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EFFECTS OF LARGE-SCALE CLIMATE

ON AVIAN POPULATION DYNAMICS

ACROSS SPECIES' NORTH AMERICAN BREEDING DISTRIBUTIONS

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ABSTRACT

Global temperature increases of $0.6\,^\circ$C over the past century and predicted increases of 2° to $6\,^\circ$C over the next century have prompted many studies on effects of global warming on the population dynamics of plants and animals. Studies of landbirds in Europe and North America have shown effects of climatic variation on productivity and survival. However, such effects have been seen to translate to changes in population densities in only a few studies of European landbirds. Thus, the extent to which global warming has the potential to cause population declines in North American landbirds has remained unclear. In the research presented here, I model 39 years of climatic data, including indices of the North Atlantic Oscillation and El Niño Southern Oscillation, and distribution-wide Breeding Bird Survey data on 21 North American landbird species, to examine potential relationships between large-scale climate change and changes in avian population densities. Results of these analyses indicate geographic variation in strength of the effect of climate on population densities, with stronger effects in regions in which climate has stronger effects on local temperatures. Results also indicate that for species exhibiting long-term declines, there is a relationship between strength of the effect of local temperatures on population densities and magnitude of population decline. Additional analyses indicate that Neotropical-Nearctic migratory species are more negatively affected by warm winter temperatures than are closely-related North American residents. These results support the hypothesis that differences in climatic effects on migrants and residents may follow from greater trophic mismatch for species that are unable to time migration in response to earlier peaks in food availability. Finally, results of this work show that species are more highly affected by densities of sympatric congeners in areas in which they are also affected by climate, indicating that increased effects of climate on food resources may increase the effects of competition between congeners. Overall, results of this research indicate that North American landbird densities are affected by annual changes in large-scale climate, such that continued increases in global temperatures have the potential to affect long-term changes in landbird population densities across the continent.

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INTRODUCTION

Global temperature increases of 0.6 ^{o}C over the past century and predicted increases of 2°

to 6 ^{o}C over the next century (IPCC 2007) have prompted many studies on the effects of

global warming on the phenology and population dynamics of plants and animals

(Walther et al. 2002; Root et al. 2003). Studies of landbird species in Europe and North

America have shown effects of variation in large-scale climate and local temperatures on

migration, breeding phenology, productivity, and survival in many species (Dunn &

Winkler 1999; Saether et al. 2000; Sillett, Holmes & Sherry 2000; Forchhammer, Post &

Stenseth 2002; Jonzen et al. 2002; Nott et al. 2002; Visser et al. 2003; Wilson & Arcese

2003; Both et al. 2004; Macmynowski et al. 2007). However, such climatic effects have

been seen to translate to changes in population densities in only a few studies of

European landbirds (Forchhammer, Post & Stenseth 1998; Saether et al. 2000; Jonzen et

al. 2002). Thus, the extent to which global warming has the potential to lead to

population declines in North American landbird species has remained unclear.

Among North American landbirds, more than 30% of Neotropical-Nearctic migratory

species have declined significantly over the past 40 years (Robbins *et al*. 1989; Askins,

Lynch & Greenberg 1990; Sauer, Hines & Fallon 2005). With species declining to this

extent, research on the factors that limit populations is imperative in focusing our

conservation efforts. To date, most of the research on factors that limit North American

migratory birds has focused on endogenous factors, including nest predation, brood

parasitism and density-dependent habitat limitation (Robinson *et al*. 1995; Sherry &

Holmes 1996; Porneluzi & Faaborg 1999); these endogenous factors are now known to

be important in limiting landbird populations and in contributing to long-term population

decline for many species. Several field studies on the effects of climate on North American landbird species have documented relationships between large-scale climate and productivity and survival at the scale of the local population (Sillett et al. 2000; Nott et al. 2002; Wilson & Arcese 2003); however, these studies showed no effect of climate on population densities, primarily because of subsequent recruitment of juveniles from other populations into the study areas (Sillett et al. 2000; Wilson & Arcese 2003). Because such field studies were necessarily conducted at relatively small geographic scales, it is possible that climatic effects on productivity or survival may cause important but undetected changes in population densities at larger, regional scales. Studies are thus needed that test for effects of climate on population densities throughout North American landbird species' distributions.

Much of the annual variation in temperatures across North America is attributable to two climate systems, the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Hurrell 1995, Trenberth & Caron 2000). Although extreme climatic events may directly affect landbird population dynamics by increasing mortality, the limiting effects of large-scale climate systems such as these are more likely mediated through climatic effects on food availability (Sillett et al. 2000; Nott et al. 2002; Jones, Doran & Holmes 2003). Food availability has been shown to impact productivity in many landbird species (e.g. Arcese & Smith 1988, Rodenhouse & Holmes 1992, Marshall et al. 2002), and both the North Atlantic Oscillation and the El Niño Southern Oscillation have been shown to affect North American landbird productivity and survival through direct annual effects on lepidopteran larvae abundance (Sillett et al. 2000, Nott et al. 2002), the

primary food resource for landbirds during breeding (Brown 1993; Hopp, Kirby & Boone 1995; Kricher 1995; Rodewald & James 1996; Hanners & Patton 1998; Nolan, Ketterson & Buerkle 1999; Cimprich, Moore & Guilfoyle 2000; Payne 2006).

In the work presented here, I test several hypotheses regarding the relationships between the NAO and ENSO and annual population densities of a total of 21 landbird species across their North American breeding distributions. The species studied are similar in life history traits, with most species breeding at 1-2 years of age, producing 1-2 clutches of eggs per summer breeding season (with clutch size generally ranging from 3 to 5 eggs), and living for a maximum of approximately 9 to 18 years (Poole 2005). As indices of annual population densities for all species studied, I used U.S. Geological Survey Breeding Bird Survey (BBS) data from physiographic regions throughout the U.S. and Canada from 1966 through 2004 (Sauer, Hines & Fallon 2005). The Breeding Bird Survey was designed to monitor long-term population trends of North American birds and is conducted annually on more than 4000 survey routes throughout 71 physiographic regions across North America, including the 49 continental U.S. states and all 13 Canadian provinces and territories. The BBS is conducted during the peak of the avian breeding season (June in most physiographic regions); each surveyed route is 24.5 miles long, with 3-minute point count surveys conducted at 0.5-mile intervals along each route. During the survey, every individual bird seen or heard within a 0.25-mile radius is recorded (http://www.pwrc.usgs.gov/bbs/about/).

Due to the large spatial and temporal extent of the BBS, routes are necessarily surveyed by different observers across routes and over time; in addition, surveys are conducted along roads, both in urban and rural areas. The Breeding Bird Survey may thus be affected by observer variability, and has the potential for biases associated with roadside habitat surveys. In addition, the likelihood of annual variability or long-term changes in route conditions may vary geographically due to geographic variation in urbanization or other habitat changes. Although such biases necessarily exist in a long-term, large-scale data set, BBS data have been collected since 1966 within a rigorous standardized protocol across species' distributions. The U.S. Geological Survey (USGS) also conducts data quality checks that identify route data which are considered acceptable for analysis. Given the potential biases that may exist, BBS data allow for elucidation of ecological relationships that is not possible at the scale of short-term or local field study sites. In addition to analyses by the USGS of the long-term population trends of North American birds, BBS data are used by the U.S. Fish and Wildlife Service and Canadian Wildlife Service to rank nation-wide avian conservation priorities, and by state Natural Heritage and Breeding Bird Atlas programs to augment their smaller databases. In addition, BBS data have been used in more than 270 peer-reviewed scientific publications to date (http://www.pwrc.usgs.gov/bbs/about/).

The research presented here utilizes modeling of long-term climate data, including the NAO and ENSO, and distribution-wide Breeding Bird Survey data on North American landbird species to examine potential relationships between annual large-scale climatic conditions and annual avian population densities. In Chapter 2, I hypothesize that climate

and local temperatures have 1-year lagged effects on annual population densities of a Neotropical-Nearctic migratory landbird species, *Coccyzus americanus*, across its breeding distribution, by influencing avian productivity in the previous year. In this study, I use density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as climate or temperature, on annual population densities (Royama 1992). I examine geographic variation in the strength of the effect of the NAO and ENSO on inter-annual fluctuations in population densities, and I test for relationships between the strength of the effects of these climate systems on regional population dynamics and the effects of the systems on local temperatures. Finally, I test for a relationship between the strength of the effect of local temperatures on annual population densities and the magnitude of long-term *C. americanus* population decline.

Based on the results of analyses of *C. americanus* population dynamics (Anders and Post 2006), in Chapter 3 I test the hypothesis that the population dynamics of multiple Neotropical-Nearctic migratory landbird species are affected by annual large-scale climate and local temperatures. If climatic effects on migratory bird populations are mediated through annual effects of climate on lepidopteran larvae, as has been seen by Sillett et al. (2000) and Nott et al. (2002), multiple landbird species should be affected by climate. In this chapter, I examine geographic variation in the strength of the relationships between ENSO and the NAO and annual fluctuations in population densities of 11 additional migratory landbird species, including both shrub-habitat and forest nesting Parulidae, Fringillidae, and *Vireo* species. I test for relationships between

the strength of the effects of the climate systems on population dynamics and the effects of the NAO and ENSO on local temperatures and precipitation. Finally, for each species I test for correlations between the strength of the effect of local temperature on annual population densities and the magnitude of long-term population decline.

In Chapter 4, I test the hypothesis that migratory landbirds are more negatively affected by warm winter temperatures than are resident landbird species. Results of analyses of yellow-billed cuckoo population densities and climate data indicated that population densities decline following warm years. Warm winter temperatures may lead to earlier spring peaks in the abundance of lepidopteran larvae, such that late-arriving migratory birds miss this peak in food availability (Stenseth & Mysterud 2002). Such trophic mismatch would lead to one-year lagged decreases in population densities of migratory birds that are unable to time their spring migration and breeding in response to food availability on the breeding grounds, as was seen by Both & Visser (2001), but this climate-induced trophic mismatch would not be seen in resident bird species that are present year-around and can time their breeding based on food availability. In this chapter, I test for differences in geographic extent and strength of effect of large-scale climate on 4 Neotropical-Nearctic migratory and 4 North American resident Cardinalinae and Turdidae species.

Finally, in Chapter 5 I test the hypothesis that climatic effects increase interspecific competition in closely-related sympatric species. Annual effects of climate on the population dynamics of collared and pied flycatchers (*Ficedula albicollis* and *F.*

hypoleuca) have been shown to influence the strength of interspecific competition between these two species in central Europe (Saetre, Post & Kral 1999). In that study, effects of climate on pied flycatchers in warm years led to increased competitive pressures from sympatric collared flycatchers. Because analyses indicated that yellow-billed cuckoo populations are negatively affected by warm temperatures, climate may increase interspecific resource competition between yellow-billed cuckoos and their congener, black-billed cuckoos (*Coccyzus erythropthalmus*) in areas of breeding sympatry. Similar effects of climate may be seen in other closely-related sympatric species in North America, pointing to additional indirect effects of climate on migratory landbird population dynamics. In this chapter, I examine annual effects of large-scale climate and congener densities in two pairs of North American sympatric congeners: yellow-billed and black-billed cuckoos (*Coccyzus americanus* and *C. erythropthalmus)*, and scarlet and summer tanagers (*Piranga olivacea* and *P. rubra*).

Because increases in global temperatures are expected to continue to escalate over the next century, identification of the impacts of increasing temperatures on population dynamics and long-term population trends is imperative, particularly for species whose populations are currently declining. The research presented here provides an understanding of the effects of large-scale climate and local temperatures on annual population densities of North American landbird species, and it provides an indication of the potential effects of continued global warming on this group of species as a whole.

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Chapter 2

DISTRIBUTION-WIDE EFFECTS OF CLIMATE ON POPULATION DENSITIES OF A DECLINING MIGRATORY LANDBIRD

Summary

1. Increases in global temperatures have created concern about effects of climatic variability on populations, and climate has been shown to affect population dynamics in an increasing number of species. Testing for effects of climate on population densities across a species' distribution allows for elucidation of effects of climate that would not be apparent at smaller spatial scales.

2. Using autoregressive population models, we tested for effects of the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) on annual population densities of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, across the species' breeding distribution over a 37-year period (1966-2002).

3. Our results indicate that both the NAO and ENSO have affected population densities of *C. americanus* across much of the species' breeding range, with the strongest effects of climate in regions in which these climate systems have the strongest effects on local temperatures. Analyses also indicate that the strength of the effect of local temperatures on *C. americanus* populations was predictive of long-term population decline, with populations that were more negatively affected by warm temperatures experiencing steeper declines.

4. Results of this study highlight the importance of distribution-wide analyses of climatic effects and demonstrate that increases in global temperatures have the potential to lead to additional population declines.

Introduction

Global temperatures have increased by approximately 0·6 °C over the 21st century and are predicted to increase by an additional 2–6 °C over the next century (Houghton *et al*. 2001). Such rapid changes in global climate have spurred research on the effects of climatic variability on the phenology and population dynamics of many species of plants and animals (Walther *et al*. 2002; Root *et al*. 2003). Studies of several species of landbirds have shown effects of variation in large-scale climate and local temperatures on migration and breeding phenology (Dunn & Winkler 1999; Forchhammer, Post & Stenseth 2002; Visser *et al*. 2003; Wilson & Arcese 2003; Both *et al.* 2004) and on population productivity and adult survival (Saether *et al*. 2000; Sillett, Holmes & Sherry 2000; Nott *et al*. 2002). However, these climatic effects have translated to changes in population densities in only a few studies (Forchhammer, Post & Stenseth 1998; Saether *et al*. 2000; Jonzen *et al*. 2002). This is perhaps not surprising, as spatial variation in biotic and abiotic factors makes it likely that ecological effects of climate are spatially heterogeneous, and most field studies are necessarily conducted at small geographical scales. Consequently, studies are needed that test for effects of climate on population densities across species' distributions.

Among North American landbirds, more than 30% of migratory species have declined significantly over the past 37 years (Robbins *et al*. 1989; Askins, Lynch & Greenberg 1990; Sauer, Hines & Fallon 2003). With species declining to this extent, research on the factors that limit populations is imperative in focusing our conservation efforts. To date, most of the research on factors that limit migratory birds in North America has focused

on endogenous factors, including nest predation, brood parasitism and density-dependent habitat limitation (Robinson *et al.* 1995; Sherry & Holmes 1996; Porneluzi & Faaborg 1999), and these endogenous factors are now known to be important in limiting migratory populations. In contrast, there is no evidence for an effect of climate on annual population densities in these species, despite several studies that have found climatic effects on phenology, productivity and survival. Thus, the extent to which changes in climate may lead to population declines in North American landbirds has remained unclear.

Here, we quantify the relationships between large-scale climate, local temperatures, and population dynamics of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, throughout its breeding distribution. Using survey data from throughout the U.S. and Canada over the past 37 years (Sauer et al. 2003), we examine the influence of annual variation in large-scale climate and local temperatures on annual *C. americanus* population densities. Much of the annual variation in temperatures across North America is attributable to two large-scale climate systems, the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Hurrell 1995; Trenberth & Caron 2000); in addition, recent evidence indicates that the NAO may be an important vehicle through which anthropogenic causes of climatic warming are manifest (Visbeck et al. 2001). Here, we document geographic variation in the strength of the NAO and ENSO on inter-annual fluctuations in population densities. We furthermore document that the strength of the effects of these climate systems on regional population dynamics is strongly correlated with the strength of the effects of these systems on local temperatures. Finally, we show that the strength of the effect of local temperatures on

annual population densities is correlated with the magnitude of population decline: the more strongly any particular population has been affected by local temperatures, the more precipitous has been that population's decline over the past 37 years.

Materials and Methods

Survey Data

Coccyzus americanus is a Neotropical migratory landbird, breeding in the United States and Canada from May through September, and wintering from Venezuela through central Argentina from October through April (Hughes 1999). Among the 137 species of long-distance migratory birds that breed in North America, *C. americanus* ranks 14th in its rate of population decline. Although declines are most severe for this species in the western U.S., it ranks 11th of 88 species in its rate of decline in the eastern U.S. (Sauer et al. 2003). As indices of annual *C. americanus* densities, we used data from the U.S. Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2002, using data from 41 physiographic regions incorporating 43 U.S. states and 3 Canadian provinces (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/). Each physiographic region was defined as a population, and annual population densities were calculated as mean number of *C. americanus* detected per survey route within a region within a year. Western cuckoo populations were excluded from analyses, as we analyzed only regions in which more than 20 cuckoos were observed in total between 1966 and 2002.

Climate and Local Temperature Data

The winter NAO index (mean of monthly NAO index values from December through March; www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter) was used to represent annual NAO conditions from 1966 through 2002, and the mean of monthly values of the Southern Oscillation Index (SOI) from May through April was used to represent annual ENSO conditions (www.cpc.ncep.noaa.gov/data/indices). Local temperature data were obtained from the U.S. National Climatic Data Center (NCDC; www.ncdc.noaa.gov/oa/climate/onlineprod/drought/ftppage.html) from NCDC divisions that overlapped the BBS physiographic regions used to define *C. americanus* populations. Mean monthly temperatures for all NCDC divisions within a BBS region were calculated, and we used mean of December through March temperatures within each year in our analyses, as both the NAO and ENSO show the strongest effects on temperatures in North America during these months (Hurrell 1995; Trenberth & Caron 2000).

Population Models

To quantify the influences of the NAO, ENSO, and local temperatures on changes in annual *C. americanus* population densities, we incorporated the climate indices and local temperatures into models of cuckoo population dynamics. We hypothesized that climate and local temperatures would have 1-year lagged effects on annual population densities on the breeding grounds by influencing cuckoo productivity in the previous year (separate analyses indicate unlagged effects of ENSO on *C. americanus* population densities, suggesting effects on survival on the wintering grounds independent of effects

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on cuckoo productivity; A.D. Anders unpublished data). We used density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as climate or temperature, on annual population densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_{t-1}) + \varepsilon_t \qquad (1)$$

where X_i are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates of the strength of statistical density dependence, b_1 quantifies the influence of climate or local temperature on population density, Y_{t-1} is the NAO index, SOI, or mean local temperature in year t-1, and ε_t represents the effects of other perturbations. Year was included as a covariate for all populations displaying a significant temporal trend (Post & Stenseth 1999). First-, second-, and third-order models were tested to determine which best predicted log annual population density for each population. We then included in the best-fit model terms for climate or local temperature to determine whether inclusion of these parameters improved model fit. Parameter coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

We next investigated whether spatial variation in the influences of the NAO and ENSO on population dynamics reflected variation in the response of local temperatures to these climate systems. We first conducted correlation analyses of the NAO index and local temperatures across the 37-year period for each of the 41 physiographic regions. Then, to

test whether the strength of the NAO's effect on annual population density is predicted by the strength of the connection between the NAO and local temperatures, we conducted a correlation analysis of the Pearson's r for each region and the NAO coefficient from the cuckoo population model for each region. We then conducted these same analyses for ENSO.

Finally, we quantified the relationship between the influence of local temperature on annual cuckoo population densities and the magnitude of long-term population change. We calculated magnitude of population change as the slope of the regression of mean population density over time, scaled by population density at the midpoint of the survey period, for each population, using only those populations that exhibited a linear trend over the period 1966-2002 ($N = 31$ populations). We then conducted a linear regression analysis of the local temperature coefficients from each population model and the slopes of the regression of population density over time for each region.

Potential Mechanisms of Climatic Effects

Although extreme climatic events may directly affect landbird population dynamics by increasing mortality, limiting effects of climate are more likely mediated through effects on food availability (Sillett et al. 2000; Jones, Doran & Holmes 2003). Food availability has been shown to impact landbird productivity (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall et al. 2002), and both the NAO and ENSO have been shown to affect North American landbird productivity through effects on lepidopteran larvae (Sillett et al. 2000; Nott et al. 2002), the primary food resource for landbirds during the

breeding season. We had thus hypothesized that the NAO and ENSO would have one-year lagged effects on annual *C. americanus* densities by affecting productivity, through effects on lepidopteran larvae abundance, the previous breeding season (Post 2004).

To determine whether climate may potentially affect cuckoo dynamics by affecting food availability, in 2003 and 2004 we collected field data on lepidopteran larvae abundance and cuckoo productivity in the Ridge and Valley region of Pennsylvania. Using two 150-ha sites, we located and monitored cuckoo territories throughout the breeding season to quantify the number of nesting attempts by each pair. Lepidopteran larvae were surveyed along randomly-located fixed transects within each cuckoo territory (*N* = 18 territories) during a two to four day period in mid- and late-June. We counted the number of caterpillars per 1,000 understory leaves and measured the length of each caterpillar to the nearest millimeter (caterpillars were not removed from the vegetation). In 2003, we surveyed a single 50 m X 1 m X 1 m transect per territory, and in 2004 we surveyed four 12.5 m X 1 m X 1 m transects per territory.

Results

Results of population models indicated that 31 *C. americanus* populations showed first-order density dependence, eight populations showed second-order density dependence, and two showed third-order density dependence. The lagged NAO climate parameter entered the best-fit population model for eight cuckoo populations, all in the southern and eastern U.S. (Fig. 1). The model coefficient quantifying the lagged effect of the NAO was positive for five of these populations and negative for three populations. The lagged

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ENSO parameter entered the best-fit model for five additional cuckoo populations, all in the north-central U.S. (Fig. 1); the model coefficient quantifying the lagged effect of ENSO was negative for all five populations.

In examining the relationship between large-scale climate, local temperatures, and population dynamics for each of the 41 *C. americanus* populations, model coefficients quantifying the lagged influences of the NAO and ENSO on annual population densities were positively related to the correlations between the NAO index and local temperatures ($r = 0.309$, $P = 0.026$; Fig. 2a) and SOI and local temperatures ($r = 0.498$, $P = 0.001$; Fig. 2b). Hence, the more strongly these large-scale climate systems affected local temperatures, the greater was their influence on *C. americanus* population dynamics. Because only positive correlations existed between the NAO index and local temperatures in all regions studied (Fig. 2a), we repeated our analysis using only those regions in which the population model NAO coefficients were positive ($N = 17$ populations). Results of this analysis also showed a significant positive correlation between the model NAO coefficients and the Pearson's r's from the NAO index and local temperature correlations ($r = 0.426$, $P = 0.044$).

Inclusion of local temperature in each population model indicated a lagged negative influence of temperature on 30 *C. americanus* populations: between 1966 and 2002, these populations experienced declines following warmer temperatures during the preceding breeding season. Linear regression analysis revealed a positive relationship between the magnitude of the influence of local temperatures on annual population densities and the

magnitude of long-term population change ($t = 4.668$, $P < 0.0001$, $R^2 = 0.429$; Fig. 3).

Hence, the more strongly local temperatures influenced a population's dynamics, the

more precipitously that population declined.

In examining the potential of food availability as a mechanism by which climate affects

annual population densities, we found that cuckoos attempted to nest on only a subset of

occupied territories in 2003 and 2004, and lepidopteran larvae abundance was higher on

those territories on which cuckoos nested than on occupied territories on which cuckoos

did not nest (repeated measures ANOVA: $F_{1,14} = 5.28$, $P = 0.037$), with no effect of year

($F_{1,14} = 2.52$, $P = 0.135$) and no interaction between year and nesting status ($F_{1,14} = 0.47$,

$P = 0.505$). Restricting the analysis to the lepidopteran survey conducted in mid-June,

when cuckoos typically initiate nesting, territories on which cuckoos subsequently nested

had higher lepidopteran larvae abundance (23.1 ± 6.8 SE caterpillars/1,000 leaves versus

7.0 ± 2.3; t-test: $t_{16} = 2.81$, $P = 0.013$) and more lepidopteran larval biomass, as indexed

by summing the lengths of caterpillars per 1000 leaves (41.2 ± 13.8 mm of

caterpillar/1,000 leaves versus 11.9 ± 4.5; $t_{16} = 2.56$, $P = 0.021$) than those territories

without nests.

Discussion

This study documents the spatially heterogeneous effects of large-scale climate on

population densities of a North American migratory landbird across the species' breeding

distribution. Our results indicate that two climate systems, the NAO and ENSO, have

affected annual population densities of *C. americanus* over the past 37 years, and that the

strength of the effect of climate on populations is correlated with the strength of the relationship between large-scale climate and local temperatures. In addition, the magnitude of the effect of local temperature on cuckoo populations is predictive of population decline: the more strongly and negatively any particular cuckoo population was affected by local temperatures on its breeding grounds, the more precipitous has been that population's decline over the past 37 years.

Geographic variation in the effects of the NAO and ENSO on cuckoo populations points to the importance of studying climatic effects at the scale of the species' distribution. Recent large-scale studies of the breeding phenology of European landbirds, including great tits *Parus major*, blue tits *P. caeruleus*, collared flycatchers *Ficedula albicollis*, and pied flycatchers *F. hypoleuca*, have shown geographic variation in effects of climate: in those areas of Europe that have experienced warming trends over the past one to two decades, landbird populations have displayed shifts in their breeding phenologies (Visser et al. 2003; Both et al. 2004). For the *Ficedula* species, there is a strong positive correlation between the extent of change in local temperatures and the extent of advancement of egg-laying date (Both et al. 2004). Field studies of North American landbirds, including black-throated blue warblers *Dendroica caerulescens* and song sparrows *Melospiza melodia*, have documented effects of climate on productivity and adult survival at the scale of the study population (Sillett et al. 2000; Wilson & Arcese 2003), but those studies showed no subsequent effect on annual population densities, primarily because of recruitment of juveniles from other areas into the study populations (Sillett et al. 2000; Wilson & Arcese 2003). Because such field studies were necessarily

conducted at relatively small geographic scales, it is possible that climatic effects on productivity or survival in these species may cause important but undetected changes in population densities at larger, regional scales.

Studies of the mechanisms by which large-scale climate could affect landbird populations have shown that the NAO and ENSO influence the abundance of lepidopteran larvae, the primary food resource for landbirds during breeding (Sillett et al. 2000; Nott et al. 2002). Research on *D. caerulescens* has shown an effect of ENSO on lepidopteran larvae abundance, and an effect of lepidopteran availability on warbler productivity (Sillett et al. 2000). Our field work with *C. americanus* indicates that only a subset of cuckoos attempted to breed in 2003 and 2004, and those territories on which cuckoos nested had more than 3 times the number and biomass of lepidopteran larvae than the occupied territories on which cuckoos did not attempt to nest. These results suggest that food availability may limit *C. americanus* productivity, as has been seen in other landbird species (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall et al. 2002).

Results of our analyses indicate that cuckoo population densities declined following warm years. There is evidence to indicate that outbreaking species of lepidopterans are more abundant in cold years: Myers (1998) found in a meta analysis of 26 outbreaking lepidopteran species that outbreaks were more likely in cold years, and Williams and Liebhold (1995) and Miller, Mo and Wallner (1989) found higher abundances of gypsy moth *Lymantria dispar* L. larvae following cooler winter and spring temperatures. *Coccyzus americanus* is known to take advantage of outbreaking species such as gypsy

moths, and warmer temperatures may act to decrease the availability of these food resources. However, it is also possible that warm winter temperatures lead to earlier spring peaks in the abundance of non-outbreaking lepidopteran species, such that *C. americanus*, a relatively late-arriving species on the breeding grounds, misses this peak in food abundance. This type of climate-induced trophic mismatch has been seen in nonmigratory *P. major* (Visser et al. 1998; Stevenson & Bryant 2000) and may be even more likely in migratory species that are unable to time their spring migration in response to food availability on the breeding grounds (Both & Visser 2001).

In conclusion, we found lagged effects of two large-scale climate systems, the NAO and ENSO, on annual *C. americanus* population densities. Geographic variation in the strength of these climate systems on cuckoo populations was underlain by geographic variation in the effects of the NAO and ENSO on local temperatures. We also found that the strength of the effect of local temperatures on populations was predictive of long-term population decline, with those populations that are more negatively affected by warm temperatures experiencing steeper declines over the past 37 years. Field data showing that cuckoo productivity is limited by lepidopteran larvae abundance point to the possibility that climate may affect *C. americanus* population densities by affecting food availability; however, data are needed to test our hypothesized mechanisms by which warm temperatures may decrease food availability. Overall, the results of this study indicate that although endogenous factors such as nest predation, brood parasitism, and habitat availability limit populations of migratory birds, exogenous factors such as large-scale climate and local temperatures also affect changes in the population densities of

these species and do so in a spatially heterogeneous manner. An understanding of the

limiting effects of climate on additional species, and knowledge of the mechanisms by

which climate has such effects, is critical in an environment of increasing climate change.

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Fig. 1. Physiographic regions in which the NAO and ENSO entered the best-fit population model for *Coccyzus americanus* populations from 1966-2002. Black outline delineates the 41 physiographic regions analyzed in this study. Dark gray indicates regions in which lagged NAO occurred in the best-fit population model; light gray indicates regions in which lagged ENSO occurred in the best-fit model (background map of BBS physiographic regions from Sauer et al. (2003)).

Fig. 2. Relationships between the lagged influences of the NAO and ENSO on *C. americanus* population dynamics and the strength of the correlations between these climate systems and local temperatures. **(a)** NAO parameter coefficient from each cuckoo population model versus strength of the Pearson's correlation between the NAO Index and local temperature within that physiographic region. **(b)** ENSO parameter coefficient from each population model versus strength of the Pearson's correlation between the Southern Oscillation Index (SOI) and local temperature within the physiographic region.

Fig. 3. Magnitude of change in *C. americanus* population density over time versus magnitude of the lagged influence of local temperature on cuckoo population dynamics within a physiographic region.

Fig. 1

Fig. 2

Fig. 3

Chapter 3

**EFFECTS OF LARGE-SCALE CLIMATE
ON ANNUAL POPULATION DENSITIES OF
NEOTROPICAL-NEARCTIC MIGRATORY LANDBIRDS
ACROSS THEIR BREEDING DISTRIBUTIONS**

Summary

1. Current and predicted increases in global temperatures have led to concern about effects of climate change on populations, and such effects of climatic variability have been shown in an increasing number of species. Examining relationships between annual climatic variation and lagged annual densities of North American landbird species across their breeding ranges will help to elucidate potential effects of climate change that have not been evident at smaller spatial scales.

2. Using autoregressive population models, I tested for 1-year lagged relationships between annual variation in the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) and annual population densities of 11 Neotropical-Nearctic migratory landbird species across their breeding distributions, using survey data from a 39-year period (1966-2004).

3. Results of these analyses indicate spatial variation at a continental scale in the relationships between ENSO and the NAO and 1-year lagged population densities of these 11 species, with the strongest relationships seen in those regions in which large-scale climate has the greatest effect on local temperatures. Analyses also indicate that for 4 of the 5 study species that have declined significantly over the past 39 years, there is a relationship between the strength of the effect of local temperatures on annual population densities and the magnitude of population decline.

4. Overall, results of this study indicate that Neotropical-Nearctic migratory warbler species (Parulidae) may be more sensitive to changes in climate than are *Vireo* or Fringillidae species, and that shrub-nesting species may be affected to a greater extent than are forest-nesting landbird species.

Introduction

In response to predicted increases in global temperatures of up to $6^{o}C$ over the next century (IPCC 2007), much research has been conducted over the past several years on the effects of climatic variability on plant and animal populations (Walther et al. 2002; Root et al. 2003). Several studies of landbird populations in Europe and North America have shown relationships between variation in large-scale climate and local temperatures and landbird migration, breeding phenology, productivity, and adult survival (Dunn & Winkler 1999; Saether et al. 2000; Sillett, Holmes & Sherry 2000; Forchhammer, Post & Stenseth 2002; Jonzen et al. 2002; Nott et al. 2002; Visser et al. 2003; Wilson & Arcese 2003; Both et al. 2004; Macmynowski et al. 2007). Climatic effects on productivity and survival have translated to changes in population densities for several species of European landbirds (Forchhammer, Post & Stenseth 1998; Saether et al. 2000; Jonzen et al. 2002). However, relationships between climatic variability and population densities of North American landbirds have been shown to date in just a single species (Anders & Post 2006). Thus, the extent to which global climate change has the potential to lead to population declines in North American landbirds has remained unclear.

Of the 137 species of Neotropical-Nearctic migratory landbirds in North America, more than 30% have experienced significant declines over the past 40 years (Robbins et al. 1989; Askins, Lynch & Greenberg 1990; Sauer, Hines & Fallon 2005). Research on the factors that affect population densities is thus imperative in focusing our conservation efforts. Field studies of several North American landbird species, including black-throated blue warblers (*Dendroica caerulescens*) and song sparrows (*Melospiza melodia*), have documented relationships between variation in large-scale climate and avian productivity and adult survival (Sillett et al. 2000, Wilson & Arcese 2003); however, these studies showed no subsequent effect on population densities, primarily because of juvenile recruitment from other populations into the study areas (Sillett et al. 2000, Wilson & Arcese 2003). Such field studies were necessarily conducted at small geographic scales; thus, it is possible that climatic effects on productivity or survival may cause changes in population densities at larger, regional scales. The single study in which climatic variability has been found to be related to population densities of a North American landbird species was conducted using survey data from throughout the species' breeding range (Anders & Post 2006); similar distribution-wide studies of additional species, then, may help to elucidate effects of large-scale climate change on North American landbirds that are not evident at smaller spatial scales.

Although extreme climatic events may directly affect landbird densities through increased mortality, effects of climate are more likely mediated through annual effects on food availability (Sillett et al. 2000; Jones, Doran & Holmes 2003). Lepidopteran larvae are the primary food resource for most North American landbird taxa during breeding,

including warblers (Parulidae), vireos (*Vireo* spp.), and buntings (Fringillidae) (Brown 1993; Hopp, Kirby & Boone 1995; Kricher 1995; Rodewald & James 1996; Hanners & Patton 1998; Nolan, Ketterson & Buerkle 1999; Cimprich, Moore & Guilfoyle 2000; Payne 2006), and large-scale climate systems have been shown to affect landbird productivity through annual direct effects on Lepidopteran larvae abundance (Sillett et al. 2000; Nott et al. 2002). The potential thus exists for large-scale climate to affect the annual population dynamics of additional species of North American landbirds through effects on food resources (Jones, Doran & Holmes 2003). To determine whether annual changes in large-scale climate are related to population densities of additional species of North American landbirds, I quantified the relationships between large-scale climate, local weather, and population dynamics of 11 Neotropical-Nearctic migratory landbird species using long-term survey data from throughout species' breeding ranges across the United States and Canada (Sauer, Hines & Fallon 2005).

Much of the annual variation and inter-annual geographic variation in local temperatures and precipitation across North America is attributable to two large-scale climate systems, the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Hurrell 1995; Trenberth & Caron 2000). In addition, the NAO appears to be an important vehicle through which human-induced climate change is manifest (Visbeck et al. 2001). Here, I document geographic variation in the strength of the relationships between ENSO and the NAO and annual fluctuations in population densities of 11 Neotropical-Nearctic migratory landbird species. I show that the strength of the relationship between ENSO and the population dynamics of 8 of these species is

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correlated with the strength of the effects of ENSO on local temperatures. Finally, I

show that for 4 of the 5 study species that have declined significantly over the past 39

years, there is a correlation between the strength of the relationship between local

temperature and annual population density and the magnitude of population decline. That

is, within each species, the more strongly annual local temperatures have affected annual

population densities, the more precipitous has been that population's decline over the past

39 years.

Materials and Methods

Survey Data

To incorporate into my study potential phylogenetic or breeding habitat differences in

effects of climate on migratory landbird species, I analyzed survey data from multiple

shrub-habitat and forest-nesting species of migratory wood warblers (Parulidae), vireos

(*Vireo* spp.), and grosbeaks/buntings (Fringillidae), using species whose breeding ranges

incorporate at least most of the central and eastern United States and southern Canada. In

choosing species in which multiple taxa within genera or families breed within different

habitat types, and for which breeding ranges incorporate a large section of North

America, my analyses were limited to the following study species: prairie warbler

(*Dendroica discolor*), common yellowthroat (*Geothlypis trichas*), black-and-white

warbler (*Mniotilta varia*), worm-eating warbler (*Helmitheros vermivorus*), white-eyed

vireo (*Vireo griseus*), Bell's vireo (*Vireo bellii*), yellow-throated vireo (*Vireo flavifrons*),

red-eyed vireo (*Vireo olivaceus*), blue grosbeak (*Guiraca caerulea*), indigo bunting

(*Passerina cyanea*), and rose-breasted grosbeak (*Pheuticus ludovicianus*) (Table 1). As

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indices of population densities within each species, I used data from the U.S. Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2004, using data from 42 physiographic regions incorporating 43 U.S. states and 3 Canadian provinces (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/). Each physiographic region was defined as a population, and annual population densities within each species were calculated as mean number of individuals detected per survey route within a region within a year.

Climate, Local Temperature, and Precipitation Data

The mean of monthly values of the Southern Oscillation Index (SOI) from May through April was used to represent annual ENSO conditions from 1966 through 2004 (www.cpc.ncep.noaa.gov/data/indices), and the winter NAO Index (mean of monthly NAO Index values from December through March; www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter) was used to represent annual NAO conditions. Local temperature and precipitation data from 1966-2004 were obtained from the U.S. National Climatic Data Center (NCDC; www.ncdc.noaa.gov/oa/climate/onlineprod/drought/ftppage.html) from NCDC divisions that overlapped the BBS physiographic regions used to define landbird populations. Mean monthly temperatures and mean precipitation for all NCDC divisions within a BBS region were calculated, and I used mean of December through March values within each year in my analyses, as both ENSO and the NAO show the strongest effects on local weather in North America during these months (Hurrell 1995; Trenberth & Caron 2000).

To quantify potential annual influences of ENSO, the NAO, and local temperatures and precipitation on annual landbird population densities, I incorporated the climate indices and local weather into models of population dynamics for each species (population sample sizes: prairie warbler $n = 20$, common yellowthroat $n = 61$, black-and-white warbler $n = 32$, worm-eating warbler $n = 16$, white-eyed vireo $n = 26$, Bell's vireo $n = 21$, yellow-throated vireo $n = 31$, red-eyed vireo $n = 49$, blue grosbeak $n = 41$, indigo bunting $n = 46$, and rose-breasted grosbeak $n = 30$ physiographic regions). I hypothesized that climate and local weather may have 1-year lagged effects on annual population densities on the breeding grounds: landbird productivity in one year would be affected by direct climatic effects on Lepidopteran larvae abundance, and such effects on avian productivity would impact landbird population densities the following year. I used density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as climate, on annual population densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_{t-1}) + \varepsilon_t \tag{1}$$

where X_i are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates of the strength of statistical density dependence, b_1 quantifies the influence of climate, local temperature, or local precipitation on population density, Y_{t-1} is the Southern Oscillation Index, NAO Index, mean local temperature, or mean precipitation in year t-1, and ε_t represents the effects of other perturbations or stochastic effects not accounted for

by other variables in the model. Year was included as a covariate for all populations displaying a significant temporal trend (Post & Stenseth 1999). First-, second-, and third-order models were tested to determine which best predicted log annual population density for each population. I then included in the best-fit model 1-year lagged terms for climate, local temperature, or local precipitation. Parameter coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

I next investigated whether spatial variation in the influences of ENSO and the NAO on population dynamics reflected variation in the response of local weather parameters to these climate systems. I first conducted correlation analyses, for each physiographic region, of the annual Southern Oscillation Index and annual local temperature, and annual SOI and local precipitation, across the 39-year period. Within each species, to test whether the strength of the relationship between ENSO and annual population density is predicted by the strength of the connection between ENSO and local temperatures, I conducted quadratic regression analyses of the SOI-local temperature Pearson's r and the population model ENSO coefficient for each population. In addition, for each region in which there was a positive correlation between SOI and local temperature, I conducted correlation analyses of the SOI-local temperature Pearson's r and the population model ENSO coefficient for each region. Similarly, I conducted correlation analyses of the SOI-local precipitation Pearson's r and population model ENSO coefficients for each species. I then conducted each of these same analyses for the NAO.

Finally, to determine the potential effects on landbird species of changes in local temperatures due to large-scale climate change, I quantified the relationship between local temperatures and annual landbird population densities and the magnitude of long-term population increase or decline for each species. I used the Breeding Bird Survey's estimates of long-term population trends (Sauer, Hines & Fallon 2005), analyzing only those populations within each species that exhibited a linear trend over the period 1966-2004 (population sample sizes: prairie warbler $n = 9$, common yellowthroat $n = 15$, black-and-white warbler $n = 13$, worm-eating warbler $n = 8$, white-eyed vireo $n = 14$, Bell's vireo $n = 9$, yellow-throated vireo $n = 12$, red-eyed vireo $n = 17$, blue grosbeak $n = 11$, indigo bunting $n = 13$, and rose-breasted grosbeak $n = 6$ physiographic regions). I then conducted linear regression analyses of the local temperature coefficients from each population model and the BBS trend estimate for each population of each species. I confined these analyses to relationships between temperature and population trends, as results of my previous analyses indicated significant relationships between precipitation-climate Pearson's r's and population model climate coefficients for only 2 of my 11 study species.

Results

Results of my population models incorporating SOI and the NAO Index indicate spatial variation in the relationships between these climate systems and annual population densities of my 11 study species, with relationships with ENSO seen throughout the U.S. and the prairie provinces of Canada, and strongest relationships with the NAO seen in the central and southeastern U.S. (Fig. 1). In my analyses of the effects of these climate

systems on local temperatures and the strength of the climate coefficients in my

population models, results of the quadratic regression analyses of the SOI-local

temperature Pearson's r's and model ENSO coefficients for all regions indicated

significant positive relationships for common yellowthroats ($F = 4.16$, $P = 0.025$, $R^2 = 0.201$) and blue grosbeaks ($F = 9.09$, $P = 0.001$, $R^2 = 0.411$) (Fig. 2). In addition,

correlation analyses between these same variables for only those regions exhibiting a

positive correlation between SOI and local temperatures indicate significant relationships

between the SOI-local temperature Pearson's r's and model ENSO coefficients for the 3

additional warbler species and for white-eyed vireos and yellow-throated vireos (prairie

warbler: $r = -0.478$, $P = 0.042$; black-and-white warbler: $r = -0.593$, $P = 0.013$; worm-

eating warbler: $r = -0.694$, $P = 0.009$; white-eyed vireo: $r = -0.407$, $P = 0.042$; yellow-

throated vireo: $r = -0.387$, $P = 0.019$) (Fig. 3). All correlations between the NAO Index

and local temperatures were positive; thus I conducted only correlation analyses, not

quadratic regressions, of the NOA Index-local temperature Pearson's r's and population

model NAO coefficients for each species. However, none of the correlation analyses

showed significant relationships between NAO-local temperature Pearson's r's and

strength of the NAO coefficients in the population models.

I conducted these same analyses between climate index-local precipitation Pearson's r's

and the population model climate coefficients for each species. Correlation analyses

between the SOI-local precipitation Pearson's r's and model ENSO coefficients indicated

a significant relationship for worm-eating warblers ($r = 0.595$, $P = 0.010$). Correlation

analyses between NAO Index-local precipitation Pearson's r's and model NAO

coefficients showed a significant correlation for common yellowthroats ($r = -0.345$, $P = 0.020$).

Finally, I analyzed for each species the relationship between local temperature and annual regional population densities and the magnitude of long-term regional population increase or decline. My results indicated a significant linear regression between population model local temperature coefficients and BBS regional population trends for common yellowthroats ($t = 2.915$, $P = 0.012$, $R^2 = 0.395$) and indigo buntings ($t = 2.401$, $P = 0.035$, $R^2 = 0.344$), and near-significant regressions for prairie warblers ($t = 2.179$, $P = 0.066$, $R^2 = 0.404$) and black-and-white warblers ($t = 2.077$, $P = 0.062$, $R^2 = 0.282$) (Fig. 4). Importantly, for these species for which there was a significant or near-significant linear relationship between strength of the local temperature parameter in the species' population models and the magnitude of long-term regional population change, all have exhibited significant declines throughout their breeding ranges from 1966-2004. For all species for which there was no relationship between strength of the population model local temperature parameters and the magnitude of long-term regional population change, each species has exhibited a significant increase or steady population trend throughout its breeding range from 1966-2004 (including worm-eating warblers, white-eyed vireos, Bell's vireos, yellow-throated vireos, red-eyed vireos, and blue grosbeaks; the single exception is the rose-breasted grosbeak, which has shown significant long-term declines throughout its range).

Discussion

This study documents spatially heterogeneous relationships between annual large-scale climate indices and 1-year lagged annual population densities of 11 Neotropical-Nearctic migratory landbird species, including shrub-habitat and forest-nesting warblers, vireos, and grosbeaks and buntings, across their North American breeding distributions. My results indicate that ENSO and the NAO have been related to lagged annual densities of some populations over the past 39 years, and that for all four warbler species, two of the vireo species, and one of the grosbeak species studied, the strength of the effect of ENSO on population densities is correlated with the strength of the effect of ENSO on local temperatures. In addition, for four of the species studied (prairie warbler, common yellowthroat, black-and-white warbler, and indigo bunting), the magnitude of the effect of local temperature on populations is predictive of long-term population decline: the more strongly and negatively any particular population's densities were related to local temperatures on its breeding grounds, the more precipitous has been that population's decline over the past 39 years. Finally and most importantly, my results show that for all four species for which there was a significant or near-significant relationship between strength of effect of local temperature on annual population densities and magnitude of long-term population change, each species has exhibited a significant decline throughout its breeding range from 1966-2004; in contrast, for the seven species for which there was no relationship between effects of local temperature and long-term population change, each species has shown stable or increasing population trends across its breeding range during that period.

Results of analyses for the 11 migratory landbird species studied here are similar to those found by Anders and Post (2006) for yellow-billed cuckoos (*Coccyzus americanus*). In that study, 1-year lagged cuckoo densities were found to be related in a spatially hetergeneous way to both ENSO and the NAO, and the strength of these relationships was correlated with the strength of the effect of these large-scale climate systems on local temperatures. As with yellow-billed cuckoos, I found relationships here between the strength of the effect of local temperature on population dynamics and migratory species' long-term population trends. Anders and Post (2006) did not analyze relationships between annual precipitation and cuckoo population dynamics. Results of such analyses in the current study, however, indicated few such relationships: there was a significant correlation between strength of the effect of ENSO on local precipitation and population model ENSO coefficients for worm-eating warblers, and a correlation between and strength of the effect of the NAO on precipitation and model NAO coefficients for common yellowthroats.

Effects of climate on landbird population dynamics have been shown in other studies to be mediated through effects of the NAO and ENSO on Lepidopteran larvae abundance (Sillett et al. 2000; Nott et al. 2002). Effects of climate, then, may potentially be seen across phylogenetic groups and throughout different breeding habitat types, as Lepidopteran larvae are the primary food resource for most landbird taxa during breeding (e.g. Brown 1993; Hopp, Kirby & Boone 1995; Kricher 1995; Rodewald & James 1996; Hanners & Patton 1998; Nolan, Ketterson & Buerkle 1999; Cimprich, Moore & Guilfoyle 2000; Payne 2006). Geographic variation in effects of climate, and variation in

strength of the effects of climate within regions, may be expected to vary among landbird species, however, as prey availability varies geographically, and exact diet varies between landbird taxa within physiographic regions. Of the species studied here, warblers (Parulidae), including shrub- and forest-breeding species, showed more significant relationships between strength of the population model local temperature parameters and long-term population change, than did the *Vireo* or Fringillidae species. In addition, the four species studied that exhibited significant relationships between strength of the effect of local temperature and strength of long-term population decline were primarily shrub-breeding species: prairie warbler, common yellowthroat, and indigo bunting; the exception was the black-and-white warbler, but this species is known to breed in young regenerating forest habitat, in addition to nesting in areas of mature forest. Thus, results of my analyses may indicate greater effects of changes in large-scale climate and local temperature on warblers, relative to vireos and grosbeaks, and on shrub-breeding relative to forest-breeding migratory landbird species.

This study is the first to document relationships between annual large-scale climate indices and annual population densities of Neotropical-Nearctic migratory landbirds at the scale of species' breeding ranges; however, results of this study support more in-depth field studies that have necessarily been conducted at smaller spatial scales. Sillett et al. (2000) found relationships between ENSO and the productivity of forest-nesting black-throated blue warblers (Parulidae: *Dendroica caerulescens*) in New Hampshire, in the northeastern U.S., and Jones et al. (2003) found relationships between the NAO and densities of multiple winter resident landbird species in that same geographic area.

Wilson and Arcese (2003) found effects of ENSO on the productivity of song sparrows (Emberizidae: *Melospiza melodia*) off of the west coast of British Columbia. Similarly, Nott et al. (2002) found relationships between ENSO and the NAO and population productivity of forest-nesting landbirds of the Pacific Northwest, including effects of ENSO on 3 Parulid warbler species (yellow warbler (*Dendroica petechia*), MacGillivray's warbler (*Oporornis tolmiei*), Wilson's warbler (*Wilsonia pusilla*)) and on western tanagers (Thraupidae: *Piranga ludoviciana*), and a relationship between the NAO and productivity in Hammond's and western flycatchers (Tyrannidae: *Empidonax hammondii* and *E. difficilis/occidentalis*).

In conclusion, I found 1-year lagged relationships between annual indices of ENSO and the NAO and annual population densities of shrub- and forest-nesting Neotropical-Nearctic migratory Parulidae, Vireo, and Fringillidae species throughout their North American breeding ranges. Geographic variation in the effects of ENSO was related to geographic variation in the strength of the effect of this climate system on local weather, including local temperatures for 7 of the 11 species, and local precipitation for 2 of the species studied. Significantly, results of my analyses indicate that for 4 of the 5 study species that have declined significantly over the past 39 years, there is a relationship between the strength of the effect of local temperatures on annual population densities and the magnitude of population decline. Overall, results of this study indicate that Parulidae species may be more sensitive to effects of changes in climate than are *Vireo* or Fringillidae species, and that shrub-nesting species may be affected to a greater extent than are forest-nesting migratory landbird species.

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Table 1. Shrub- and forest-breeding species of migratory warblers, vireos, and grosbeaks for which relationships were examined between large-scale climate, local weather, and annual population densities.

	Shrub breeding habitat	Forest breeding habitat
Parulidae species:	prairie warbler (*Dendroica discolor*)	black-and-white warbler (*Mniotilta varia*)
	common yellowthroat (*Geothlypis trichas*)	worm-eating warbler (*Helmitheros vermivorus*)
***Vireo* species:**	white-eyed vireo (*Vireo griseus*)	yellow-throated vireo (*Vireo flavifrons*)
	Bell's vireo (*Vireo bellii*)	red-eyed vireo (*Vireo olivaceus*)
Fringillidae species:	blue grosbeak (*Guiraca caerulea*)	rose-breasted grosbeak (*Pheucticus ludovicianus*)
	indigo bunting (*Passerina cyanea*)	

Fig. 1. Physiographic regions in which ENSO and the NAO entered best-fit population

models for the 11 Neotropical-Nearctic migratory landbird species studied (data from

1966-2004). Black outlines indicate all regions that were analyzed for each species

studied. Light grey fill indicates regions in which the 1-year lagged Southern Oscillation

Index occurred in the best-fit population model; dark grey fill indicates regions in which

the 1-year lagged NAO Index occurred in the best-fit model; and black fill indicates

regions in which both climate indices occurred in the best-fit model (background map of

BBS regions from Sauer et al. (2005)).

Fig. 2. Quadratic regression analyses indicated significant positive relationships between

local temperature-Southern Oscillation Index Pearson's r's and population model

Southern Oscillation Index coefficients for common yellowthroats ($F = 4.16$, $P = 0.025$,

$R^2 = 0.201$) and blue grosbeaks ($F = 9.09$, $P = 0.001$, $R^2 = 0.411$).

Fig. 3. Correlation analyses indicated significant relationships between local temperature-

Southern Oscillation Index Pearson's r's and population model SOI coefficients for prairie

warblers ($r = -0.478$, $P = 0.042$), black-and-white warblers ($r = -0.593$, $P = 0.013$),

worm-eating warblers ($r = -0.694$, $P = 0.009$, white-eyed vireos ($r = -0.407$, $P = 0.042$),

and yellow-throated vireos ($r = -0.387$, $P = 0.019$).

Fig. 4. Linear regression analyses showed significant relationships between population

model local temperature coefficients and BBS long-term regional population trends for

common yellowthroats ($t = 2.915$, $P = 0.012$, $R^2 = 0.395$) and indigo buntings ($t = 2.401$,

$P = 0.035$, $R^2 = 0.344$), and near-significant relationships for prairie warblers ($t = 2.179$,

$P = 0.066$, $R^2 = 0.404$) and black-and-white warblers ($t = 2.077$, $P = 0.062$, $R^2 = 0.282$).

Each of these 4 species has exhibited significant declines throughout their breeding

ranges from 1966-2004.

Fig. 1

a. prairie warbler

b. black-and-white warbler

c. common yellowthroat

d. worm-eating warbler

e. white-eyed vireo

f. yellow-throated vireo

g. Bell's vireo

h. red-eyed vireo

i. blue grosbeak

j. rose-breasted grosbeak

k. indigo bunting

Fig. 2

Common yellowthroat
(Parulidae: *Geothlypis trichas*)

Blue grosbeak
(Fringillidae: *Guiraca caerulea*)

Fig. 3

Prairie warbler
(Parulidae: *Dendroica discolor*)

White-eyed vireo
(Vireonidae: *Vireo griseus*)

Black-and-white warbler
(Perulidae: *Mniotilta varia*)

Yellow-throated vireo
(Vireonidae: *Vireo flavifrons*)

Worm-eating warbler
(Perulidae: *Helmitheros vermivorus*)

Fig. 4

Common yellowthroat
(Parulidae: *Geothlypis trichas*)

long-term population trend

population model local temp coefficient

Prairie warbler
(Parulidae: *Dendroica discolor*)

long-term population trend

population model local temp coefficient

Indigo bunting
(Fringillidae: *Passerina cyanea*)

long-term population trend

population model local temp coefficient

Black-and-white warbler
(Parulidae: *Mniotilta varia*)

long-term population trend

population model local temp coefficient

Chapter 4

GREATER EFFECTS OF LARGE-SCALE CLIMATE
ON LONG-DISTANCE MIGRATORY VERSUS RESIDENT
NORTH AMERICAN LANDBIRD SPECIES:
POTENTIAL EFFECTS OF TROPHIC MISMATCH

Summary

1. Changes in global temperatures over the past several decades have been seen to shift the breeding phenology of many plant and animal species; however, for species that migrate long distances from non-breeding to breeding areas, shifts in phenology to adjust to effects of climate change may be constrained by the timing of migration. Such constraints can lead to decreases in productivity or survival if a species' breeding phenology becomes mismatched with that of its prey species.

2. To determine whether long-distance migratory species may be more likely to suffer effects of such climate-induced trophic mismatch, I examined the relationship between winter temperatures and 1-year lagged annual population densities of four Neotropical-Nearctic migratory landbirds and four resident or short-distance migratory North American landbird species throughout their breeding ranges from 1966-2004.

3. Results of my analyses indicate that more long-distance migrant populations experienced significant 1-year lagged declines following warm winter temperatures than did populations of resident or short-distance migratory landbirds; in addition, the strength of effects of warm winter temperatures were greater for long-distance migrants than for resident or short-distance migratory landbird populations. Because the phenology of Lepidopteran species, the main food resource for most landbird taxa during breeding, is known to be affected by winter temperatures, greater negative effects of warm winters on long-distance migrants may be due at least in part to the species' inability to time their

migration based on the timing of availability of Lepidopteran food resources on the breeding grounds.

4. Of the 137 species of Neotropical-Nearctic long-distance migratory landbirds, more than 30% have experienced significant declines over the past 40 years. An understanding of the role of increasing temperatures and of increasing annual variability in temperatures will help us to better determine the proximate causes of population decline and better predict future responses to global climate change.

Introduction

Global temperatures have increased by 0.6°C over the past century (IPCC 2007), and many studies have documented changes in the phenology of plant and animal species in response to this warming (Dunn & Winkler 1999; Forchhammer, Post & Stenseth 1999; Walther et al. 2002; Root et al. 2003; Visser et al. 2003; Wilson & Arcese 2003; Both et al. 2004). Although some species may shift their timing of breeding or other life history traits to successfully adjust to environmental effects of changes in global climate, species that migrate long distances may be constrained in the extent to which their phenology may shift (Both & Visser 2001; Post & Forchhammer in press). Although timing of breeding may change based on effects of temperature on the breeding grounds, the timing of migration to the breeding area is, for many migratory species, based on endogenous traits or on climatic conditions in the non-breeding area. Thus, although the phenology of food resources on the breeding grounds may shift in response to warming, long-distance migratory species may be unable to adequately respond to these changes, leading to a mismatch between trophic levels within the ecosystem (Stenseth & Mysterud 2002).

Within long-distance migratory landbird species, such constraint in the timing of migration has been seen in the European pied flycatcher (*Ficedula hypoleuca*): although spring temperatures in the Netherlands have increased over the past 20 years, exerting selection for earlier breeding dates in this species, a phenological shift that would maximize fitness based on timing of availability of food resources has been constrained by the timing of arrival of this long-distance migrant on the breeding grounds (Both & Visser 2001). For North American landbird species, both short-and long-distance migratory species have shifted the timing of their spring migration in response to global warming over the past century; however, short-distance migratory species arrive on their breeding territories an average of 13 days earlier, while long-distance migrants arrive an average of only 4 days earlier, compared to arrival dates of the early twentieth century (Butler 2003). Analyses of the population dynamics of a Neotropical-Nearctic long-distance migrant, the yellow-billed cuckoo (*Coccyzus americanus*), in relation to local temperatures on the breeding grounds indicate that population densities exhibit a 1-year lagged decline following warm winters (Anders & Post 2006). Warm winter temperatures may lead to earlier spring peaks in the abundance of Lepidopteran larvae (Miller, Mo & Wallner 1989; Nott et al. 2002; Jones, Doran & Holmes 2003; Forister & Shapiro 2003), the primary food resource for most landbird taxa during breeding (e.g. Roth, Johnson & Underwood 1996; Gowaty & Plissner 1998; Hughes 1999; Sallabanks & James 1999), such that yellow-billed cuckoos, which are likely unable to time their migration based on food availability on the breeding grounds, miss this peak in food availability, leading to decreases in productivity or adult survival.

In this study, I examine the relationship between local winter temperatures and annual population densities of Neotropical-Nearctic migratory landbirds and resident or short-distance migratory landbirds in North America. If warm winter temperatures shift the phenology of Lepidopteran species, leading to earlier spring peaks in the abundance of Lepidopteran larvae (e.g. Miller, Mo & Wallner 1989; Forister & Shapiro 2003), long-distance migratory birds that are unable to shift their timing of migration in response to this earlier peak in food availability (e.g. Both & Visser 2001) may experience lower productivity and/or lower survival rates during that breeding season. This decrease in productivity or survival would lead to one-year lagged decreases in population densities of these migratory species. In contrast, such changes in population densities due to climate-induced trophic mismatch should not be seen in resident or short-distance migratory landbird species that are present in North America year-around and can thus time their breeding based upon food availability (Stenseth & Mysterud 2002).

Materials and Methods

Survey Data

To test whether Neotropical-Nearctic migratory landbird species are potentially more negatively affected by warm winter temperatures than are resident or short-distance migratory North American species, a pattern expected if long-distance migrants, but not residents, suffer from trophic mismatch in warm years, I analyzed long-term survey data from throughout the breeding ranges for both long-distance migratory and resident or short-distant migratory species. To obtain a large sample size of populations for each

species, and to allow for examination of geographic effects, I used species whose breeding ranges incorporate at least most of the central and eastern United States and southern Canada. In choosing multiple migratory and resident study species while controlling for phylogeny, and taking into account geographic extent of the breeding range, my analyses were limited to species within the subfamily Cardinalinae (family Emberizidae) and within the family Turdidae. These species include the long-distance migratory rose-breasted grosbeak (*Pheuticus ludovicianus*) (Wyatt & Francis 2002) and blue grosbeak (*Guiraca caerulea;*) (Ingold 1993), the non-migratory northern cardinal (*Cardinalis cardinalis*) (Halkin & Linville 1999), and short-distance migratory eastern towhee (*Pipilo erythrophthalmus*) (Greenlaw 1996), as well as the long-distance migratory wood thrush (*Hylocichla mustelina*) (Roth, Johnson & Underwood 1996) and veery (*Catharus fuscescens*) (Bevier, Poole & Moskoff 2004) and the short-distance migratory eastern bluebird (*Sialis sialis*) (Gowaty & Plissner 1998) and American robin (*Turdus migratorius*) (Sallabanks & James 1999) (Table 1). As indices of population densities within each species, I used data from the U.S. Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2004, using data from a total of 40 physiographic regions incorporating 43 U.S. states and 3 Canadian provinces (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/), with a mean of 78 survey routes per physiographic region. Each physiographic region was defined as a population, and annual population densities within each species were calculated as mean number of individuals detected per survey route within a region within a year.

Local Temperature Data

Local temperature data from 1966-2004 were obtained from the U.S. National Climatic

Data Center (NCDC; www.ncdc.noaa.gov/oa/climate/onlineprod/drought/ftppage.html)

from NCDC divisions that overlapped the BBS physiographic regions used to define

landbird populations. Mean monthly temperatures for all NCDC divisions within a BBS

region were calculated, and I used mean of December through March (winter

temperature) values within each year in my analyses. In addition to winter temperatures

affecting the timing and availability of landbird Lepidopteran food resources (Miller, Mo

& Wallner 1989; Nott et al. 2002; Jones, Doran & Holmes 2003; Forister & Shapiro

2003), large-scale climate systems are known to show the strongest effects on local

temperatures in North America during these months (Hurrell 1995; Trenberth & Caron

2000).

Population Models

To quantify the potential influences of local winter temperatures on changes in annual

landbird population densities, I incorporated local temperature into models of population

dynamics for each species (population sample sizes: rose-breasted grosbeak $n = 29$, blue

grosbeak $n = 41$, northern cardinal $n = 39$, eastern towhee $n = 45$, wood thrush $n = 29$,

veery $n = 33$, eastern bluebird $n = 42$, American robin $n = 62$ physiographic regions). I

hypothesized that local temperature would have a 1-year lagged effect on annual

population densities on the breeding grounds: landbird productivity in one year would be

affected by direct climatic effects on Lepidopteran larvae (Miller, Mo & Wallner 1989;

Nott et al. 2002; Jones, Doran & Holmes 2003; Forister & Shapiro 2003), the main food

resource for most landbird taxa during breeding (e.g. Roth, Johnson & Underwood 1996; Gowaty & Plissner 1998; Hughes 1999; Sallabanks & James 1999), and such effects on avian productivity would affect landbird population densities the following year. I used density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as temperature, on annual population densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_{t-1}) + \varepsilon_t \qquad (1)$$

where X_i are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates of the strength of statistical density dependence, b_1 quantifies the influence of local temperature on population density, Y_{t-1} is mean local temperature in year t-1, and ε_t represents the effects of other perturbations or stochastic effects not accounted for by other variables in the model. Year was included as a covariate for all populations displaying a significant temporal trend (Post & Stenseth 1999). First-, second-, and third-order models were tested to determine which best predicted log annual population density for each population. I then included in the best-fit model the 1-year lagged term for local temperature. Parameter coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

I next examined whether the strength of the population model winter temperature coefficients differed between Neotropical-Nearctic migratory and resident or short-

distance migratory species. I first examined the proportion of populations of each species for which the lagged local temperature term (b_1) entered the best-fit population model. I conducted a Chi-square analysis to determine whether these proportions differed between the four long-distance migratory species (rose-breasted grosbeak, blue grosbeak, wood thrush, and veery), and the four resident or short-distance migratory species (northern cardinal, eastern towhee, eastern bluebird, and American robin). I next tested for differences in the strength of the effect of local temperatures (the magnitude of b_1) between the four long-distance migratory species and four resident or short-distance migratory species. I conducted an analysis of variance of population model temperature coefficients for all populations of all species, with migratory status (long-distance migrant or short-distance migrant/resident) as a fixed-effects factor.

Next, because populations of long-distance migrants breeding at lower latitudes within the North American breeding range arrive earlier on their breeding territories than do populations that breed at higher latitudes, I tested for differences in the strength of the population model temperature coefficients by latitude within each species, hypothesizing that populations at higher latitudes may be more strongly affected by warm winter temperatures, due to greater trophic mismatch caused by later arrival on the breeding territories. Such differences in effects on populations across species' breeding ranges would exemplify a nonlinear trophic mismatch response by latitude described by Stenseth and Mysterud (2002). For each long-distance migratory species, I conducted linear regression analyses of the population model temperature coefficients and the mean latitude of the BBS survey routes within each physiographic region. To determine

whether differences in population densities occur across a latitudinal gradient that might

mask potential relationships between trophic mismatch and latitude, I conducted

correlation analyses between physiographic region population densities and latitude for

each Neotropical-Nearctic migratory species.

Finally, because previous studies have shown relationships between the strength of the

effect of annual temperatures on annual population densities and the extent of long-term

population decline for several long-distance migratory landbird species (Anders & Post

2006; Chapter 3 this volume), I tested for this relationship with each of the eight species

studied here, including the North American resident and short-distance migratory species.

I used the Breeding Bird Survey's estimates of long-term population trends (Sauer, Hines

& Fallon 2005), analyzing only those populations within each species that exhibited a

linear trend over the period 1966-2004 (population sample sizes: rose-breasted grosbeak

$n = 12$, blue grosbeak $n = 12$, northern cardinal $n = 12$, eastern towhee $n = 9$, wood thrush

$n = 13$, veery $n = 9$, eastern bluebird $n = 12$, American robin $n = 17$ physiographic

regions). I then conducted linear regression analyses of negative population model

temperature coefficients and the BBS trend estimate for each population of each species.

Results

Results of analysis of autoregressive population models for Neotropical-Nearctic and

North American resident or short-distance migratory landbird species indicate that 1-year

lagged local temperatures entered the best-fit population models for a significantly

greater proportion of populations of long-distance migratory species than resident or

short-distance migratory species ($z = 2.327$; $P = 0.020$) (Fig. 1). In examining differences

in the strength of the population model local temperature coefficients for all study

populations of long-distance migrants versus resident or short-distance migratory species,

results of an analysis of variance indicated a near-significant difference ($F_{1,230} = 3.455$, P

$= 0.064$) (Fig. 2), with a negative mean model temperature coefficient for long-distance

migrants (indicating a decrease in annual population densities with increasing local

temperature), and a positive mean coefficient for resident and short-distance migratory

species (indicating an increase in annual population densities with increasing local

temperature).

In testing the hypothesis that populations of Neotropical-Nearctic migratory species

breeding at higher latitudes may experience stronger effects of warm winter temperatures

(due to greater trophic mismatch following later arrival on the breeding territories),

results of linear regression analyses for each species indicated no significant relationships

between mean latitude of the study population and strength of the population model

temperature coefficient (rose-breasted grosbeak: $t = 1.838$, $P = 0.087$, $R^2 = 0.194$; blue

grosbeak: $t = 0.998$, $P = 0.342$, $R^2 = 0.091$; wood thrush: $t = 1.458$, $P = 0.171$, $R^2 = 0.150$;

veery: $t = 1.906$, $P = 0.086$, $R^2 = 0.266$). Although the linear regression analysis of model

temperature coefficients versus latitude approached significance for the veery, the

relationship was in the opposite direction than predicted, with populations at lower

latitudes experiencing stronger lagged effects of warm winter temperatures. In testing

whether latitudinal gradients in population densities exist for any of the four migratory

study species, which may potentially mask relationships between trophic mismatch and

latitude, correlation analyses indicated a significant positive relationship between population density and latitude for rose-breasted grosbeaks ($r = 0.626$, $P = 0.001$); however, subsequent analysis indicated no correlation between strength of the local temperature coefficient and latitude for this species ($r = -0.216$, $P = 0.290$).

Finally, analyses of the relationships between strength of the effect of local temperatures on annual population densities and extent of long-term population change indicated significant relationships for two of the eight study species. Linear regression analyses of negative population model temperature coefficients and BBS trend data from 1966-2004 indicate that for the veery, a Neotropical-Nearctic migratory species, the stronger the negative relationship between warm winter temperatures and annual population densities, the greater has been that population's decline over the 39-year period ($t = 4.058$, $P = 0.005$) (Fig. 3a). This relationship was also seen for the short-distance migratory species, the eastern towhee ($t = 3.283$, $P = 0.013$) (Fig. 3b).

Discussion

Results of this study suggest that populations of long-distance Neotropical-Nearctic migratory landbird species may be more strongly affected by warm winter temperatures on the breeding grounds than are closely-related North American resident or short-distance migratory species. My comparison of annual population densities of long-distance migratory and resident or short-distance migratory Cardinalinae and Turdidae species over a 39-year period throughout the species' breeding ranges (Sauer, Hines & Fallon 2005) indicate that Neotropical-Nearctic migratory populations experienced more

and greater 1-year lagged declines following warm winter temperatures than did populations of resident or short-distance migratory landbirds. Because the phenology of Lepidopteran species, the main food resource for most landbird taxa during breeding, is known to be affected by winter temperatures (Miller, Mo & Wallner 1989; Nott et al. 2002; Jones, Doran & Holmes 2003; Forister & Shapiro 2003), greater negative effects of warm winters on Neotropical-Nearctic migratory landbirds may be due at least in part to the species' inability to time their migration based on the timing of availability of Lepidopteran food resources on the breeding territories (Both & Visser 2001; Stenseth & Mysterud 2002). This potential causal mechanism would parallel results found for the European long-distance migrant, the pied flycatcher, in which the study population was seen to suffer from increasing trophic mismatch with prey species on the breeding territories as winter temperatures increased over a 20-year period; pied flycatcher breeding date was seen to advance significantly, but a match with the shifting peak in food availability was limited overall by timing of arrival of this long-distance migratory species on the breeding grounds (Both & Visser 2001).

Differences in the degree to which such trophic mismatch affects populations might be expected to vary by latitude (Stenseth & Mysterud 2002), as, across my study species, individuals breeding at higher latitudes arrive on their breeding territories several weeks later than do individuals breeding at more southerly latitudes (Ingold 1993; Roth, Johnson & Underwood 1996; Wyatt & Francis 2002; Bevier, Poole & Moskoff 2004). Results of my analyses, however, indicate no significant relationship between breeding latitude and lagged effect of warm winter temperatures on population densities for any of

my Cardinalinae or Turdidae study species. The lack of a relationship between latitude and degree of effect of warm winter temperatures on migratory landbirds may be due to a concomitant shift in the phenology of Lepidopteran species at varying latitudes, with more northerly insect populations exhibiting a later phenological shift than southerly populations due to differences in local temperatures across the latitudinal range. Additional studies of the relationships between Lepidopteran abundance and climate across the North American continent need to be conducted, however, in order to test this hypothesis.

As with previously-studied North American landbird taxa (Anders & Post 2006; Chapter 3 this volume), results of analyses of Cardinalinae and Turdidae species indicate significant relationships, for a subset of the species, between the strength of the negative effect of warm winter temperatures on annual population densities, and the extent of a populations' long-term decline: for both the veery, a Neotropical-Nearctic migratory species, and the eastern towhee, a short-distance migrant, the stronger the negative relationship between warm temperatures and population densities, the more precipitously did that population decline during the period 1966-2004. This relationship between annual effects of warm winter temperatures and long-term population decline has been seen in several Neotropical-Nearctic migratory landbird taxa, including the yellow-billed cuckoo [Cuculiformes: Cuculidae] (Anders & Post 2006); common yellowthroat (*Geothlypis trichas*), prairie warbler (*Dendroica discolor*), and black-and-white warbler (*Mniotilta varia*) [Passeriformes: Parulidae]; and indigo bunting (*Passerina cyanea*) [Passeriformes: Fringillidae] (Chapter 3 this volume).

Overall, results of my study suggest that long-distance Neotropical-Nearctic migratory landbird species may have been more negatively affected by warm winter temperatures across their breeding ranges over the period 1966-2004 than were closely-related North American resident or short-distance migratory species. This difference in effect of warm winter temperatures between these groups may follow from greater trophic mismatch for long-distance migratory species that are unable to time their migration to the breeding grounds in response to earlier peaks in the availability of Lepidopteran food resources following warm winters (Stenseth & Mysterud 2002; Post & Forchhammer 2007). Although differences in the degree of effect of trophic mismatch may potentially vary by latitude, with more northerly populations experiencing greater trophic mismatch due to later arrival on the breeding territories, such a pattern was not seen in the Cardinalinae and Turdidae species studied here. Finally, as in previous analyses of other long-distance migratory species (Anders & Post 2006; Chapter 3 this volume), a relationship was found in this study between the strength of the negative annual effects of warm winter temperatures and the extent of long-term population decline: for the veery, a long-distance migrant, but also for the eastern towhee, a short-distance migrant, the greater the effect of warm local temperatures on population densities, the greater was that population's decline over the period 1966-2004. Of the 137 species of Neotropical-Nearctic migratory landbirds, more than 30% have exhibited significant declines over the past 40 years (Robbins et al. 1989; Askins, Lynch & Greenberg 1990; Sauer, Hines & Fallon 2005). An understanding of the role of increasing temperatures and of increasing

annual variability in temperatures will help us to better determine the proximate causes of

these population declines and better predict future responses to changes in global climate.

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Table 1. Neotropical-Nearctic migratory and resident or short-distance migratory landbird species used in this study to compare differences in the potential effects of warm winter temperatures on 1-year lagged population densities.

	Neotropical-Nearctic migratory species	**North American resident species**
Cardinalinae:	rose-breasted grosbeak (*Pheuticus ludovicianus*)	northern cardinal (*Cardinalis cardinalis*)
	blue grosbeak (*Guiraca caerulea*)	eastern towhee (*Pipilo erythrophthalmus*)
Turdidae:	wood thrush *(Hylocichla mustelina*)	eastern bluebird *(Sialis sialis*)
	veery (*Catharus fuscescens*)	American robin (*Turdus migratorius*)

Fig. 1. Physiographic regions in which 1-year lagged local winter temperatures entered the best fit population model for Neotropical-Nearctic migratory landbirds (a-d) and resident or short-distance migratory species (e-h). Light gray indicates physiographic regions studied for each species, and dark gray indicates regions in which temperature entered the best-fit model (background map of BBS physiographic regions from Sauer et al. (2005)). Chi-square analysis indicated a significant difference in the proportion of populations of Neotropical-Nearctic migrants versus resident or short-distance migratory landbirds for which local temperature entered the best-fit population model.

Fig. 2. Mean values of 1-year lagged local winter temperature coefficients from models of all populations of Neotropical-Nearctic migratory and resident or short-distance migratory landbird species studied. A negative mean model coefficient for Neotropical-Nearctic migrants indicates decreasing annual population densities with increasing local temperature, and a positive mean coefficient for resident/short-distance migratory species indicates an increase in annual population densities with increasing local temperature. An analysis of variance indicated near-significant differences in the strength of the effect of local temperature on annual population densities for long-distance migratory versus resident or short-distance migratory species.

Fig. 3. BBS long-term population trends versus population model temperature coefficients for the veery and eastern towhee. For both species, the greater the effect of 1-year lagged local winter temperatures on annual population densities, the more precipitous has been that population's long-term decline over the period 1966-2004.

Fig. 1

a. rose-breasted grosbeak

e. northern cardinal

b. blue grosbeak

f. eastern towhee

c. wood thrush

g. eastern bluebird

d. veery

h. American robin

Fig. 2

Fig. 3

a. veery

b. eastern towhee

Chapter 5

LIMITING EFFECTS OF CONGENER DENSITIES
GREATER FOR POPULATIONS ALSO AFFECTED BY
LARGE-SCALE CLIMATE

Summary

1. In addition to affecting population phenology, productivity, and survival, changes in large-scale climate have the potential to impact indirect interspecific competition through effects on food resources.

2. To determine whether annual changes in large-scale climate potentially affect population densities of landbirds through effects on interspecific competition, I quantified relationships between annual indices of the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO), and annual population densities of two pairs of North American sympatric congeners: yellow-billed and black-billed cuckoos (*Coccyzus americanus* and *C. erythropthalmus)*, and scarlet and summer tanagers (*Piranga olivacea* and *P. rubra*).

3. Results of these analyses show common geographic patterns of relationships between these climate systems and annual population densities of all four study species. Effects of climate and congener densities were unpaired for black-billed cuckoos, but the behaviorally-dominant yellow-billed cuckoo was affected by congener densities to a greater extent in regions in which this species' densities were also affected by climate. Both tanager species experienced the greatest negative effects of congener densities in regions in which the species also experienced climatic effects.

4. Overall, results of this study indicate that increased effects of climate on resources such as food availability may act to increase the effect of indirect competition from sympatric congeners on North American landbird species.

Introduction

Studies of many species of landbirds in Europe and North America have shown effects of changes in large-scale climate on phenology, productivity, and survival within populations (Dunn & Winkler 1999; Saether et al. 2000; Sillett, Holmes & Sherry 2000; Jonzen et al. 2002; Forchammer, Post & Stenseth 2002; Nott et al. 2002; Visser et al. 2003; Wilson & Arcese 2003; Both et al. 2004; Macmynowski et al. 2007). Such effects of climate have been shown to be mediated in some North American birds through effects on food availability (Sillett, Holmes & Sherry 2000; Nott et al. 2002; Jones, Doran & Holmes 2003), with climatic variability affecting annual abundance of Lepidopteran larvae (Sillett, Holmes & Sherry 2000; Nott et al. 2002), the primary food resource for most landbird taxa during breeding (e.g. Robinson 1996; Hughes 1999; Mowbray 1999; Hughes 2001)**.** Because of its effects on food resources, climate has the potential not only to affect within-species population productivity and survival, but also to increase indirect interspecific competition for resources.

Effects of climate on interspecific interactions are most likely to occur among closely-related species whose ranges overlap and whose breeding ecologies are similar. The population dynamics of two congeneric European species, the collared flycatcher and pied flycatcher (*Ficedula albicollis* and *F. hypoleuca*), have been shown to be affected by

large-scale climate through its influence on the strength of interspecific competition (Saetre, Post & Kral 1999). In that study, effects of climate on pied flycatchers in warm years led to increased competitive pressures from the sympatric and socially-dominant collared flycatcher. In North America, analyses of climatic effects on yellow-billed cuckoo (*Coccyzus americanus*) populations indicated that population densities of this species are negatively affected by warm winter temperatures (Anders & Post 2006). Climate thus has the potential to increase indirect interspecific resource competition between yellow-billed cuckoos and their sympatric congener, the black-billed cuckoo (*Coccyzus erythropthalmus*), following warm winters. Similar effects of climate may also exist in other closely-related sympatric species in North America.

To determine whether changes in large-scale climate affect population densities of North American landbird species through effects on interspecific competition, I quantified relationships between large-scale climatic variability and population dynamics in yellow-billed and black-billed cuckoos, and in another pair of sympatric congeners, scarlet and summer tanagers (*Piranga olivacea* and *P. rubra*). Much of the annual variation in climatic conditions across North America is attributable to two climate systems, the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Hurrell 1995; Trenberth & Caron 2000). Using a 39-year data set of population surveys from throughout the United States and Canada (Sauer, Hines & Fallon 2005), I assessed the importance of congener population densities and ENSO and the NAO on annual population densities of yellow-billed and black-billed cuckoos, and on scarlet and summer tanagers, throughout their sympatric breeding ranges.

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Materials and Methods

Study Species

Yellow-billed and black-billed cuckoos are Neotropical-Nearctic migratory landbirds, breeding in North America from May through September, and wintering in Venezuela and Colombia, south into central Argentina, from October through April (Hughes 1999, 2001). The breeding range of the yellow-billed cuckoo extends from Texas and the Gulf Coast states in the south, north through the Midwestern states and along the East Coast through Maine, and into southern Manitoba, Ontario, and Quebec. The breeding range of the black-billed cuckoo is situated north relative to the yellow-billed cuckoo range, extending from northern Oklahoma and southern Missouri in the south, east through the Appalachian Mountains of western North Carolina, and north through central Alberta to Prince Edward Island and Nova Scotia (Hughes 2001). Within these ranges, yellow-billed cuckoo densities are highest in the southern and Midwestern U.S. (Hughes 1999), while black-billed cuckoos are most numerous in the more northern latitudes (Hall 1983, Robbins and Easterla 1992); however, there is extensive overlap between these congeneric species in the central and northern U.S. and southern Canada (Fig. 1) (Sauer, Hines & Fallon 2005).

In terms of breeding ecology, the two cuckoo species are quite similar, with breeding and foraging habitat consisting primarily of mixed deciduous-coniferous forests and pine and hemlock woodlands (Hughes 1999, 2001). In both species, nesting occurs primarily from late May through August, with a peak in June and July. In both species, males and

females contribute to nest-building, and clutch size is 2 to 3 eggs (rarely 4 or 5). Both

adults contribute to incubation during the 10 to 11 day incubation period, and both adults

brood and feed nestlings during the 6 to 7 day nestling period (Hughes 1999, 2001).

Foraging is done mainly in the canopy, and primary food items include Lepidopteran

adults and larvae, grasshoppers (Orthoptera), crickets (Gryllidae), katydids

(Tettigoniidae), and annual and periodical cicadas (Cicadidae) (Hughes 1999, 2001). The

black-billed cuckoo is more slender than the yellow-billed cuckoo (*C. erythropthalmus*:

28-31 cm length, 45-55 g versus *C. americanus*: 26-30 cm length, 55-65 g) (Hughes

1999, 2001), and although the species use similar breeding habitat, yellow-billed cuckoos

are behaviorally-dominant and more often nest in the forest interior, while black-billed

cuckoo nests are generally built along forest edges or in hedgerows or thickets (personal

observation; Hughes 1999, 2001).

Scarlet and summer tanagers are also long-distance Neotropical-Nearctic migratory

species, breeding in North America from early May to mid-August and wintering from

central America, south through southern Bolivia and Brazil, from September through

April (Robinson 1996; Mowbray 1999). The scarlet tanager breeding range extends from

northern Mississippi, Alabama, and Georgia, west to eastern Oklahoma, and north

through Minnesota and southern Manitoba and Ontario, and along the eastern seaboard

into northern Maine, New Brunswick, and Nova Scotia (Fig. 2). Summer tanager

breeding distribution lies south relative to its congener's range, extending from southern

Texas and the Gulf Coast states, north through Kansas and Iowa, and along the east coast

of the U.S. through Virginia and Maryland (Fig. 2). These two *Piranga* species breed

sympatrically throughout the central U.S., from the northern Gulf Coast states north through Missouri and east to Maryland.

The breeding ecology of scarlet and summer tanagers is also very similar, with breeding and foraging habitat consisting mainly of deciduous forest and pine-oak woodlands (Robinson 1996; Mowbray 1999). Both tanager species nest from early May through mid-August, with a peak in June. In both species, clutch size is generally 4, with a range of 3 to 5 eggs. Females incubate during the 10 to 11 day incubation period, and both adults feed nestlings during the 9 to 12 day nestling period (Robinson 1996; Mowbray 1999). Foraging is done in the canopy, and primary food items include Hymenopteran adults and larvae, Lepidopteran larvae, and spiders. The two tanager species are similar in size, with a body mass range of 25-30 g (Robinson 1996; Mowbray 1999), and although the species use similar breeding habitat, scarlet tanagers more often nest in large tracts of mature forest, while summer tanager nests may nest near forest gaps or edges. Interspecific competition for breeding territories has been inferred in these *Piranga* species by highly aggressive responses to experimental interspecific song playback by both scarlet and summer tanagers (Shy 1984).

Survey Data

As indices of annual population densities of yellow-billed and black-billed cuckoos and scarlet and summer tanagers, I used data from the U.S. Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2004, using data from a total of 28 physiographic regions incorporating 38 U.S. states and 7 Canadian provinces

(ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/; Sauer, Hines & Fallon 2005). I

present population models for each species only in areas of congeneric sympatry: for the

cuckoo species, this includes 26 BBS regions, and for the tanager species the area of

sympatry includes 14 BBS regions. Each physiographic region was defined as a

population, and annual population densities within each species were calculated as mean

number of individuals detected per survey route within a region within a year.

Climate Data

The mean of monthly values of the Southern Oscillation Index (SOI) from May through

April was used to represent annual ENSO conditions from 1966 through 2004

(www.cpc.ncep.noaa.gov/data/indices), and the winter NAO Index (mean of monthly

NAO Index values from December through March;

www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter) was used to represent annual

NAO conditions.

Population Models

To quantify the influences of congeneric population densities and climate on changes in

annual cuckoo and tanager population densities, I incorporated congener population

density, the Southern Oscillation Index, and the North Atlantic Oscillation Index into

models of population dynamics for each species (population sample sizes: yellow-billed

cuckoo $n = 26$, black- billed cuckoo $n = 26$, scarlet tanager $n = 14$, summer tanager $n =$

14 physiographic regions). I hypothesized that congener densities and climate would have

1-year lagged effects on annual population densities on the breeding grounds by

influencing a species' productivity in the previous year. I used density-dependent

autoregressive population models, which allow for examination of the strength of

previous population densities and other factors, such as climate, on annual population

densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_{t-1}) + b_2(Z_{t-1}) + \varepsilon_t \qquad (1)$$

where X_i are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates

of the strength of statistical intraspecific density dependence, b_1 quantifies the influence

of congener density, Y_{t-1} is congener density in year t-1, b_2 quantifies the influence of

climate on population density, Z_{t-1} is the Southern Oscillation Index or NAO Index in

year t-1, and ε_t represents the effects of other perturbations or stochastic effects not

accounted for by other variables in the model. Year was included as a covariate for all

populations displaying a significant temporal trend (Post & Stenseth 1999). First-,

second-, and third-order autoregressive models were tested to determine which best

predicted log annual population density for each population. I then included in the best-fit

model lagged terms for congener population density and ENSO or the NAO. Parameter

coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model

fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

Results

Results of my autoregressive population models indicated that most populations of all

four study species display first-order population dynamics; that is, a 1-year lagged effect

of within-species densities best predicted annual population densities (Tables 1 & 2). First-order autoregressive coefficients (1-year-lagged within-species effects) were negative (< 1) for all populations of all four species, as were all second- and third-order coefficients (2- and 3-year-lagged within-species effects) (Tables 1 & 2).

One-year lagged effects of congener densities on annual population dynamics were also negative (< 1) for almost all populations of all four species (the exception was a positive 1-year lagged effect of black-billed cuckoo density on yellow-billed cuckoos in the High Plains region (region 36)). That is, for almost all populations of all species, higher congener densities in one year were associated with decreased study species densities the following year (Tables 1 and 2).

Effects of ENSO and the NAO were variable among the four species, but these climate systems displayed similar geographic trends between species: ENSO occurred in best-fit population models in the central and north-central U.S. for all four species, and the NAO occurred in best-fit models in the southern and eastern U.S. and in the western prairie states (Figures 3 & 4). Model coefficients of the NAO parameter were negative for most populations of each species (high values of the NAO index led to 1-year lagged decreases in population density); for the yellow-billed cuckoo, two of the six NAO parameter coefficients were positive, as was the single significant NAO coefficient for a scarlet tanager population model (Tables 1 & 2). Two BBS regions exhibited effects of the NAO on multiple species: in the Black Prairie region (region 40), both yellow- and black-billed cuckoo populations were affected by the NAO; for both species, the NAO model

coefficient was negative. In the Highland Rim (region 14), the NAO had opposite effects on cuckoos and tanagers: for yellow-billed cuckoos, the NAO model coefficient was positive, while for summer tanagers the NAO coefficient was negative. ENSO also had opposite effects on the cuckoo and tanager species: ENSO model coefficients were positive for both tanager species (Table 2), but ENSO coefficients were negative for all but one population of one of the cuckoo species (Table 1).

In examining effects of both climate and congener densities on population densities, within the cuckoo species, yellow-billed cuckoos were negatively affected by black-billed cuckoo densities in eleven regions; of these eleven regions, four were also significantly affected by ENSO (regions 16, 17, 22, and 32), and three were affected by the NAO (regions 11, 12, and 40) (Table 1, Fig. 3a). In contrast, black-billed cuckoo populations were negatively affected by yellow-billed cuckoo densities in many regions in which climate did not impact black-billed cuckoo populations (a total of ten regions; Table 1, Fig. 3b). Within the tanager species, scarlet tanagers were most negatively affected by summer tanager densities in a region in which scarlet tanager densities were also impacted by ENSO (region 15; Fig. 4a). Summer tanager populations experienced negative effects of scarlet tanager density in six regions, and of these six regions, four were also strongly affected by climate: three by ENSO and one by the NAO (Table 2; Fig. 4b).

Discussion

Results of my population models indicate spatial variation in the effects of large-scale climate and congener densities on population densities of my study species across their breeding ranges. However, common patterns emerge for both *Coccyzus* and *Piranga* species. First, effects of ENSO were most pronounced in the central portion of the U.S. in the Midwest and Upper Midwest. In contrast, effects of the NAO are seen in the southern U.S., north along the East Coast, and in the western prairie states of Kansas and Colorado north through North Dakota.

Interestingly, ENSO and the NAO appeared to have opposite effects on cuckoos and tanagers. For all scarlet and summer tanager populations that were affected by ENSO, the ENSO coefficient in each population model was positive (that is, high values of the Southern Oscillation Index led to 1-year lagged increases in tanager populations). For the cuckoo species, however, ENSO coefficients were negative for all but one population (high values of SOI led to 1-year lagged decreases in cuckoo densities). In addition, in the one physiographic region in which both cuckoos and tanagers were affected by the NAO (the Highland Rim; region 14), the NAO had opposite effects on yellow-billed cuckoos and summer tanagers: the NAO model coefficient was positive for the cuckoo species, but negative for the tanager species. Such opposite effects of large-scale climate systems on species within different avian foraging guilds has been seen in other studies (Jonzen et al. 2002; Nott et al. 2002; Macmynowski et al. 2007); such differences may be due to varying effects of climate on specific avian prey species, although additional work is needed to test this hypothesis.

In examining relationships between the effects of both climate and congener densities on a species' population dynamics, for the *Coccyzus* species, the behaviorally-dominant yellow-billed cuckoo was affected by population densities of its sympatric congener primarily in regions in which yellow-billed cuckoos were also affected by climate: of the eleven regions in which yellow-billed cuckoos were negatively affected by black-billed cuckoos, seven regions were also affected by ENSO or the NAO. In contrast, black-billed cuckoo populations were negatively affected by densities of their congener in thirteen regions, only three of which also experienced effects of ENSO or the NAO. Within the *Piranga* species, both scarlet and summer tanagers experienced the greatest negative effects of congener densities in regions in which they were also affected by ENSO: the Lexington Plain (region 15) for scarlet tanagers, and the Till Plains (region 31) for summer tanagers.

Previous research has found that densities of some populations of yellow-billed cuckoos decline following warm winters (Anders & Post 2006). *Coccyzus* cuckoos are known to feed on the larvae of outbreaking Lepidopteran species such as gypsy moths *Lymantria dispar* L, and evidence indicates that such outbreaking Lepidopterans are more abundant after cold winters (Miller, Mo & Wallner 1989; Williams and Liebhold 1995; Myers 1998). Thus, in physiographic regions in which yellow-billed cuckoos show a lagged effect of annual climatic conditions (likely mediated by effects of food availability on population productivity), this normally behaviorally-dominant species may be more prone to competitive effects from its sympatric congener, relative to regions in which

yellow-billed cuckoo populations are not as highly-affected by climatic conditions. Although the *Piranga* species displayed opposite effects of ENSO and the NAO on population densities relative to the *Coccyzus* cuckoos (again, possibly indicating different effects of these two climate systems on food availability for these two genera), both scarlet and summer tanagers were similarly affected by a combination of climate and congener density, being more strongly negatively affected by their sympatric congeners in regions in which the species were also impacted by annual climatic variability.

Results of this study are similar to those found by Saetre, Post & Kral (1999), in which pied flycatchers were more strongly affected by interspecific competition with their sympatric congener, the collared flycatcher, in years following warm winters. However, while Saetre, Post & Kral (1999) found negative effects of the socially-dominant species, the collared flycatcher, on its sympatric congener, I found greater effects of the socially-submissive species, the black-billed cuckoo, on the population dynamics of its sympatric congener in regions in which yellow-billed cuckoos were also impacted by climate.

In summary, although I found spatial variation in the effects of large-scale climate and congener densities on *Coccyzus* and *Piranga* species, I found common patterns of effects of ENSO and the NAO on all four species, with ENSO having greatest effects in the Midwest and Upper Midwest of the United States, and the NAO having greater impacts in the southern and eastern U.S. and in the western prairie states. While the effects of climate and congener densities were unpaired for black-billed cuckoos, the behaviorally-dominant yellow-billed cuckoo was affected by congener densities to a greater extent in

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regions in which this species also experienced significant effects of climate. Both scarlet and summer tanagers experienced the greatest negative effects of congener densities in regions in which the species were also impacted by climate. Thus, increased effects of climate on resources such as food availability may act to increase the impact of indirect competition from sympatric congeners on these species. Additional field research with sympatric populations of these or other congeneric species may provide insights into the exact mechanisms by which climatic variability affects population densities. Such research is key in predicting the effects of increasing climate change on avian population and community dynamics.

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Table 1. Yellow-billed and black-billed cuckoo best-fit population models and model coefficients. Delta AIC values for each parameter indicate the decrease in model AIC (increase in model fit) contributed by that parameter.

BBS Region	Region Name	Yellow-billed Cuckoo (YBCU) Best-fit population model	Autoregressive coeffs (a1, a2, a3)	Congener coeff (b1)	ENSO coeff (b2)	NAO coeff (b2)	Best-fit AIC	Congener Δ AIC	ENSO Δ AIC	NAO Δ AIC
9	Glaciated Coastal Plain	AR(1)	0.415				20.23			
10	Northern Piedmont	AR(1)	0.590				8.27			
11	Southern Piedmont	AR(1) + BBCU + NAO	0.536	-0.347		0.024	-31.02	2.40		2.14
12	Southern New England	AR(1) + BBCU + NAO	0.122	0.156		-0.064	16.83	0.44		5.04
13	Ridge and Valley	AR(1)	0.342				-67.60			
14	Highland Rim	AR(3) + NAO	0.331, 0.066, -0.504			0.015	-75.14			2.89
15	Lexington Plain	AR(1)	0.182				-14.87			
16	Great Lakes Plain	AR(1) + BBCU + ENSO	0.321	-0.069	-0.051		-8.42	16.11	0.40	
17	Driftless Area	AR(1) + BBCU + ENSO	-0.091	0.224	-0.080		6.11	7.50	1.32	
18	St. Lawrence River Plain	AR(1)	0.318				7.28			
19	Ozark-Ouachita Plateau	AR(3)	0.422, 0.193, -0.457				-61.49			
20	Great Lakes Transition	AR(2) + BBCU	-0.087, -0.415	0.151			-14.75	6.65		
21	Cumberland Plateau	AR(2)	0.224, -0.269				-31.52			
22	Ohio Hills	AR(1) + BBCU + ENSO	0.135	0.003	-0.079		-14.83	0.44	3.14	
23	Blue Ridge Mountains	AR(1)	0.336				4.74			
24	Allegheny Plateau	AR(1) + BBCU	0.298	0.008			-6.47	1.30		
27	Northern New England	AR(1)	0.282				21.94			
28	N. Spruce-Hardwoods	AR(1) + BBCU	-0.047	0.284			31.66	6.46		
31	Till Plains	AR(1) + BBCU	0.469	0.007			-31.92	5.41		
32	Dissected Till Plains	AR(1) + BBCU + ENSO	0.703	-0.069	-0.033		-56.67	0.61	2.54	
33	Osage Plain-Cross Timbers	AR(1)	0.337				-79.64			
34	High Plains Border	AR(1)	0.232				-23.18			
35	Rolling Red Prairies	AR(2) + NAO	0.639, -0.329			-0.012	-62.88			0.45
36	High Plains	AR(1) + BBCU + NAO	-0.363	2.750		-0.082	12.71	5.16		4.60
37	Drift Prairie	AR(1)	-0.445				6.47			
40	Black Prairie	AR(1) + BBCU + NAO	0.443	0.190		-0.059	24.47	1.96		2.51

BBS Region	Region Name	Black-billed Cuckoo (BBCU) Best-fit population model	Autoregressive coeff (a1, a2, a3)	Congener coeff (b1)	ENSO coeff (b2)	NAO coeff (b2)	Best-fit AIC	Congener Δ AIC	ENSO Δ AIC	NAO Δ AIC
9	Glaciated Coastal Plain	AR(1)	-0.100				20.13			
10	Northern Piedmont	AR(1) + YBCU + NAO	-0.074	0.097		-0.062	35.96	0.44		2.00
11	Southern Piedmont	AR(3)	0.338, 0.517, -0.693				4.63			
12	Southern New England	AR(1) + YBCU	0.150	0.380			-2.44	10.45		
13	Ridge and Valley	AR(2) + NAO	0.803, -0.391			-0.019	-17.15			0.23
14	Highland Rim	AR(3) + YBCU	0.816, -0.872, 0.452	0.029			4.47	0.16		
15	Lexington Plain	AR(1) + YBCU	-0.175	0.001			19.71	2.02		
16	Great Lakes Plain	AR(1) + ENSO	0.106		-0.057		-30.04		2.32	
17	Driftless Area	AR(1) + YBCU	0.131	-0.089			-8.24	6.56		
18	St. Lawrence River Plain	AR(1) + YBCU	0.238	0.272			-35.79	4.78		
19	Ozark-Ouachita Plateau	AR(1) + YBCU + ENSO	-0.951	0.067	0.176		-11.00	6.65	6.62	
20	Great Lakes Transition	AR(2)	0.645, -0.252				-38.65			
21	Cumberland Plateau	AR(1)	-0.047				19.95			
22	Ohio Hills	AR(1) + YBCU	-0.113	0.030			9.76	0.36		
23	Blue Ridge Mountains	AR(1) + YBCU	0.270	-0.150			-1.85	4.93		
24	Allegheny Plateau	AR(1) + ENSO	0.459		-0.052		-13.02		0.87	
27	Northern New England	AR(1) + ENSO	0.282		-0.123		38.42		1.78	
28	N. Spruce-Hardwoods	AR(1) + YBCU	0.463	0.433			-6.80	3.71		
31	Till Plains	AR(1) + YBCU + ENSO	-0.264	0.031	-0.096		-2.00	9.01	3.77	
32	Dissected Till Plains	AR(1) + YBCU	0.063	0.099			-6.97	2.68		
33	Osage Plain-Cross Timbers	AR(2)	-0.040, 0.289				15.21			
34	High Plains Border	AR(1) + YBCU	-0.197	0.094			9.72	1.42		
35	Rolling Red Prairies	AR(1)	0.365				1.88			
36	High Plains	AR(1) + ENSO	0.058		-0.270		6.93		5.45	
37	Drift Prairie	AR(1)	0.544				13.35			
40	Black Prairie	AR(1) + NAO	0.696			-0.025	-5.55			0.37

Table 2. Scarlet and summer tanager best-fit population models and model coefficients. Delta AIC values for each parameter indicate the decrease in model AIC (increase in model fit) contributed by that parameter.

		Scarlet Tanager (SCTA)	Autoregressive coeffs	Congener coeff	ENSO coeff	NAO coeff				
BBS Region	Region Name	Best-fit population model	(a1, a2, a3)	(b1)	(b2)	(b2)	Best-fit AIC	Congener Δ AIC	ENSO Δ AIC	NAO Δ AIC
4	Upper Coastal Plain	AR(1)+SUTA	0.716	0.060			-103.2	-9.88		
5	Mississippi Alluvial Plain	AR(1)+ENSO	-0.609		0.053		-13.55		-0.74	
10	Northern Piedmont	AR(3)+ENSO	0.607, 0.385, -0.446		0.044		-75.43		-11.07	
11	Southern Piedmont	AR(1)	-0.156				-52.18			
13	Ridge and Valley	AR(1)	0.686				-100.02			
14	Highland Rim	AR(1)	0.378				-58.89			
15	Lexington Plain	AR(2)+SUTA+ENSO	0.216, 0.372	-0.042	0.042		-22.58	-1.11	-0.61	
19	Ozark-Ouachita Plateau	AR(1)+SUTA	0.226	0.033			-38.69	-5.62		
21	Cumberland Plateau	AR(1)	0.025				-68.69			
22	Ohio Hills	AR(1)	0.447				-63.31			
23	Blue Ridge Mountains	AR(2)+SUTA	0.438, 0.150	0.034			-69.26	-6.91		
31	Till Plains	AR(1)+SUTA	-0.089	0.779			-26.09	-0.59		
32	Dissected Till Plains	AR(2)+NAO	-0.056, 0.381			0.028	5.84			0.29
33	Osage Plain-Cross Timbers	AR(1)	0.328				3.83			

		Summer Tanager (SUTA)	Autoregressive coeffs	Congener coeff	ENSO coeff	NAO coeff				
BBS Region	Region Name	Best-fit population model	(a1, a2, a3)	(b1)	(b2)	(b2)	Best-fit AIC	Congener Δ AIC	ENSO Δ AIC	NAO Δ AIC
4	Upper Coastal Plain	AR(2)+SCTA+NAO	0.380, 0.156	0.076		-0.005	-142.48	-12.08		-1.01
5	Mississippi Alluvial Plain	AR(1)+SCTA	0.012	0.630			-39.16	-5.41		
10	Northern Piedmont	AR(1)	0.440				3.88			
11	Southern Piedmont	AR(1)	0.579				-102.32			
13	Ridge and Valley	AR(1)+SCTA+ENSO	0.411	0.052	0.023		-69.34	-4.92	-0.21	
14	Highland Rim	AR(1)+NAO	0.500			-0.008	-113.53			-1.23
15	Lexington Plain	AR(1)	0.373				-30.46			
19	Ozark-Ouachita Plateau	AR(2)+SCTA+ENSO	0.382, -0.413	0.042	0.015		-108.04	-1.24	-1.16	
21	Cumberland Plateau	AR(1)+SCTA	0.314	-0.002			-51.52	-0.30		
22	Ohio Hills	AR(1)+NAO	0.145			-0.032	-30.28			-4.45
23	Blue Ridge Mountains	AR(1)+NAO	-0.014			-0.036	8.47			-1.05
31	Till Plains	AR(1)+SCTA+ENSO	0.463	-1.420	0.067		15.92	-2.63	-0.27	
32	Dissected Till Plains	AR(1)	0.054				9.05			
33	Osage Plain-Cross Timbers	AR(2)	0.428, 0.296				-40.57			

Fig. 1. From Sauer et al. (2005): breeding range of (a) yellow-billed cuckoos (*Coccyzus americanus*) and (b) black-billed cuckoos (*C. erythropthalmus*) based on Breeding Bird Survey (BBS) data from 1994-2003. Darker areas refer to regions of higher density (density values in key refer to numbers of individual birds detected annually per BBS route).
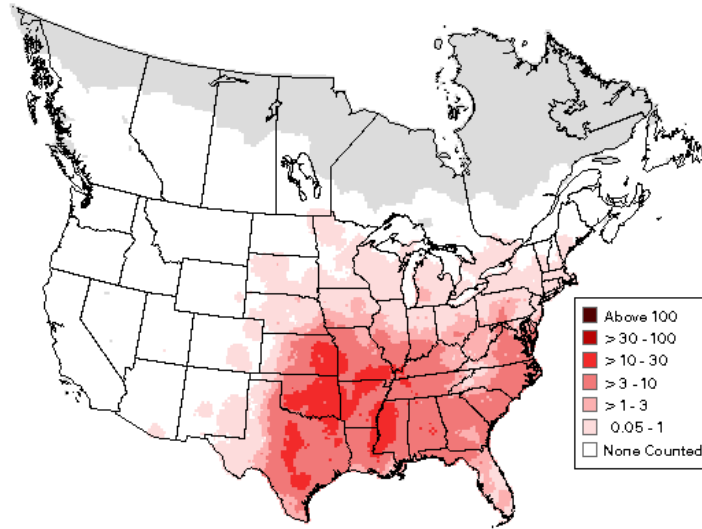
Fig. 2. From Sauer et al. (2005): breeding range of (a) scarlet tanagers (*Piranga olivacea*) and (b) summer tanagers (*P. rubra*) based on Breeding Bird Survey (BBS) data from 1994-2003. Darker areas refer to regions of higher density (density values in key refer to numbers of individual birds detected annually per BBS route).

Fig. 3. Parameters entering the best-fit population models for (a) yellow-billed cuckoos (*Coccyzus americanus*) and (b) black-billed cuckoos (*C. erythropthalmus*) for each physiographic region in which the congeners are sympatric. Dark gray indicates a negative congener coefficient in the best-fit model. Diagonal hatching indicates an ENSO coefficient, and horizontal hatching an NAO coefficient, in the best-fit population model for that region. Light gray indicates the remaining areas of sympatry (background map of BBS physiographic regions from Sauer et al. (2005)).

Fig. 4. Parameters entering the best-fit population models for (a) scarlet tanagers (*Piranga olivacea*) and (b) summer tanagers (*P. rubra*) for each physiographic region in which the two species are sympatric. Dark gray indicates a negative congener coefficient in the best-fit model. Diagonal hatching indicates an ENSO coefficient, and horizontal

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hatching an NAO coefficient, in the best-fit population model for that region. Light gray indicates the remaining areas of sympatry (background map of BBS physiographic regions from Sauer et al. (2005)).

Fig. 1.

a. yellow-billed cuckoo
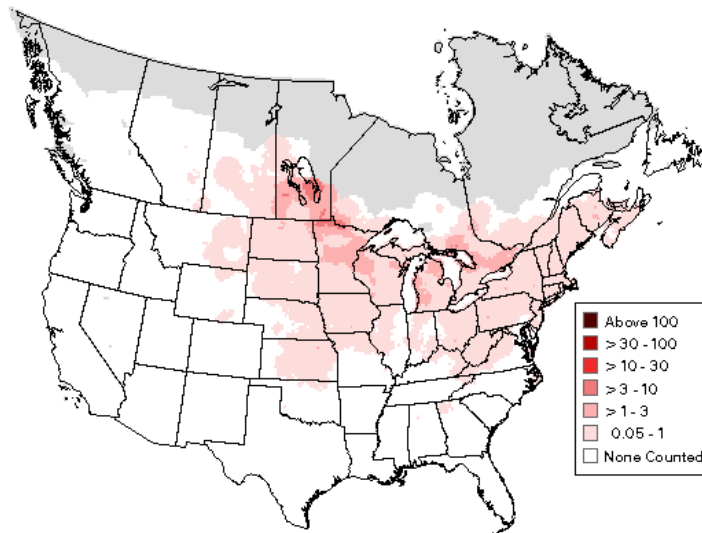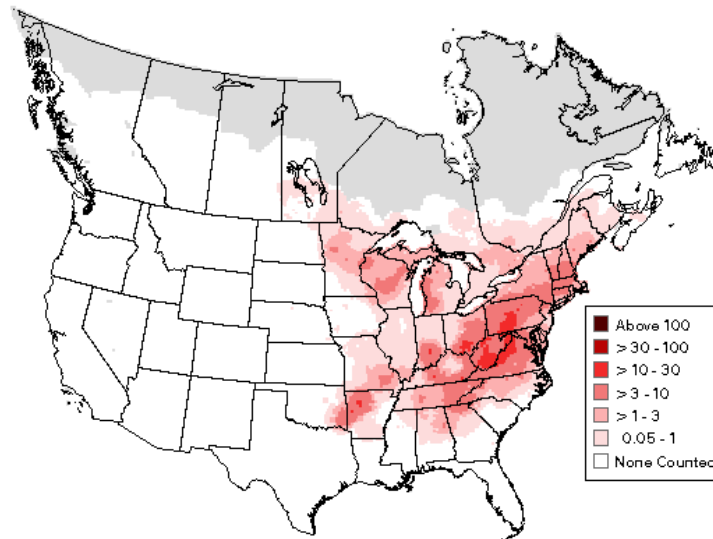

b. black-billed cuckoo
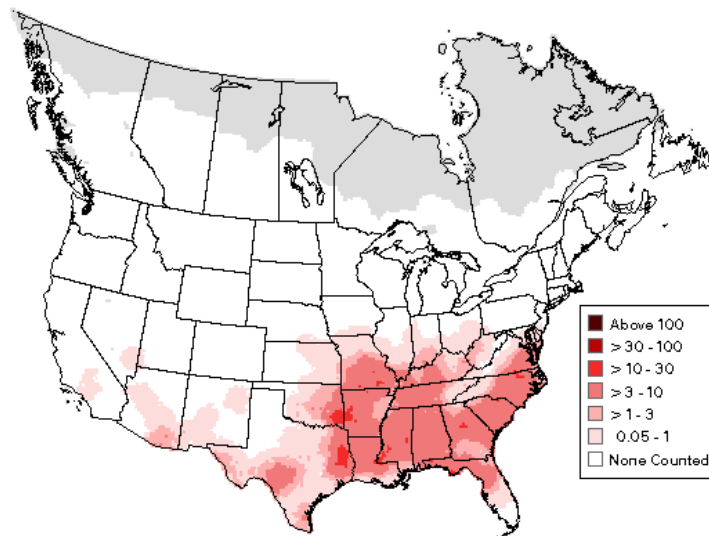
Fig. 2.

a. scarlet tanager
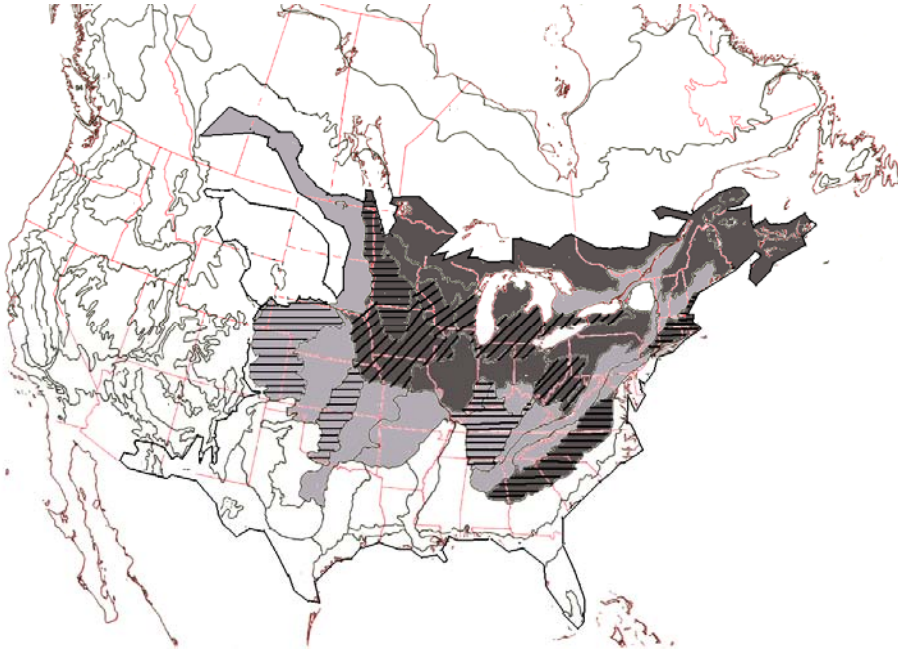

b. summer tanager
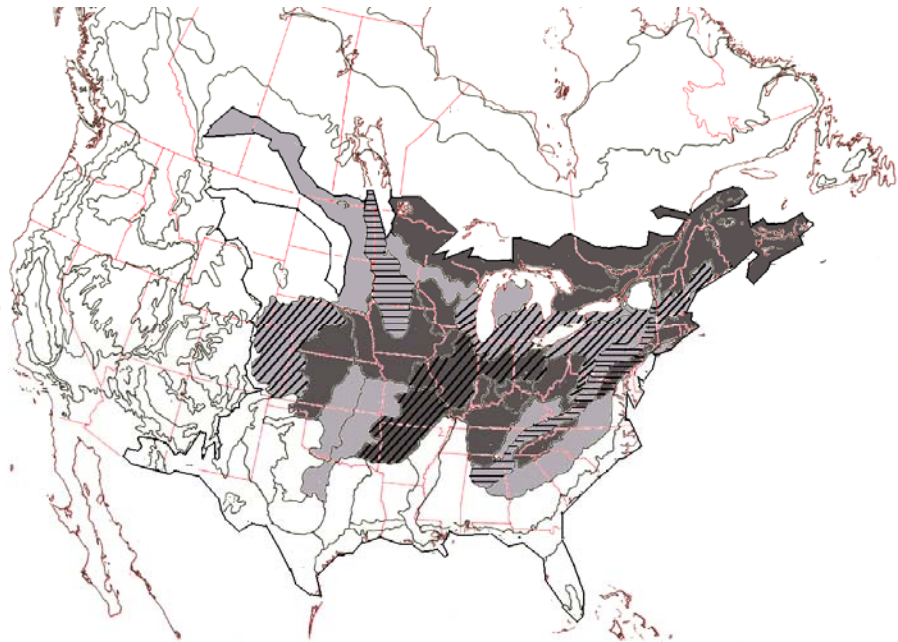
Fig. 3.

a. yellow-billed cuckoo
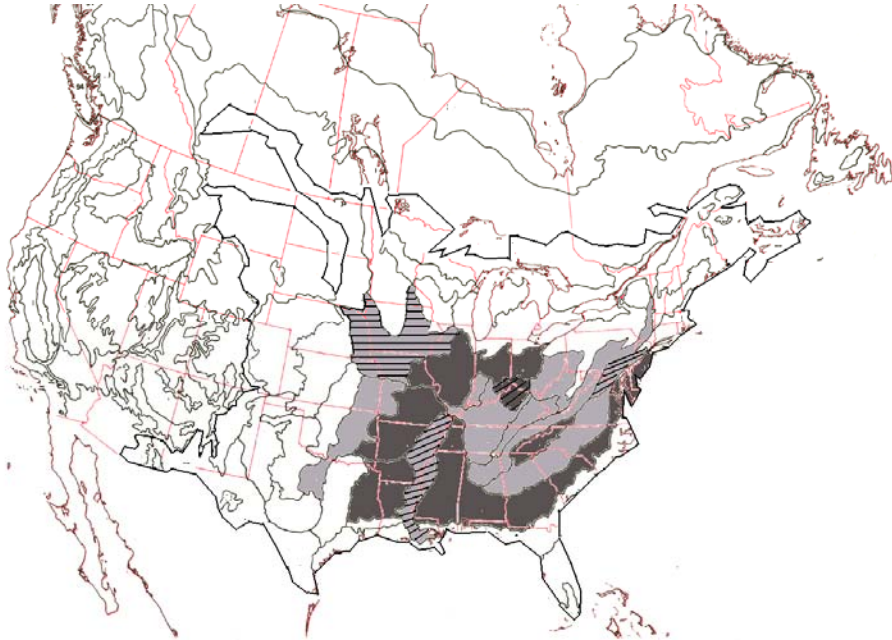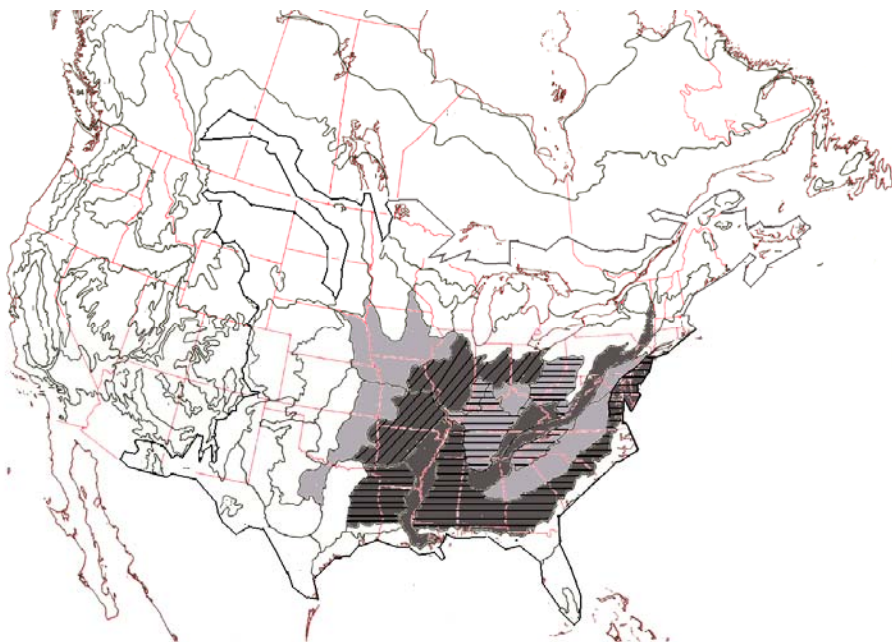

b. black-billed cuckoo

Fig. 4.

a. scarlet tanager

b. summer tanager

Chapter 6

CONCLUSIONS

The research presented here is the first to examine effects of large-scale climate on North American landbirds across species' breeding distributions. Distribution-wide analyses of long-term avian survey data in conjunction with long-term climate data allow for examination of climatic effects on annual population densities, and do so without effects of juvenile recruitment potentially masking population density changes. In addition to elucidating effects of climate on a suite of long-distance migratory species, these analyses have also allowed for comparisons of climatic effects on Neotropical-Nearctic and North American resident landbird species to determine whether warmer winter temperatures more strongly affect migratory species, potentially through mechanisms of trophic mismatch. Finally, these analyses have allowed for examination of potential indirect effects of climate on North American landbird species, through increases in interspecific competition between sympatric congeners, again at the scale of species' breeding distributions.

Through autoregressive population modeling, using Breeding Bird Survey data and indices of the North Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO) from 1966-2002, in Chapter 2 I found 1-year lagged relationships between both of these large-scale climate systems and annual population densities of the yellow-billed cuckoo (*Coccyzus americanus*). Geographic variation in the strength of the NAO and ENSO on cuckoo populations was underlain by geographic variation in the effects of these climate systems on local temperatures. Importantly, I also found that the strength of the effect of local temperatures on populations was predictive of long-term population

decline, with those populations that are more negatively affected by warm temperatures experiencing steeper declines over a 37-year period.

In a similar way, the results of Chapter 3 indicate that 1-year lagged relationships also exist between the NAO and ENSO and annual population densities of 11 additional North American landbird species, including shrub- and forest-nesting Parulidae, *Vireo*, and Fringillidae species throughout their North American breeding ranges. As was found for yellow-billed cuckoos, geographic variation in the effects of ENSO was related to geographic variation in the strength of the effect of this climate system on local weather, including local temperatures for 7 of the 11 species, and local precipitation for 2 of the species studied. Results of these analyses also indicate that for 4 of the 5 study species that have declined significantly over the past 39 years, there is a relationship between the strength of the effect of local temperatures on annual population densities and the magnitude of population decline. Overall, results of this chapter indicate that warbler species (Parulidae) may be more sensitive to effects of changes in climate than are *Vireo* or Fringillidae species, and that shrub-nesting species may be affected to a greater extent than are forest-nesting landbirds.

Results of Chapter 4 suggest that long-distance Neotropical-Nearctic migratory landbird species may have been more negatively affected by warm winter temperatures across their breeding ranges over the period 1966-2004 than were closely-related North American resident or short-distance migratory species. These results may provide support for the hypothesis that differences in climatic effects on long-distance migratory and

resident species may follow from greater trophic mismatch for long-distance migrants that are unable to time their migration to the breeding grounds in response to earlier peaks in the availability of food resources. Although additional research is needed, however, on the mechanisms by which Neotropical-Nearctic migratory landbird species are more strongly affected by climate and local temperatures.

Finally, the results of Chapter 5 indicate that 3 of the 4 species studied were more highly affected by sympatric congener densities in areas in which the species were also affected by large-scale climate. Effects of climate and sympatric congener densities were unpaired for black-billed cuckoos (*Coccyzus erythropthalmus*), but yellow-billed cuckoos were affected by congener densities to a greater extent in regions in which yellow-billed cuckoo densities were also affected by ENSO or the NAO. The two sympatric tanager species, scarlet and summer tanagers (*Piranga olivacea* and *P. rubra*), both experienced the greatest negative effects of congener densities in regions in which the species were also affected by climate, with summer tanagers in particular exhibiting stronger congener effects in regions in which summer tanagers are more strongly affected by ENSO. Results of this chapter thus indicate that increased effects of climate on resources such as food availability may increase the effect of competition from sympatric congeners on North American landbird species.

Overall, the results of this research indicate that North American landbird densities are affected by annual changes in large-scale climate, such that continued increases in global temperatures have the potential to affect long-term changes in landbird population

densities on the continent. Use of long-term, distribution-wide avian survey data allowed

for elucidation of the effects of large-scale climate that had not, previously, been evident

from field studies conducted at restricted local scales. Additional field research on the

mechanisms by which climate affects landbird population densities, and an understanding

of the limiting effects of climate on additional North American species, are critical in an

environment of increasing climate change.

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