Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird

Scott Wilson,[1,4] Shannon L. LaDeau,[2] Anders P. Tøttrup,[3] and Peter P. Marra[1]

[1]*Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008 USA*
[2]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[3]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen,
Universitetsparken 15, DK-2100 Copenhagen, Denmark*

Abstract. Geographic variation in the population dynamics of a species can result from regional variability in climate and how it affects reproduction and survival. Identifying such effects for migratory birds requires the integration of population models with knowledge of migratory connectivity between breeding and nonbreeding areas. We used Bayesian hierarchical models with 26 years of Breeding Bird Survey data (1982–2007) to investigate the impacts of breeding- and nonbreeding-season climate on abundance of American Redstarts (*Setophaga ruticilla*) across the species range. We focused on 15 populations defined by Bird Conservation Regions, and we included variation across routes and observers as well as temporal trends and climate effects. American Redstart populations that breed in eastern North America showed increased abundance following winters with higher plant productivity in the Caribbean where they are expected to overwinter. In contrast, western breeding populations showed little response to conditions in their expected wintering areas in west Mexico, perhaps reflecting lower migratory connectivity or differential effects of winter rainfall on individuals across the species range. Unlike the case with winter climate, we found few effects of temperature prior to arrival in spring (March–April) or during the nesting period (May–June) on abundance the following year. Eight populations showed significant changes in abundance, with the steepest declines in the Atlantic Northern Forest (−3.4%/yr) and the greatest increases in the Prairie Hardwood Transition (4%/yr). This study emphasizes how the effects of climate on populations of migratory birds are context dependent and can vary depending on geographic location and the period of the annual cycle. Such knowledge is essential for predicting regional variation in how populations of a species might vary in their response to climate change.

Key words: American Redstart; Breeding Bird Survey; climate; hierarchical models; migratory connectivity; Neotropical migrant; population dynamics; Setophaga ruticilla.

Introduction

Identifying the causes of fluctuations in population size requires an understanding of limiting factors operating throughout the annual cycle. Much of our knowledge of population limitation in birds comes from species that are more or less sedentary year-round because individuals can be monitored among seasons and years (Newton 1998, Böhning-Gaese et al. 2000). This task is far more challenging for long-distance migrants because of the vast distances they move among seasons. A typical individual will spend about three months on the breeding grounds, six to seven months on the wintering grounds, and the remainder on spring and fall migration. At each of these stages, they face a multitude of factors that can influence fitness (e.g., Sillett

et al. 2000, Marra and Holmes 2001, Latta and Faaborg 2002, Hannon et al. 2009), and events during one stage of the annual cycle can carry over to affect performance during subsequent stages (Marra et al. 1998, Reudink et al. 2009). While detailed studies on the breeding or nonbreeding grounds have helped our understanding of the factors affecting reproduction and survival for specific populations, the difficulty of tracking individuals among seasons means we still have a limited understanding of how different factors interact between seasons of the annual cycle and how they vary across a species range.

Climate is one factor known to influence reproduction and survival of songbirds (reviewed in Newton 1998). For species breeding in north temperate regions, warmer temperatures typically result in an earlier onset of breeding (Both et al. 2004, Dunn 2004), which can enhance productivity because it increases the opportunities for multiple broods or re-nesting after failure (Wilson and Arcese 2003). Temperature and precipitation can also directly influence nestling and fledgling

survival via inclement weather and effects on food abundance (Morrison and Bolger 2002, Collister and Wilson 2007). Many long-distance migrants spend the nonbreeding season in regions with interannual variability in rainfall, which often has cascading effects on plant productivity, arthropod abundance, and ultimately the condition (Brown and Sherry 2006, Studds and Marra 2007) and survival (Szep et al. 2006) of birds. We know less about the effects of climate during migration (but see Tøttrup et al. 2008), but mortality is thought to be high during this period (Sillett and Holmes 2002) and severe weather en route may be a frequent cause (e.g., Wiedenfield and Wiedenfield 1995).

The impact of breeding or nonbreeding-season climate may vary for populations across a species range, dependent on the frequency and extent of weather anomalies. Only recently have we begun to focus on the effects of climate on the dynamics of migratory bird populations over large spatial scales (Anders and Post 2006, Link and Sauer 2007), and there have been no studies directly linking winter climatic conditions to the abundance of Nearctic–Neotropical migrants across the breeding range of a species. Such analyses first require that we understand migratory connectivity: where specific breeding populations of migrants winter, and where wintering populations of migrants breed (Webster et al. 2002). Advances in stable isotopes analyses over the past decade have improved our knowledge of migratory connectivity for some species (Chamberlain et al. 1997, Rubenstein et al. 2002, Norris et al. 2006), allowing for a more precise examination of how climatic events in one period influence that same regional population in a subsequent period of the annual cycle.

We combined knowledge on migratory connectivity with data from the North American Breeding Bird Survey (BBS) to provide the first study on the role of breeding and nonbreeding-season climate on the range-wide population dynamics of a Neotropical migrant songbird, the American Redstart. This species breeds in second-growth deciduous and mixed forests, and its breeding distribution covers much of eastern North America, the boreal forest and mountainous regions of western Canada, and the northwestern United States (Sherry and Holmes 1997). Redstarts have a broad winter range but the highest numbers are observed in the Caribbean and western Mexico, with lower numbers elsewhere in Central America, northern South America, and southern Florida (Sherry and Holmes 1997). Isotopic studies have examined the connectivity between breeding and nonbreeding populations, with strong evidence for an east–west migratory divide (Norris et al. 2006). Populations that breed in western North America primarily overwinter in Mexico and northern Central America, while those from the Midwest and eastern North America overwinter in the Caribbean, with lower numbers in southern Central America and northern South America.

Objectives and predictions

We first consider the effects of breeding-season temperature on population abundance the following year. We predicted that warmer temperatures in early spring (March–April) and during the nesting period (May–June) in year t would lead to higher abundance in year $t + 1$, and expected this effect to be most pronounced for populations in the colder northern or western parts of the species' range. We then consider whether plant productivity during the nonbreeding period, as indicated by the Normalized Difference Vegetation Index, NDVI (Pettorelli et al. 2005), influenced the abundance of redstarts in the following breeding season. Our previous work on the nonbreeding grounds has identified a strong relationship between rainfall, plant productivity, insect abundance, and redstart performance (Studds and Marra 2007, 2011). As a measure of net primary productivity, and thus indirectly an index of food availability between years, the NDVI should provide a reliable measure of the ecological conditions experienced by American Redstarts. Based on migratory connectivity in this species (Norris et al. 2006), we predicted that populations breeding in western North America would show a positive response to the previous winter NDVI in western Mexico, while those in eastern North America would show a positive response to the NDVI in the Caribbean.

Methods

Survey data

We analyzed 26 years of data (1982–2007) from the Breeding Bird Survey using hierarchical Bayesian approaches (Gelman et al. 2004, Link and Barker 2010). These methods have previously been applied to the North American Breeding Bird Survey (Link and Sauer 2002, LaDeau et al. 2007), the Audubon Society Christmas Bird Count (Link and Sauer 2007), and the May Breeding Waterfowl Survey (Sæther et al. 2008). The North American Breeding Bird Survey was initiated in 1966 and is conducted annually during the breeding period in May and June (Sauer et al. 2006). The survey is based on ~40.2 km (24.5 miles) roadside routes with a three-minute point count conducted every 0.8 km for a total of 50 counts. The number of individuals for a species is typically summed across all 50 counts to provide a single abundance per route as the sampling unit.

We analyzed BBS data according to populations defined by Bird Conservation Regions (BCR), and each BCR contained multiple routes each surveyed for a variable number of years. BCRs were developed for the North American Bird Conservation Initiative and are based on eco-regions described by the Commission for Environmental Cooperation (1997). BCRs are well suited for defining a population, because they capture the habitat and environmental conditions in a region,

TABLE 1. Mean abundance, breeding-season temperature, and temporal trend of American Redstarts for 15 populations defined by Bird Conservation Region (BCR) across the species range.

BCR strata	BCR name	No. BBS routes	Mean no. redstarts/route	Breeding temperature (°C)	Temporal trend (% change/yr)
10N	Canadian Northern Rockies (1)	54	8.19	3.60/12.68	0.40 (−1.59, 2.10)
10S	U.S. Northern Rockies (1)	51	1.13	3.15/12.15	**−1.90 (−3.42, −0.36)**
6W	Western Boreal Taiga Plains (1)	49	2.34	0.34/12.71	0.40 (−2.66, 2.60)
6E	Eastern Boreal Taiga Plains (1)	35	5.65	−1.85/12.78	**3.90 (1.60, 6.20)**
17	Badlands and Prairies (1)	29	1.62	4.65/17.34	**−2.36 (−4.61, −0.29)**
12W	Western Boreal Hardwood Transition (1,2)	201	6.25	1.46/14.79	**1.50 (0.70, 2.20)**
12E	Eastern Boreal Hardwood Transition (2)	45	5.22	−0.65/13.84	−0.90 (−2.27, 0.40)
13	Lower Great Lakes/St. Lawrence Plain (2)	153	2.99	3.65/16.06	0.30 (−0.71, 1.00)
14	Atlantic Northern Forest (2)	245	11.56	1.63/15.59	**−3.42 (−4.06, −2.93)**
23	Prairie Hardwood Transition (2)	121	1.52	5.34/14.21	**4.00 (3.10, 4.90)**
30	New England/Mid-Atlantic Coast (2)	89	1.94	6.88/17.67	−0.29 (−1.32, 0.60)
28N	Northern Appalachian Mountains (2)	308	4.11	7.15/17.43	**1.20 (0.60, 1.70)**
26	Mississippi Alluvial Valley (2)	16	2.06	14.95/23.77	−1.97 (−5.31, 1.20)
28S	Southern Appalachian Mountains (2)	54	1.13	10.31/19.76	**−2.02 (−3.69, −0.42)**
27W	Southeastern Coastal Plain (2)	61	1.19	15.89/23.83	−0.50 (−2.72, 1.70)

Notes: See Fig. 1 for the location of the Bird Conservation Regions (BCR) used in this analysis. Numbers in parentheses following the BCR description refer to the approximate west–east wintering location for the majority of individuals from each breeding area (based on Norris et al. [2006]): 1, Mexico and northern Central America; 2, Caribbean. Numbers of BBS routes used in analyses for each population are given. The two values separated by a slash in the breeding temperature column are the means for March–April and May–June, respectively, 1982–2007. Temporal trends include the mean with 95% credible interval in parentheses. Values in boldface type indicate significant trends with credible intervals not overlapping zero.

and therefore reflect the expected variation in suitable habitat and climate experienced by redstarts across their breeding range. Because some BCRs were large, we further subdivided them into a northern/southern or an eastern/western component based on state or provincial boundaries (Table 1). The locations of these splits were as follows: (1) Northern Rockies (BCR 10), U.S./Canada border; (2) Boreal Taiga Plains (BCR 6), Alberta/Saskatchewan border; (3) Boreal Hardwood Transition (BCR 12), U.S./Canada border between Lake Superior and Lake Huron; (4) Appalachian Mountains (BCR 28), borders of Kentucky/Tennessee and Virginia/North Carolina (see Table 1 for further detail on BCR designations). To avoid including populations where the vast majority of counts were 0, we only used information from a BCR if the average number of redstarts detected per route per year was more than one individual and the BCR contained at least five routes that met these criteria. Following this, we did not include the BCRs along the periphery of the species' range including numbers: 4, 5, 9, 11, 16, 18, 21, 22, 24, 25, and 29. In the Western Boreal Taiga Plains (BCR 6 west), redstarts were rare north of the Alberta–Northwest Territories border, and we did not include any routes for this region. Similarly, in the Southeastern Coastal Plain (BCR 27), we did not include any routes from states north of South Carolina because redstart abundance was very low on those routes. American Redstarts were common in the Boreal Softwood Shield (BCR 8), but we did not include those data in this analysis because there were few BBS routes and those were restricted to small portions of the BCR. In total we analyzed data for 15 separate populations (Fig. 1) and these had an average of 101 routes (minimum, 16; maximum, 308) and a mean of 15.59 years of coverage

per route. We restricted our analyses to the years 1982–2007 because that was the time period over which NDVI data were available from the wintering grounds.

Climatic conditions

To assess the effects of winter conditions on the abundance of redstarts, we used the Global Inventory Modeling and Mapping Studies Satellite Drift Corrected and NOAA-16 incorporated Normalized Difference Vegetation Index (NDVI) (Tucker et al. 2005) from December through March as a proxy measure for the actual environmental conditions in the wintering areas during the dry season. The NDVI is the difference (in reflectance) between the AVHRR near-infrared and visible bands divided by the sum of these two bands. Thus, it provides a measure of the degree of absorption by chlorophyll in red wavelengths and is proportional to leaf chlorophyll density. The relationship between NDVI and rainfall is strongest in drier regions and can be influenced by other factors such as water and cloud cover (Santos and Negri 1997). For our purposes, the NDVI was used as a relative measure to look at annual changes in abundance in relation to annual changes in the NDVI for each region, thus removing inter-region variability in the mean value of the index.

The NDVI data used in this study are provided as bimonthly 14-day means at a 1.0° resolution. For comparative purposes, the geographic area over which the NDVI was measured was similar between Cuba and southwestern Mexico. In the latter case, the region for analysis extended from 16° to 21° N latitude and within 250 km of the Pacific coast. Within these regions we extracted the average values from December through March for the grid cells in the region and used this value to represent a single nonbreeding-season measure for the
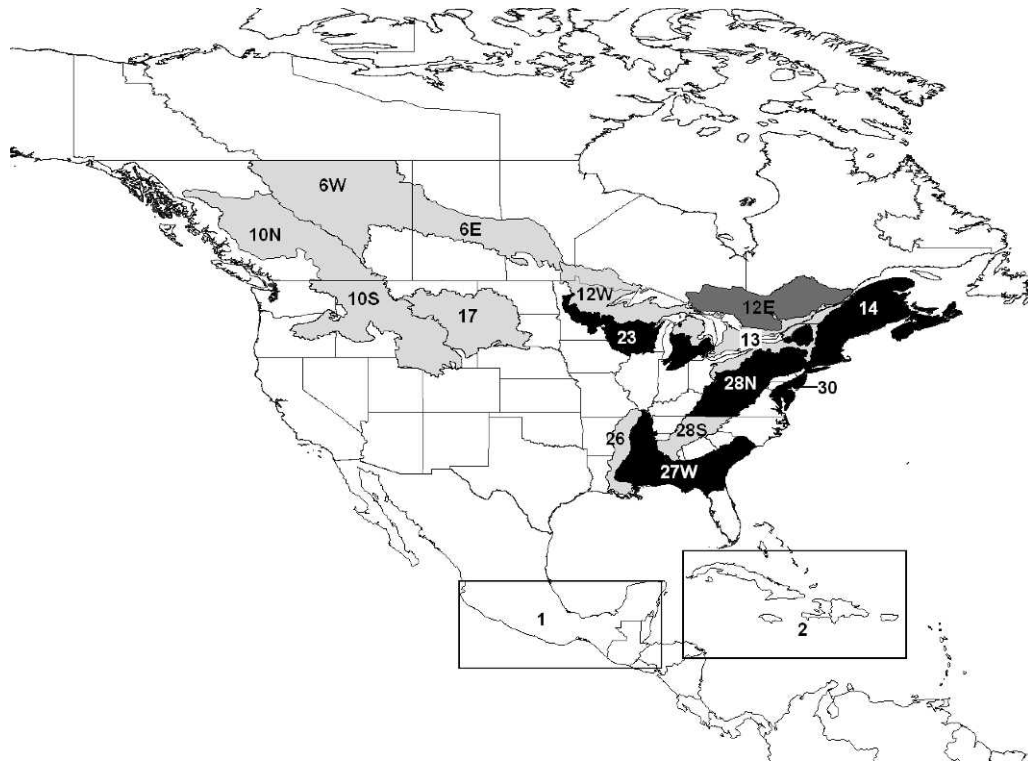
Fɪɢ. 1.   Response of American Redstarts (*Setophaga ruticilla*) to the Normalized Difference Vegetation Index (NDVI) from December through March in Cuba, representing the western Caribbean. The NDVI is a measure of plant productivity and indicates wetter conditions during the winter dry season. Redstart populations that had a positive response to winter conditions in the western Caribbean are shown in black for the 95% level and dark gray for the 90% level (see *Methods*). Populations in light gray all had intervals that overlapped zero. No populations showed significant responses to the NDVI in western Mexico. The areas enclosed in boxes (areas 1 and 2) indicate the expected wintering areas for populations from different parts of the breeding range, that is, breeding populations in the west overwinter in the area of box 1, and populations in the east generally overwinter in box 2 (see Table 1 and Norris et al. [2006]).

conditions in the Caribbean (represented by Cuba) and Western Mexico. These values were standardized prior to analysis. Within years the NDVI is correlated over larger areas, and thus the values for Cuba would describe conditions over most of the Greater Antilles (e.g., the Cuba–Jamaica correlation coefficient is 0.71), while those in west Mexico would also reflect conditions in adjacent areas of Mexico and northern Central America. One outlier year was present in the data for Cuba, with a standardized value of −3.67. To avoid undue influence on the analyses, we replaced the value in this year with the average NDVI value for Cuba. Separate analyses with and without the outlier indicated that there was little difference in the results for the two cases.

To examine the role of breeding-season temperature, we used mean bimonthly values over two periods: (1) March–April, which represents effects on early spring conditions prior to arrival, and (2) May–June, which represents conditions during the main nesting period. Data on breeding-season temperature was specific to each population. For all populations, we used the average estimate of three climate stations that were approximately located near the center of the BCR encompassing that population. For BCRs within the

United States, we obtained climate data from the United States Historical Climatology Network (*available online*),[5] while for Canadian BCRs we used information from Environment Canada (*available online*).[6] Within years, temperature tends to be correlated over large spatial scales, and thus our averaged values over the three stations should describe the conditions experienced by individuals in each year. All temperature data were standardized prior to analysis.

Statistical analyses

Breeding Bird Survey data were modeled as hierarchical over-dispersed Poisson variables, and models were fit using Markov Chain Monte Carlo (MCMC) methods in WinBUGS 1.4.3 (Lunn et al. 2000). Hierarchical Bayesian approaches are particularly useful for population time series analyses because they provide a robust framework to account for sources of variation at multiple scales, such as BBS routes within popula-

---

[5] ⟨http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html⟩
[6] ⟨http://www.climate.weatheroffice.gc.ca/climateData/canada_e.html⟩

tions (Link and Sauer 2002, 2007). Observed values are specified as parameters, which are themselves governed by hyper-parameters (Gelman et al. 2004, Clark 2005, Link and Barker 2010).

We ran MCMC analyses to quantify support for each of the specified predictions, following a common model structure. We let C_{it} denote the observed redstart count on route i and time t where $i = 1,\ldots, N$, $t = 1,\ldots, T$, and N and T are the number of routes and the number of years observed, respectively. Conditioned on the model, counts (C_{it}) are independent across years and routes. We assumed that each of these conditional distributions for C_{it} was Poisson with mean μ_{it}:

$$C_{it} \sim \text{Poisson}(\mu_{it}).$$

Then, the full model for expected log abundance used to test our predictions regarding location and importance of winter plant productivity as well as breeding-season temperature is

$$\log(\mu_{it}) = \beta_{0 \text{ pop}} + \beta_{1 \text{ pop}} \times \text{year} + \beta_{2 \text{ pop}} \times \text{NDVI}_{\text{Cuba } t}$$
$$+ \beta_{3 \text{ pop}} \times \text{NDVI}_{\text{Mexico } t}$$
$$+ \beta_{4 \text{ pop}} \times \text{temp}_{\text{Mar-Apr pop } t-1}$$
$$+ \beta_{5 \text{ pop}} \times \text{temp}_{\text{May-Jun pop } t-1} + \beta_6 \times \text{first year}_{i,t}$$
$$+ \text{route}_i + \text{observer}_{i,t} + \text{noise}_{i,t}.$$

The base process model includes population-specific estimates for intercept (β_0), linear trend (β_1), and population-specific parameters ($\beta_{x\text{pop}}$) representing annual winter-season NDVI in a particular location x (as specified in *Introduction: Objectives and predictions*), or previous breeding-season temperature, indexed by breeding-population geography. For temperature variables, we have included "pop" as a subscript under the Temp covariate to note that temperatures are specific to the BCR containing that population. Subscripts with t indicate variables with an influence in the current year, while $t - 1$ indicates an influence from the previous year. All population-specific parameters are drawn from a common probability distribution with global mean and variance parameters. We assumed conditionally conjugate (vague) prior distributions for all parameters determining the μ_{it}, for all $x = 1,\ldots, X$ covariate effects for all $p = 1,\ldots, P$ populations (including β_{0-5}):

$$\beta_x \sim \mathcal{N}(\mu_x, \tau_x^2).$$

All μ_x were normally distributed with mean 0 and variance 10^3. BBS observers differ in skill at detecting birds, and failure to account for this can lead to errors in the estimate of the coefficients (Link and Sauer 2002, 2007). Observer effects (observer$_{it}$) and unexplained route-specific variability (route$_i$) were both treated as normally distributed random variables, with mean 0 and precision τ_{obs}^2 and τ_{route}^2. There is also evidence that observer identity has a temporal effect, where counts made during an individual's first year of service differ from subsequent years (Link and

Sauer 2007). To incorporate this influence, we treated an individual's first year (first year$_{it}$) as a binary indicator variable (β_6). The precision parameters (τ^2) for β_{0-5}, observer, route, and noise effects were given vague (proper) inverse gamma prior distributions (Berger 1985) with parameters (0.001, 0.001).

We used 95% credible intervals (CIs) generated from the posterior distribution of parameter estimates. Parameters were interpreted to have a significant influence when 95% CIs did not include zero, although we also consider 90% intervals as potential effects for the breeding and nonbreeding-season climate variables. We ran two Markov chains for the model, each for 125 000 iterations and examined model convergence and performance through individual parameter histories, Gelman-Rubin diagnostics, and the degree of autocorrelation (Gelman et al. 2004, Link and Barker 2010). Convergence was typically reached within 1000–5000 iterations, but we used a higher burn-in period of about 25 000 iterations before drawing samples from the posterior distribution.

Results

Our analysis was based on 1511 BBS routes performed by 2377 observers across the 15 populations. A total of 111 038 redstarts were detected on these routes between 1982 and 2007 and there was considerable variability in abundance (birds per route) across the range (Tables 1 and 2). Redstarts were most abundant in the Atlantic Northern Forest (BCR 14), the Boreal Hardwood Transition (BCRs 12 east/west) and the Canadian Northern Rockies (BCR 10 north). They were less common in southern and midwestern regions.

Observer and route level variance

Variation among BBS observers was high, with a posterior median = 0.89 (posterior SD = 0.03) and accounting for ~24% of the variance in the model. There was also a strong, negative, first-year effect for observers ($\beta_{\text{firstyr}} = -0.087$, 95% CI = $-0.122, -0.050$), indicating that American Redstarts are less likely to be reported in an individual's first year of service compared to their subsequent years. Route level variability within strata also accounted for considerable variability in the model (32%) with a posterior median = 1.18 (posterior SD = 0.03).

Breeding and nonbreeding-season conditions

Temperature during early spring and the nesting period had little influence on the abundance of redstarts in the following year. No population showed a significant positive response to either temperature covariate at the 95% level, but surprisingly, birds in the northern Appalachians showed a significant negative response to temperature in March and April. Birds in the U.S. Northern Rockies displayed a significant positive response to early spring temperature at the 90% level, possibly indicating a weak effect of warmer conditions at that time of year.

TABLE 2. Model parameter estimates for American Redstarts showing abundance in relation to climatic conditions in the Caribbean (represented by Cuba) and western Mexico during the previous winter and temperatures during the previous breeding season.

Population (BCR)	$\beta_{2\ pop} \times$ NDVI$_{Cuba\ t}$	$\beta_{3\ pop} \times$ NDVI$_{Mexico\ t}$	$\beta_{4\ pop} \times$ Temp$_{Mar–Apr\ pop\ t-1}$	$\beta_{5\ pop} \times$ Temp$_{May–Jun\ pop\ t-1}$
10N	0.000 (−0.080, 0.064)	−0.011 (−0.063, 0.035)	−0.033 (−0.081, 0.011)	0.011 (−0.028, 0.050)
10S	0.044 (−0.033, 0.130)	−0.007 (−0.071, 0.045)	0.052 (−0.007, 0.128)†	0.022 (−0.025, 0.079)
6W	0.036 (−0.046, 0.119)	0.018 (−0.036, 0.084)	0.044 (−0.014, 0.121)	−0.001 (−0.051, 0.044)
6	0.008 (−0.090, 0.081)	−0.008 (−0.070, 0.044)	0.015 (−0.037, 0.073)	−0.014 (−0.076, 0.033)
17	0.033 (−0.055, 0.117)	−0.014 (−0.096, 0.042)	0.015 (−0.048, 0.087)	−0.007(−0.070, 0.042)
12W	−0.004 (−0.049, 0.037)	0.011 (−0.020, 0.042)	−0.007(−0.035, 0.021)	0.013 (−0.014, 0.039)
12E	0.052 (−0.011, 0.129)†	0.022 (−0.027, 0.080)	0.000 (−0.050, 0.051)	−0.007 (−0.053, 0.034)
13	0.037 (−0.016, 0.065)	0.010 (−0.027, 0.049)	−0.004 (−0.039, 0.029)	0.020 (−0.011, 0.052)
14	**0.051 (0.019, 0.083)**	−0.004 (−0.031, 0.022)	0.014 (−0.006, 0.033)	0.006 (−0.012, 0.024)
23	**0.059 (0.000, 0.129)**	0.015 (−0.027, 0.061)	−0.020 (−0.065, 0.024)	0.017 (−0.021, 0.058)
30	**0.060 (0.002, 0.120)**	0.009 (−0.039, 0.058)	0.009 (−0.035, 0.055)	0.015 (−0.023, 0.055)
28N	**0.045 (0.008, 0.082)**	0.008 (−0.021, 0.038)	**−0.026 (−0.047, −0.005)**	−0.002 (−0.024, 0.020)
26	0.046 (−0.044, 0.151)	0.023 (−0.036, 0.105)	0.004 (−0.071, 0.083)	−0.005 (−0.072, 0.049)
28S	0.035 (−0.047, 0.118)	0.028 (−0.026, 0.103)	−0.039 (−0.115, 0.019)	0.008 (−0.042, 0.060)
27W	**0.073 (0.002, 0.179)**	0.016 (−0.040, 0.083)	0.004 (−0.054, 0.063)	0.003 (−0.046, 0.049)

Notes: Values shown are the median estimates from the posterior distribution with 95% lower and upper credible intervals in parentheses. Strata in boldface type indicate 95% credible intervals not overlapping zero for that particular variable. See Table 1 for BCR descriptions.

† Significant at the 90% level.

Although there was little evidence of breeding-season temperature, we found strong support for an effect of winter conditions on abundance in the eastern part of the breeding range. As predicted, six of the eastern populations showed a strong positive relationship to the NDVI in the Caribbean including five at the 95% significance level and one at the 90% level. There were no western populations with a positive relationship between abundance and the NDVI in Caribbean. Contrary to our predictions, the western populations did not show a positive association with the NDVI in Mexico, nor did any of the eastern breeding populations.

Temporal trends

Distinct temporal patterns, beyond the interannual temperature and NDVI effects, were observed for 8 of the 15 populations (Fig. 2, Table 1). The strongest declines were observed in the Atlantic northern forest, where redstarts were the most abundant but also decreasing at a rate of −3.4% per year. Redstarts also showed significant declines in the U.S. Northern Rockies (−1.9%), Badlands and Prairies (−2.4%), and the southern Appalachian Mountains (−2.0%). Increasing abundance was observed along a band stretching from the southern boreal region of the Prairie provinces (Eastern Boreal Taiga Plains, 3.9% per year), through the midwestern states (Prairie Hardwood Transition, 4.0%/yr; Western Boreal Hardwood Transition, 1.5%/yr) and into the Northern Appalachian states (1.2%/yr).

DISCUSSION

Population response to nonbreeding-season climate

Understanding how birds and other organisms might respond to a changing climate necessitates studying their potential responses to climate throughout the annual cycle. This study is one of the first large-scale examples to show how the abundance of a Nearctic–Neotropical migrant is influenced by the environmental conditions experienced during the previous nonbreeding period. American Redstarts that breed in eastern North America and largely overwinter in the Greater Antilles of the Caribbean were more abundant following winters with higher plant productivity, as indexed by the NDVI. Long-term research on American Redstarts on the nonbreeding grounds in Jamaica has helped identify the mechanism by which rainfall affects individual performance in this region. Precipitation during the December through March dry season varies from <40 mm to >200 mm per year (Meteorological Service of Jamaica; *available online*).[7] This change in rainfall determines plant productivity and can lead to a fivefold variation in the abundance of arthropods, which is correlated with changes in overwinter condition and timing of departure on spring migration (Studds and Marra 2007, 2011). The effects of variable precipitation are often most distinct in lower-quality scrub habitat where females predominate due to exclusion by dominant males in mangroves (Marra and Holmes 2001). At a larger scale across Jamaica, redstart body condition in late winter and survival are linked, and survival tends to be higher in more productive habitats (Johnson et al. 2006). Studies on other Neotropical migrants in the Caribbean have found similar effects of nonbreeding-season climate. In Jamaica, Black-throated Blue Warblers (*Dendroica caerulescens*) have higher annual survival following wetter La Niña phases of the El Niño Southern Oscillation (ENSO), likely due to greater food

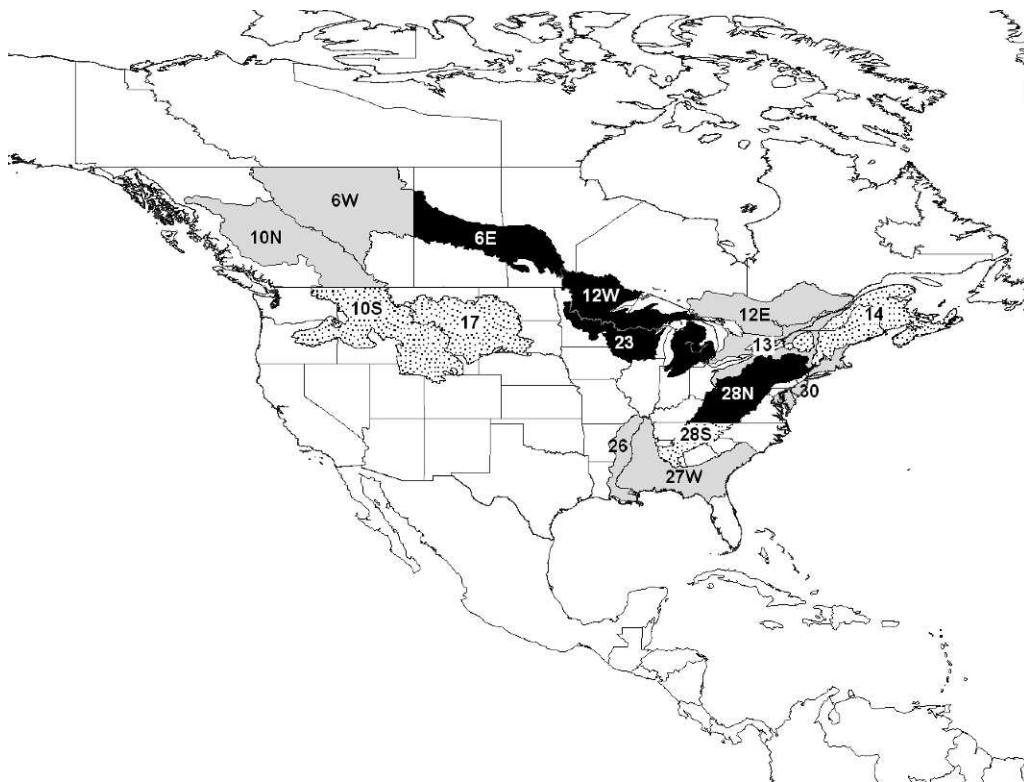[7] ⟨http://www.metservice.gov.jm⟩

Fig. 2. Temporal trends for American Redstart (*Setophaga ruticilla*) populations across the breeding range from 1982 to 2007. Significant trends were inferred from coefficients that had nonoverlapping 95% credible intervals. Increasing populations are noted in black, and decreasing populations are noted with stippling. Populations in solid gray all had credible intervals that overlapped zero.

availability (Sillett et al. 2000). Also in Jamaica, Brown and Sherry (2006) demonstrated that variation in rainfall affected food supply and overwinter condition of Ovenbirds (*Seiurus aurocapillus*), while in Puerto Rico, Northern Waterthrush (*Seiurus noveboracensis*) overwintering in drier habitats had a greater decline in body mass and a lower rate of fat deposition prior to migration than individuals in wetter habitats (Smith et al. 2010).

Our results are also consistent with smaller-scale studies of breeding populations that have shown how performance metrics or abundance is affected by conditions on the wintering grounds. In North America, studies on Yellow Warblers (*Dendroica petechia*) in Manitoba found positive relationships between adult survival and La Niña phases of the ENSO cycle, with the suggestion that the ENSO affects survival via local effects on rainfall on the wintering grounds (Mazzerole et al. 2005). For a population of Barn Swallows in Denmark, Szep et al. (2006) showed that survival was positively correlated with the NDVI in parts of the nonbreeding range in South Africa. Several other species of European songbirds have earlier first arrival dates in the breeding areas following winters with higher precipitation on the nonbreeding grounds in sub-Saharan West Africa (Saino et al. 2004, Gordo et al.

2005). Unlike the case with American Redstarts, there have been no detailed field studies for these species on the nonbreeding grounds, and therefore it is not clear as to the exact mechanism by which winter climate influences the condition or behavior of individuals during this period.

Although we found distinct effects of winter conditions in the Caribbean on the abundance of eastern breeding populations, we did not find any evidence for an effect of conditions in west Mexico on the abundance of western populations. Several nonexclusive factors might lead to variation in how populations respond to winter climate or our ability to detect those effects. Connecting winter effects to spring abundance requires moderately strong migratory connectivity, but the strength of connectivity may vary across the range. For example, birds from eastern breeding populations are believed to primarily overwinter in the Caribbean or along the Caribbean coast of northern Central America, while those from western breeding populations appear to be more dispersed and occur along the Pacific and Caribbean coasts of Mexico and northern Central America (Norris et al. 2006). If individuals from western populations overwinter over a larger area, then it would be more difficult to capture environmental effects with a single covariate.

It is also possible that precipitation gradients have unexpected consequences on individuals in these ecologically complex ecosystems. American Redstarts occupy a diverse range of habitats on the nonbreeding grounds (Sherry and Holmes 1997, Marra et al. 1998, Johnson et al. 2006) and the type of trophic cascade that has been observed in Jamaica may not be consistent in other parts of the nonbreeding range. This might be especially true if redstarts in these other regions are more likely to utilize wetter habitats such as humid forest or mangroves where variation in rainfall may be less likely to influence food abundance. The NDVI may also be a less reliable measure of the annual variability in ecological conditions in these types of habitats (Santos and Negri 1997). The extent to which climate affects demography across sites is also dependent on the relative strengths of other regulating or limiting factors, such as density dependence, predation or competition (Dugger et al. 2004, Wilson and Arcese 2006, Sæther et al. 2008). We know little about how such factors vary across the wintering range for Neotropical migrants.

Population response to breeding-season climate

Although we predicted that temperature in early spring (March–April) and the breeding period (May–June) would influence population size in colder parts of the range, we found little evidence for this. Only birds in one population (U.S. Northern Rockies, BCR 10S) showed a significant positive response to temperature at the 90% level, while another (Northern Appalachian States, BCR 28N) actually showed a negative response at the 95% level. Because these effects were not observed for any nearby population, it is not clear whether they represent a true biological response or were simply a sampling artifact.

Many studies have examined the impacts of breeding-season climate on reproductive success of songbirds, and it is clear that temperature can influence some components of reproduction such as timing of breeding (Both et al. 2004, Dunn 2004) and nestling growth and survival (Veistola et al. 1997, McCarty and Winkler 1999). It is less clear as to the circumstances under which the effects of temperature on breeding translate to an influence on population size in the following year. Breeding dates of resident Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia respond strongly to temperature, with subsequent effects on the number of breeding attempts and reproductive output. However, there is little influence on population size because of density-dependent effects on juvenile recruitment (Wilson and Arcese 2003). Other studies have found positive effects of temperature on population size. In New Hampshire, fecundity of Black-throated Blue Warblers is higher during La Niña phases of the El Niño Southern Oscillation, which translates into greater numbers of yearling breeders in the following breeding season (Sillett et al. 2000). In a range-wide analysis of Yellow-billed Cuckoos (*Coccyzus americanus*), Anders and Post

(2006) found that abundance for some populations was higher following years of colder temperatures during the breeding period. The mechanism in this case was believed to be a negative effect of temperature on outbreaks of a key lepidopteran food source.

A long-standing debate exists on the role of breeding vs. nonbreeding periods on the dynamics of migratory bird populations (Greenberg and Marra 2005). Preliminary analysis of data on reproduction and survival of American Redstarts from breeding and nonbreeding sites in New Hampshire and Jamaica, respectively, suggest that population growth is more sensitive to changes in adult survival during the nonbreeding season (P. P. Marra, T. S. Sillett and S. Wilson, *unpublished data*). If winter plant productivity and spring/summer temperatures are comparable measures for these two periods of the annual cycle, then our results appear to suggest that American Redstarts in eastern North America are more susceptible to variability in environmental conditions during the nonbreeding season. However, a complete analysis on the role of climate in driving population dynamics throughout the annual cycle requires consideration of other components such as breeding-season rainfall, which can influence breeding productivity for songbirds (Morrison and Bolger 2002, Collister and Wilson 2007). Rainfall tends to be variable over small geographic scales, and it was not possible to isolate a single value that could be used as a covariate for each population in this study. It is also possible that breeding-season temperature affects abundance in the following year, but at large spatial scales it is difficult to identify a single covariate to represent that effect. Additional studies that investigate temperature effects across spatial gradients would improve our knowledge and our ability to detect temperature effects across geographic scales.

Temporal trends

American Redstarts are generally common and not the focus of conservation efforts. However, we showed considerable declines of 2–4% annually over the past three decades for some parts of the breeding range, including the northeastern states/Maritime Provinces, and the Rocky Mountain region south of the United States–Canada border. Such changes may be related to large-scale habitat change. Redstarts generally prefer mid-successional forest, and long-term studies at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire have indicated declines for this species as forests have aged (Holmes and Sherry 2001). Increasing abundance along the southern edge of the boreal forest and the midwestern states may similarly be due to an increase in the availability of suitable habitat. Temporal trends might also be due to habitat change on the wintering grounds, which has been implicated for some species (Robbins et al. 1992).

Large-scale analyses of temporal change in abundance are well suited for examining broad, geographic patterns

that can then be utilized to design fine-scale studies to focus on the cause of population change within smaller regions. At present, long-term surveys on the breeding grounds are typically used to assess population declines on the breeding and nonbreeding grounds. While there has been a slight increase in the number of long-term surveys on the nonbreeding grounds, they are still few in number, and further emphasis on surveys across the nonbreeding range would greatly improve our ability to identify which populations of Neotropical migrants are declining, and examine the causes of declines.

Conclusion

To our knowledge, this is the first study to demonstrate range-wide effects of nonbreeding-season climatic conditions on the abundance of a Nearctic–Neotropical migrant over large spatial scales. As our understanding of migratory connectivity continues to improve we will be able to ask more detailed questions on which populations of a species are most influenced by climate and at what period of the annual cycle. For Nearctic–Neotropical migrants, these analyses will be further aided by longer time series of abundance on the breeding and especially the nonbreeding grounds. A greater understanding of geographic variation in population response to climate will be valuable for predicting the effects of climate change, because not all regions are expected to respond similarly.

Literature Cited

Anders, A. D., and E. Post. 2006. Distribution-wide effects of climate on population densities of a declining migratory landbird. Journal of Animal Ecology 75:221–227.

Berger, J. O. 1985. Statistical decision theory and Bayesian analysis. Springer-Verlag, New York, New York, USA.

Böhning-Gaese, K., B. Halbe, N. Lemoine, and R. Oberrath. 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evolutionary Ecology Research 2:823–839.

Both, C., et al. 2004. Large scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B 271:1657–1662.

Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32.

Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109:132–141.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8:2–14.

Collister, D. M., and S. Wilson. 2007. Contributions of weather and predation to reduced breeding success in a threatened northern Loggerhead Shrike population. Avian Conservation and Ecology 2:11.

Commission for Environmental Cooperation. 1997. Ecological regions of North America: toward a common perspective. Commission for Environmental Cooperation, Montreal, Quebec, Canada.

Dugger, K. M., J. Faaborg, W. J. Arendt, and K. A. Hobson. 2004. Understanding survival and abundance of overwintering warblers: does rainfall matter? Condor 106:744–760.

Dunn, P. O. 2004. Breeding dates and reproductive performance. Advances in Ecological Research 35:69–87.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Gordo, O., L. Brotons, X. Ferrer, and P. Comas. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology 11:12–21.

Greenberg, R., and P. P. Marra. 2005. Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press, Baltimore, Maryland, USA.

Hannon, S. J., S. Wilson, and C. A. McCallum. 2009. Does cowbird parasitism increase predation risk to American redstart nests? Oikos 118:1035–1043.

Holmes, R. T., and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. Auk 118:589–609.

Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conservation Biology 20:1433–1444.

LaDeau, S. L., A. M. Kilpatrick, and P. P. Marra. 2007. West Nile virus emergence and large-scale declines of North American bird populations. Nature 447:710–713.

Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May Warblers wintering in multiple habitats. Ecology 83:2502–2515.

Link, W. A., and R. J. Barker. 2010. Bayesian inference with ecological applications. Academic Press, London, UK.

Link, W. A., and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832–2840.

Link, W. A., and J. R. Sauer. 2007. Seasonal components of avian population change: joint analysis of two large-scale monitoring programs. Ecology 88:49–55.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS – a Bayesian modeling framework: concepts, structure and extensibility. Statistics and Computing 10:325–337.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in a migrant passerine bird during the non-breeding season. Auk 118:92–104.

Mazzerole, D. F., K. W. Dufour, K. A. Hobson, and H. E. den Haan. 2005. Effects of large-scale fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. Journal of Avian Biology 36:155–163.

McCarty, J. P., and D. W. Winkler. 1999. Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. Ibis 141:286–296.

Morrison, S. A., and D. T. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133:315–324.

Newton, I. 1998. Population limitation in birds. Academic Press, London, UK.

Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Ornithological Monographs 61:14–28.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological response to environmental change. Trends in Ecology and Evolution 20:503–510.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B 276:1619–1626.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549–562 *in* J. M. Hagan III and D. W. Johnson, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Rubenstein, D. R., C. P. Chamberlain, R. T. Holmes, M. P. Ayres, J. R. Waldbauer, G. R. Graves, and N. C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. Science 295:1062–1065.

Sæther, B. E., M. Lillegård, V. Grøtan, M. C. Drever, S. Engan, T. D. Nudds, and K. M. Podruzny. 2008. Geographical gradients in the population dynamics of North American prairie ducks. Journal of Animal Ecology 77:869–882.

Saino, N., T. Tźep, M. Romano, D. Rubolini, F. Spina, and A. P. Møller. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters 7:21–25.

Santos, P., and A. J. Negri. 1997. A comparison of the normalized difference vegetation index and rainfall for the Amazon and northeastern Brazil. Journal of Applied Meteorology 36:958–965.

Sauer, J. R., J. E. Hines, and J. Fallon. 2006. The North American Breeding Bird Survey, results and analysis 1996-2006, version 6.2.2006.U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sherry, T. S., and R. T. Holmes. 1997. American Redstart (*Setophaga ruticilla*). In: A. Poole and F. Gill, editors. Birds of North America, No. 277A. The Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2010. Moisture as a determinant of habitat quality for a non-breeding Neotropical migratory songbird. Ecology 91:2874–2882.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115–122.

Studds, C. E., and P. P. Marra. 2011. Rainfall induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B. *In press*.

Szep, T., A. P. Møller, S. Piper, R. Nuttall, Z. D. Szabó, and P. L. Pap. 2006. Searching for potential wintering and migration areas of a Danish Barn Swallow population in South Africa by correlating NDVI with survival estimates. Journal of Ornithology 147:245–253.

Tøttrup, A. P., K. Thorup, K. Rainio, R. Yosef, E. Lehikoinen, and C. Rahbek. 2008. Avian migrants adjust migration in response to environmental conditions en route. Biology Letters 4:685–688.

Tucker, C. J., J. E. Pinzon, M. E. Brown, D. Slayback, E. W. Pak, R. Mahoney, E. Vermote, and N. El Saleous. 2005. An Extended AVHRR 8-km NDVI Data Set Compatible with MODIS and SPOT Vegetation NDVI Data. International Journal of Remote Sensing 26:4485–4498.

Veistola, S., E. Lehikoinen, and T. Eeva. 1997. Weather and breeding success at high latitudes–the pied flycatcher *Ficedula hypoleuca* and the Siberian tit *Parus cinctus*. Ornis Fennica 74:89–98.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–82.

Wiedenfield, D. A., and M. G. Wiedenfield. 1995. Large kill of Neotropical migrants by tornado and storm in Louisiana, April 1993. Journal of Field Ornithology 66:70–80.

Wilson, S., and P. Arcese. 2003. El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). Proceedings of the National Academy of Sciences USA 100:11139–11142.

Wilson, S., and P. Arcese. 2006. Nest depredation, brood parasitism and reproductive variation in island populations of song sparrows (*Melospiza melodia*). Auk 123:784–794.