter values and mean monthly temperatures in March and April for spring values. To approximate temperatures encountered in Central American wintering grounds, we searched for weather stations in the Global Historical Climatology Network (see Acknowledgments) located near the center of the ruby-throat's winter range (southern Mexico to northern Panama)

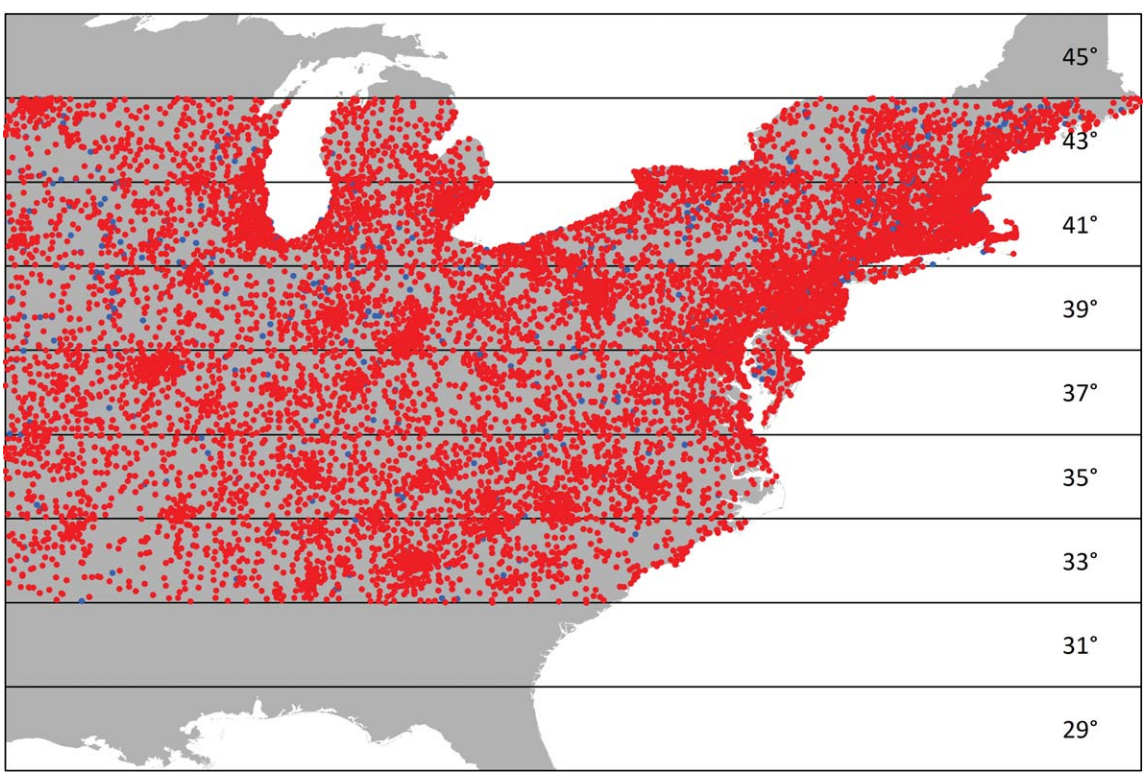

FIG. 1. Locations within our study region (33–44°N, 67–94°W) where Ruby-throated Hummingbird arrivals were reported by the North American Bird Phenology Program (1880–1969; blue) and Journey North (2001–2010; red). Numbers represent approximate degrees north latitude. First arrivals in our study were grouped by period and 1° latitudinal band.

that reported long-term monthly temperature records from 1895 to 2010. In general, such stations were scarce. Only one (Aerop. Interna, GHCN Station no. 41476644000, 20.98°N, –89.65°W, Yucatan, Mexico) met our criteria and was therefore used to approximate temperatures on the ruby-throat's wintering grounds. We used mean February temperatures to approximate temperatures on wintering grounds because February is typically the last full month in which ruby-throats overwinter prior to their departure to North America (Robinson et al. 1996).

Statistical analyses.—We compared mean arrival dates by latitudinal band using standard least-squares regression with period as a predictor. We initially examined mean arrival dates by decade and noted that arrivals in our recent period were significantly earlier than mean arrival dates in each of the previous decades. Therefore, to simplify our output, we grouped arrival dates into a pre- and post-climate-change period based on noted similarities of arrival dates within periods and a general consensus that a climatic change point occurred in the mid-1970s, after which many phenological events began to advance (Walther et al. 2002, Gordo and Sanz 2009). To adjust for micro-scale differences within bands, we included latitude, longitude, and elevation in our models, along with possible interaction terms. To examine remaining variability in arrival date, we then explored differences among the environmental variables associated with arrival dates (winter and spring temperature on breeding grounds, precipitation on breeding grounds, and temperature on wintering grounds) by latitudinal band and period and noted that environmental variable means differed between periods.

Given the mean differences in both arrival dates and environmental variables, we used stepwise variable selection techniques to identify sets of environmental variables that were related to arrival date at each latitudinal band. Initial analyses indicated that relationships between environmental variables and bird arrivals were inconsistent between periods and that there was a high correlation among environmental variables. Therefore, we analyzed the relationship between arrival date and weather variables separately, for each period and band combination, using standard least-squares regression. All statistical analyses were conducted using JMP, version 9.0 (SAS Institute 2010).

Migratory rates were calculated by subtracting mean arrival times at adjacent latitudinal bands and dividing by 111 km (the approximate length of 1° of latitude). Total migratory passage time was calculated by subtracting mean arrival dates at 33°N from those at 44.99°N for each period. To compare arrival dates graphically, we generated a smoothed raster map from point data for each period using inverse distance weighting (IDW) in ARCGIS, a procedure that assigns values to raster cells on the basis of known values of surrounding cells. For our IDW models, we calculated mean arrivals by period and climate division and included all divisions between 29 and 46°N that had a minimum of 10 arrival points per period; this included 99 climate divisions from the historical and 195 climate divisions from the recent period. Although variability was higher for mean arrival dates between 29 and 32°N and between 45 and 46°N in our historical period, we chose to include these data in this analysis for comparative purposes. We assigned each mean arrival date a latitude and longitude based on the centroid of the climate division it represented. For our graphical analysis, we considered a 9-cell search radius and delineated arrivals using an 8-day interval.

RESULTS

Mean first arrival dates differed dramatically between periods at all latitudes (Fig. 2), with ruby-throats arriving 11.4–18.2 days earlier in the recent period (Table 1). Moreover, differences in first arrival date varied by latitude (Fig. 3). At lower and middle latitudes, ruby-throats arrived ~15 days earlier in the recent period, but at higher latitudes they arrived ~11.5 days earlier (Table 1). Hummingbirds, on average, took 33.8 days to travel between 33 and 45°N during the historical period (= 36.2 km day^{-1}) and 38.0 days (= 32.1 km day^{-1}) to travel between 33 and 45°N in recent times.

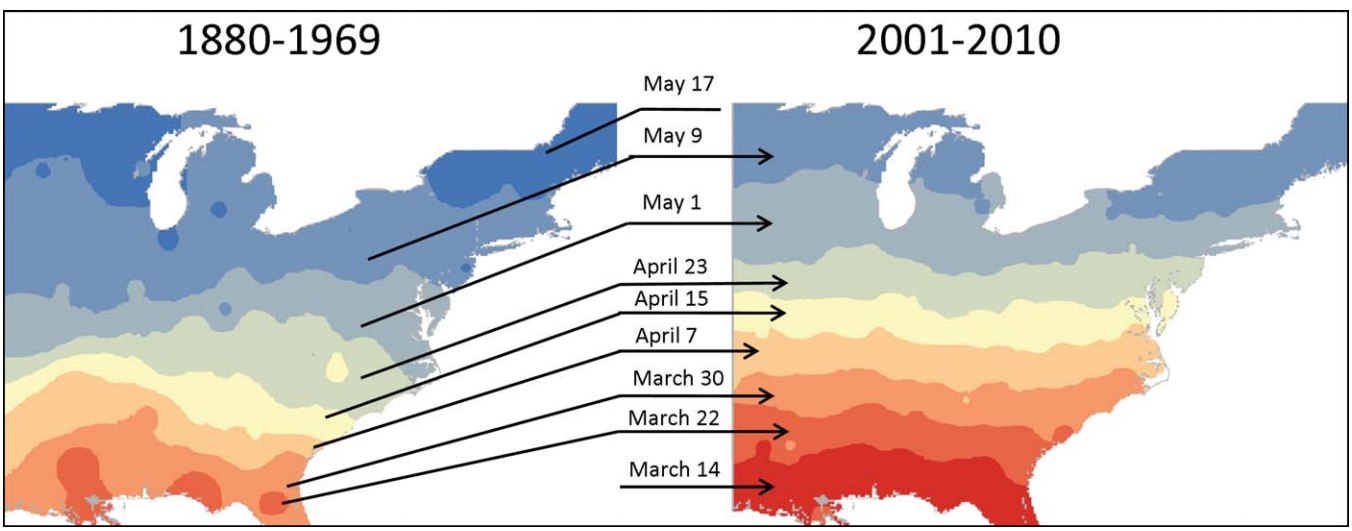

FIG. 2. A depiction of mean first arrival dates of Ruby-throated Hummingbirds in eastern North America, 1880–1969 and 2001–2010. Arrival dates were advanced at all latitudes. This figure was generated using inverse-distance weighted (IDW) interpolation in ARCGIS, version 10.

TABLE 1. First arrival dates of Ruby-throated Hummingbirds in North America reported by latitude for the historical (1880–1969) and recent (2001–2010) periods. Differences in mean arrivals were compared using *t*-tests.

	First arrivals 1880–1969			First arrivals 2001–2010			Difference		
Latitude	*n*	DOY [a]	SE	*n*	DOY [a]	SE	Days earlier	SE	*P*
33	83	104.9	1.16	1,138	89.3	0.27	15.6	1.19	<0.001
34	75	112.3	1.22	1,778	94.1	0.20	18.2	1.24	<0.001
35	169	112.6	0.70	2,475	99.5	0.16	13.1	0.72	<0.001
36	118	117.3	0.92	1,996	102.2	0.18	15.1	0.93	<0.001
37	129	121.8	0.75	1,974	106.5	0.17	15.3	0.76	<0.001
38	191	125.7	0.70	2,694	111.1	0.15	14.6	0.71	<0.001
39	298	128.8	0.51	3,308	115.5	0.14	13.3	0.53	<0.001
40	569	135.0	0.42	3,057	118.7	0.14	16.3	0.44	<0.001
41	898	135.2	0.28	4,225	121.5	0.11	13.7	0.30	<0.001
42	1,009	135.9	0.23	4,007	124.2	0.11	11.7	0.25	<0.001
43	564	137.6	0.26	2,618	125.9	0.12	11.7	0.29	<0.001
44	488	138.7	0.31	1,768	127.3	0.14	11.4	0.34	<0.001

[a] Arrival dates expressed as day of year (DOY) and corrected for leap years; for example, 95 = 5 April.

Migratory rate (inversely related to passage days; Fig. 4) increased at higher latitudes in both periods.

Climate variables associated with arrival differed between periods, with warmer winters and warmer and wetter springs reported in recent times at higher latitudes (Table 2). In general, winter and spring temperatures were highly correlated in both periods ($r = 0.85$, df = 34 and 926, $P < 0.0001$). On average, February temperatures on Central American wintering grounds were 0.90 ± 0.02°C (SE) warmer for arrivals in recent times ($P < 0.0001$) than in the historical period. Several weather variables predicted arrival dates at various latitudes during the recent period (Table 3A). Most notably, birds arrived earlier in warmer winters and springs at lower latitudes, but later in warmer winters and springs at higher latitudes. Wetter springs were correlated with earlier arrivals at 33 and 34°N, but with later arrivals at 37 and 40°N (Table 3). In general, birds arrived earlier when February wintering-ground temperatures were warmer. Weather variables during the historical period were less predictive of avian arrivals; although some trends were similar to the recent period, only 4 of 48 possible variables were significant at our 12 latitudes (Table 3B).

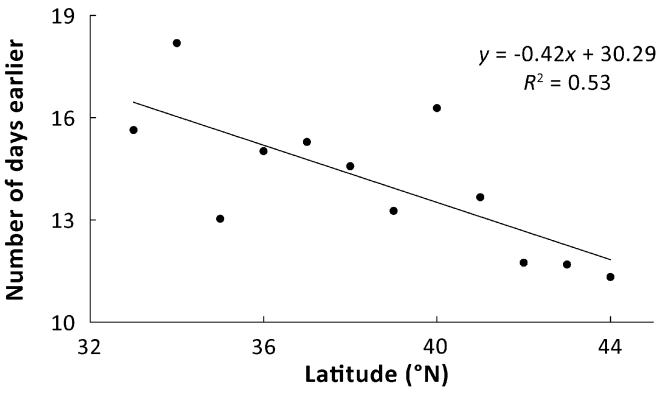

FIG. 3. Migration advancement in Ruby-throated Hummingbirds, 1880–1969 and 2001–2010, by 1° latitudinal band. Linear regression line shows that changes in first arrival dates are less pronounced in northern latitudes.

DISCUSSION

Understanding how species and ecosystems respond across spatial and temporal scales is one of the challenges facing climate-change research (Primack et al. 2009). The innate urgency of birds to complete northward migration in time for breeding activities to occur when food and other resources are plentiful is constrained by availability of suitable temperatures and sufficient food at a variety of latitudes en route (Hüppop and Winkel 2006, Tøttrup et al. 2008). Our findings demonstrate that Ruby-throated Hummingbirds arrive at breeding areas throughout the eastern United States 11.4 to 18.2 days earlier than they did historically (Fig. 1), a result generally consistent with site-specific reports at various latitudes. For example, we report an 11.8-day advancement in ruby-throat migration at 42°N, whereas Ledneva et al. (2004) reported an 18.4-day advancement in Middleborough, Massachusetts (41.89°N, 70.91°W), from 1970 to 2002;

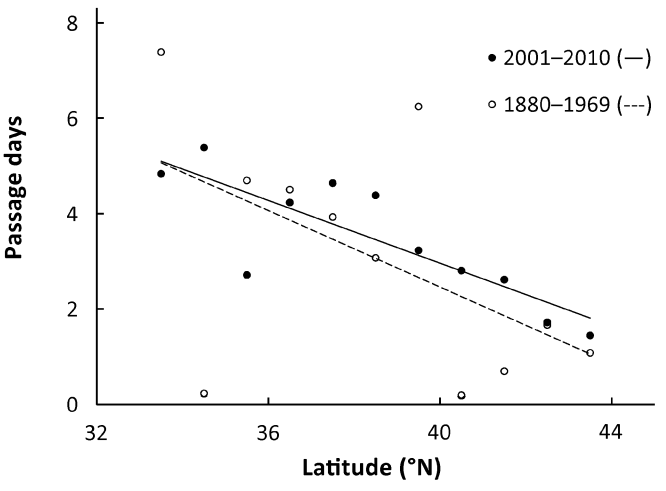

FIG. 4. Number of passage days spent between 1° latitude intervals during spring migration by first-arriving Ruby-throated Hummingbirds. Linear regression lines indicate that migration rates increased (i.e., fewer passage days) in northern latitudes in both 1880–1969 and 2001–2010.

TABLE 2. Differences (Diff.) in climate variables in the region between 33 and 45°N and from 67 to 94°W, between historical (1880–1969) and recent (2001–2010) periods.

	Winter temperature (°C) [a]				Spring temperature (°C) [b]				Spring precipitation (cm) [c]			
Latitude	Diff. [d]	SE	*P*	Trend [e]	Diff. [d]	SE	*P*	Trend [e]	Diff. [d]	SE	*P*	Trend [e]
33	–0.69	0.23	0.003	Colder	0.14	0.15	0.37		–4.98	1.42	<0.001	Dryer
34	–1.01	0.22	<0.001	Colder	0.19	0.14	0.17		–3.21	1.30	0.01	Dryer
35	0.26	0.15	0.08		0.83	0.09	<0.001	Warmer	–4.22	0.72	<0.001	Dryer
36	0.48	0.20	0.02	Warmer	1.14	0.13	<0.001	Warmer	–4.65	1.17	<0.001	Dryer
37	–0.08	0.20	0.69		0.53	0.12	<0.001	Warmer	0.37	1.17	0.75	
38	0.63	0.18	<0.001	Warmer	1.41	0.10	<0.001	Warmer	0.92	0.79	0.24	
39	0.36	0.14	0.01	Warmer	1.28	0.08	<00001	Warmer	0.67	0.55	0.22	
40	0.26	0.12	0.04	Warmer	1.14	0.07	<0.001	Warmer	1.29	0.42	0.002	Wetter
41	0.43	0.09	<0.001	Warmer	1.31	0.06	<0.001	Warmer	4.76	0.36	<0.001	Wetter
42	0.90	0.08	<0.001	Warmer	1.25	0.05	<0.001	Warmer	4.04	0.29	<0.001	Wetter
43	1.31	0.12	<0.001	Warmer	1.27	0.08	<0.001	Warmer	1.98	0.37	<0.001	Wetter
44	2.82	0.16	<0.001	Warmer	1.69	0.11	<0.001	Warmer	2.62	0.42	<0.001	Wetter

[a] Mean January and February temperatures on North American breeding grounds.
[b] Mean March and April temperatures on North American breeding grounds.
[c] Mean sum of February–April precipitation in North American breeding grounds.
[d] Differences calculated by subtracting 1880–1969 climate means from 2001–2010 climate means.
[e] Summary of how recent climate data (2001–2010) compare with historical climate data (1880–1969).

Butler (2003) reported a 6.3-day shift in Worcester, Massachusetts (42.26°N, –71.80°W), from 1932 to 1993. Butler (2003) also reported a modest 2-day shift ($P = 0.05$) toward earlier arrivals at Cayuga Lake Basin, New York (42.92°N, –76.73°W), but arrival periods were grouped differently (i.e., 1903–1950 and 1951–1993) than in our study. At 44°N, we report an 11.4-day advancement, whereas Wilson et al. (2000) found a 4-day advancement in Maine (~44°N, 70°W; comparing intervals 1899–1911 and 1994–1997) and Swanson and Palmer (2009) found an 18.1-day advancement in South Dakota (~44°N, 100°W; between 1971 and 2006). Swanson and Palmer (2009) found no evidence that ruby-throats arrived earlier in Minnesota between 1964 and 2005 and, although Minnesota (~46°N, 95°W) is outside our study region, this result is somewhat consistent with our finding that advancement in arrival dates declines at higher latitudes (Fig. 3).

Effects of climate on hummingbird arrivals.—Our findings are consistent with a growing body of evidence that winters and springs are warming in recent years, especially at higher latitudes (i.e., above 35°N; Karl and Trenberth 2003, Loarie et al. 2009; Table 2). Earlier hummingbird arrivals in our study were correlated with weather variables in both periods (Table 3), consistent with a general trend reported across bird taxa (Gordo 2007, Lehikoinen and Sparks 2010). Photoperiod has long been regarded as the primary cue that triggers migration in birds (Farner 1964), with weather variables such as temperature and precipitation helping to fine tune migration timing (Tøttrup et al. 2010, Knudsen et al. 2011). Interestingly, our results showed that weather variables affected arrival dates to a greater extent in recent times, with 29 of 48 metrics significant in the recent period, compared with only 4 of 48 in the historical period (Table 3), which may suggest that local-scale weather or climate-related cues are emerging as factors of increasing importance to ruby-throats, both in North America and on Central American wintering grounds.

During our recent period (2001–2010), birds arrived earlier to most latitudes when February temperatures were higher in their wintering grounds prior to departure (Table 3). Few studies have used temperature on the wintering ground to predict migratory arrival to North America, because long-term data from tropical areas in the western hemisphere are limited (Gordo 2007). Evidence from Europe, however, suggests that migrants return earlier when winters are warmer in Africa (Boyd 2003, Cotton 2003, Balbontín et al. 2009). Our results also show that recent arrivals are earlier when winters and springs are warmer in North America, but only at lower latitudes (Table 3), which suggests that migration of Ruby-throated Hummingbirds is likely constrained by weather or foraging conditions en route (Marra et al. 2005, Tøttrup et al. 2008).

Ruby-throats migrated north at a rate of 32.1 km day^{-1} during the recent period, a rate similar to the 32.2 km day^{-1} (or 20 miles day^{-1}) reported by the popular citizen-science website hummingbirds.net. Our results suggest that migration occurred faster historically (36.2 km day^{-1}), meaning that hummingbirds currently take ~4 additional days to travel between 33 and 45°N. It is somewhat surprising that the migratory rate has slowed in recent times, even though the migratory period occurs much earlier in the spring (Fig. 2), given recent increases in ruby-throat populations and the likelihood that competition for food may be intensified. An increase in the provision of sugar water along migration routes in recent times may partially explain this delay. If so, periodic stops along the migratory route to refuel at feeders could help reduce mortality during migration and allow hummingbirds to arrive in breeding areas in better condition and to better compete for nesting territories.

Our data also show that warmer winter temperatures advance migration below 40°N but delay hummingbird migration above 40°N (Table 3A). It is possible that a failure to meet winter chilling requirements of plants, due to recent warmer winters in the eastern United States, may delay bud break for some plant species (Morin et al. 2009, Harrington et al. 2010, Cook et al. 2012) below 40°N (Zhang et al. 2007), meaning that migratory birds, such as hummingbirds, may extend their stopover periods to obtain sufficient food to complete migration (Strode 2003) or in response to another plant phenology cue. We report a migratory delay (i.e., an increase in the number of passage days; Fig. 4) between 37°N and 39°N in the recent period, which appears to be consistent with this hypothesis. Spring temperatures were also correlated with later arrivals at mid- and high latitudes, but

TABLE 3. Significant predictors ($P < 0.05$) of Ruby-throated Hummingbird arrival dates in (A) recent (2001–2010) and (B) historical (1880–1969) periods. We used regression models to identify the environmental variables that predicted arrival date at each latitudinal band. Latitude, longitude, and elevation were included as covariates to adjust for possible regional effects within latitudinal bands.

	Winter temperature (°C) [a]			Spring temperature (°C) [b]			Spring precipitation (cm) [c]			Wintering grounds temp. (°C) [d]		
Latitude	Slope (SE)	*P*	Description	Slope (SE)	*P*	Description	Slope (SE)	*P*	Description	Slope (SE)	*P*	Description
(A) Recent data (2001–2010)												
33	–0.92 (0.18)	<0.001	↑Temp, Earlier	–1.36 (0.28)	<0.001	↑Temp, Earlier	–0.13 (0.03)	<0.001	↑Precip, Earlier	–0.81 (0.25)	0.001	↑Temp, Earlier
34	–0.64 (0.14)	<0.001	↑Temp, Earlier	–0.22 (0.23)	0.33		–0.06 (0.02)	0.02	↑Precip, Earlier	–0.21 (0.20)	0.29	
35	–0.53 (0.10)	<0.001	↑Temp, Earlier	–0.40 (0.17)	0.02	↑Temp, Earlier	–0.03 (0.02)	0.20		0.02 (0.16)	0.88	
36	–0.25 (0.12)	0.03	↑Temp, Earlier	0.19 (0.18)	0.28		0.03 (0.02)	0.10		0.17 (0.18)	0.32	
37	–0.54 (0.10)	<0.001	↑Temp, Earlier	–0.02 (0.17)	0.92		0.04 (0.02)	0.008	↑Precip, Later	–0.06 (0.17)	0.72	
38	–0.55 (0.08)	<0.001	↑Temp, Earlier	0.42 (0.14)	0.003	↑Temp, Later	0.03 (0.02)	0.12		–0.41 (0.15)	0.008	↑Temp, Earlier
39	–0.36 (0.07)	<0.001	↑Temp, Earlier	0.33 (0.14)	0.01	↑Temp, Later	0.02 (0.02)	0.18		–0.39 (0.14)	0.006	↑Temp, Earlier
40	–0.07 (0.07)	0.35		0.01 (0.13)	0.95		0.09 (0.02)	<0.001	↑Precip, Later	–0.29 (0.14)	0.04	↑Temp, Earlier
41	0.02 (0.05)	0.66		0.33 (0.09)	<0.001	↑Temp, Later	0.02 (0.01)	0.18		–0.48 (0.11)	<0.001	↑Temp, Earlier
42	0.23 (0.05)	<0.001	↑Temp, Later	0.50 (0.09)	<0.001	↑Temp, Later	–0.03 (0.01)	0.08		–0.73 (0.12)	<0.001	↑Temp, Earlier
43	0.19 (0.05)	<0.001	↑Temp, Later	0.29 (0.08)	<0.001	↑Temp, Later	–0.02 (0.02)	0.33		–0.53 (0.12)	<0.001	↑Temp, Earlier
44	0.04 (0.05)	0.40		0.30 (0.08)	<0.001	↑Temp, Later	–0.02 (0.02)	0.37		–0.75 (0.13)	<0.001	↑Temp, Earlier
(B) Historical data (1880–1969)												
33	0.90 (0.63)	0.16		1.03 (0.88)	0.25		–0.21 (0.10)	0.04	↑Precip, Earlier	–0.98 (1.03)	0.34	
34	0.72 (0.48)	0.14		–0.18 (0.93)	0.85		-0.19 (0.10)	0.07		1.40 (0.98)	0.16	
35	–0.28 (0.33)	0.39		–0.20 (0.48)	0.68		0.03 (0.08)	0.70		–0.10 (0.63)	0.87	
36	–0.18 (0.33)	0.60		0.27 (0.44)	0.54		–0.06 (0.10)	0.52		0.16 (0.80)	0.84	
37	–0.08 (0.40)	0.84		0.32 (0.54)	0.55		0.14 (0.12)	0.25		–0.01 (0.67)	0.99	
38	0.08 (0.28)	0.77		–0.10 (0.44)	0.81		0.08 (0.11)	0.44		–0.02 (0.65)	0.98	
39	0.07 (0.27)	0.80		0.34 (0.38)	0.37		–0.07 (0.09)	0.43		–0.15 (0.59)	0.80	
40	0.38 (0.13)	0.004	↑Temp, Later	0.16 (0.19)	0.39		–0.06 (0.05)	0.28		-0.09 (0.28)	0.75	
41	0.17 (0.11)	0.13		–0.19 (0.16)	0.23		–0.03 (0.05)	0.49		0.35 (0.22)	0.11	
42	0.04 (0.09)	0.65		0.15 (0.13)	0.25		–0.01 (0.04)	0.79		0.20 (0.19)	0.27	
43	0.06 (0.10)	0.55		–0.25 (0.14)	0.07		0.02 (0.04)	0.66		–0.17 (0.23)	0.46	
44	0.26 (0.11)	0.02	↑Temp, Later	–0.16 (0.14)	0.27		0.03 (0.04)	0.42		–0.50 (0.23)	0.04	↑Temp, Earlier

[a] Mean January and February temperatures on North American breeding grounds.
[b] Mean March and April temperatures on North American breeding grounds.
[c] Mean sum of February–April precipitation on North American breeding grounds.
[d] Mean February temperature in Yucatan, Mexico (20.98°N, –89.65°W), used to approximate temperatures in wintering grounds.

this may be because spring and winter temperatures were highly correlated in our study and the mechanism that best explains the migratory delay is the warming winter temperature. Another possibility is that some birds delay migration in years with high productivity and extend stopovers to take advantage of improved foraging conditions (Tøttrup et al. 2008, Robson and Barriocanal 2011). Regardless of the mechanism(s) governing these interactions, ruby-throats appear to arrive later in relation to spring conditions at northern latitudes, which may indicate a mismatch between hummingbird arrival and initial availability of food. Our results demonstrate the importance of considering latitude and possible reasons for stopover when interpreting migratory studies that assess phenology.

Using first arrival dates and a growing hummingbird population.—We have obviated a common criticism that first arrival dates are affected by differences in observer effort across space (Gordo and Sanz 2006, Dickinson et al. 2010) by comparing mean first arrival dates of ruby-throats (based on ≥75 observations per band; Table 1), instead of using first arrival dates of individuals. Other biases of using first arrival dates were impossible to address in our study, such as the tendency for early migrants to be influenced more by climate change (Vähätalo et al. 2004, Tøttrup et al. 2010) and the tendency for first arrival dates to advance more than mean or median migration dates (Lehikoinen et al. 2004, Rubolini et al. 2007, Miller-Rushing et al. 2008). Even so, we are confident that our results illustrate biologically meaningful spatial and temporal patterns and note that a study of this spatial and temporal magnitude (Fig. 2) would be nearly impossible to conduct without using first arrival dates.

We also point out the population size of ruby-throats has more than doubled in the eastern United States since 1966, according to data from the North American Breeding Bird Survey (Sauer et al. 2011). We chose not to include population size in our analyses because we lacked a reliable estimate of hummingbird populations from 1880 to 1966. Swanson and Palmer (2009) reported that first arrival dates advanced in 7 of 10 species with increasing populations (and in 16 of 28 species with stable populations) from 1964 to 2006 in Minnesota and South Dakota. Although increasing populations are often correlated with higher detection probabilities among citizen volunteers (Tryjanowski and Sparks 2001, Tryjanowski et al. 2005, Miller-Rushing et al. 2008), we find it unlikely that population changes, alone, sufficiently explain the dramatic migratory advancement that we report here.

Backyard bird feeding, expanding winter ranges, and other data limitations.—An important consideration when interpreting our results is the increase in popularity of backyard bird feeding in the United States in past decades (Robb et al. 2008). Although we are confident that data reporters in our historical period (1880–1969) were competent naturalists, it is likely that fewer historical observations were made at feeders, perhaps decreasing the likelihood that early-arriving birds were immediately detected. Many of our recent arrivals were also reported online (compared with historical arrival records that were submitted by mail), perhaps encouraging some observers to be more vigilant when ruby-throats were reported nearby (L. Chambers pers. comm.), and perhaps increasing the effort among competitive observers seeking to report the first hummingbird arrival in a particular area (Schaffner 2009). Unfortunately, the data that we used did not include detailed observer information that would have allowed demographic comparisons to be made between observers from different periods, such as differences in observer age, income, and gender (Cooper and Smith 2010), factors that may have contributed to the discretionary time observers had to look for birds. In addition, important demographic data about hummingbird populations (e.g., age classes of birds, sex ratios, and whether birds were local breeders or migrating birds) that likely varied by latitude and period were unmeasurable in our study and could have influenced the changes in hummingbird migration that we report.

It is also possible that the winter ranges of hummingbirds could be advancing northward into the southern United States as bird feeders and warming winter temperatures provide more predictable food resources (Parmesan and Yohe 2003). A more northerly winter range could potentially decrease the distance and time that a hummingbird needs to migrate and cause birds to arrive earlier to their breeding grounds (Robb et al. 2008, Visser et al. 2009), although birds would still face similar environmental constraints in migrating northward. It is even possible that some ruby-throats have changed their migratory routes altogether (i.e., migrating over land through Mexico and Texas rather than over the Gulf of Mexico; Zelt et al. 2012). Although we were not able to account for this possibility, we defined our study area as north of 33°N, which almost certainly eliminated the chance for wintering birds to be reported as first arrivals (Hauser and Currie 1966, Robinson et al. 1996).

We have demonstrated a major phenological shift in the past century for the ruby-throat that is most pronounced at lower latitudes and is largely related to climate. Extended migratory stopovers in mid-latitudes during warmer winters, when spring is earlier in the north, may present a double effect on synchrony between birds and their breeding habitats. Taken together, our results demonstrate advanced migration arrival dates but with spatial variation for Ruby-throated Hummingbirds and suggest that local-scale weather-related cues, in both North American breeding and Central American wintering grounds, are emerging as factors of increasing importance to bird phenology. Large-scale comparative studies such as this could help conservationists and policy makers identify where ecosystem services provided by birds (e.g., pollination and pest suppression) are most likely to be impeded and help inform management decisions.

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