Université d'Ottawa · University of Ottawa

# Université d'Ottawa · University of Ottawa

FACULTÉ DES ÉTUDES SUPÉRIEURES
ET POSTDOCTORALES

FACULTY OF GRADUATE AND
POSTDOCTORAL STUDIES

Tania Teresa SENDEL
AUTEUR DE LA THÈSE - AUTHOR OF THESIS

M. Sc. (Biology)
GRADE - DEGREE

Department of Biology
FACULTÉ, ÉCOLE, DÉPARTEMENT - FACULTY, SCHOOL, DEPARTMENT

TITRE DE LA THÈSE - TITLE OF THE THESIS

Is Climate Responsible for Local Changes in Passerine Abundance in North America?

D. Currie
DIRECTEUR DE LA THÈSE - THESIS SUPERVISOR

CO-DIRECTEUR DE LA THÈSE - THESIS CO-SUPERVISOR

EXAMINATEURS DE LA THÈSE - THESIS EXAMINERS

P. Catling
L. Fahrig
J. Kerr

J.-M. De Koninck, Ph.D.
LE DOYEN DE LA FACULTÉ DES ÉTUDES SUPÉRIEURES ET POSTDOCTORALES
DEAN OF THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

# Is climate change responsible for local changes in passerine abundance in North America?

Tania Teresa Sendel

Thesis submitted to the Faculty of Graduate and Post-doctoral Studies, University of Ottawa, in partial fulfillment of the requirements for the M.Sc. degree in the

Ottawa-Carleton Institute of Biology
Ottawa, Ontario, Canada
May, 2004

Supervisor

Candidate

Université d'Ottawa · University of Ottawa

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

*Your file Votre référence*
*ISBN: 0-494-01601-9*
*Our file Notre référence*
*ISBN: 0-494-01601-9*

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

## Acknowledgements

I would like to thank my supervisor Dr. David J. Currie for his guidance and support. Thank you to my committee members, Drs. Paul Catling, Lenore Fahrig, Charles Francis, and Jeff Houlahahn, who offered insight and direction. A special thank you to Dr. Anthony Francis who provided useful advice on both the conceptual framework and practicalities of obtaining my data, and who saved me an enormous amount of grief by writing code to automate the calculation of the trend data and associated stats. Thank you to Dr. Jeremy Kerr who bailed me out when I needed saving and who was always ready with useful tips. I owe great thanks to Dr. Gajewski for his advice and for suggesting that I use climate data from the University of Delaware Center for Climatic Research. Thank you to the Canadian Wildlife Service and the United States Geological Survey who jointly administer the North American Breeding Bird Survey, for the bird data. And of course thank you to all my labmates who provided feedback and encouragement.

Funding for this work was provided through an NSERC grant to Dr. David J. Currie.

# Abstract

Human impacts such as habitat loss, species invasions and climate change are thought to be leading to biodiversity losses. However, little is known about the relative magnitudes of these effects. The purpose of this study is to determine to what extent climate change may have been responsible for observed changes in avian species' abundances. I investigated this question using data from the North American Breeding Bird Survey, one of the largest and most comprehensive biodiversity databases available. I found that 40% of the bird populations studied show significant linear changes in abundance from 1970 to 1999. Over the same period, temperature shows significant linear changes at 13% of the survey routes studied, whereas precipitation does not show significant trends. I analyzed the spatial relationships between abundance and climate and found that they are not strong (median $R^2 = 0.119$) but are generally consistent through time. Temporal trends in abundance were only very weakly related to trends in either temperature or temperature sub-optimality from 1970 to 1999. I found that temperature change is spatially autocorrelated over very long distances, whereas abundance change is autocorrelated over much shorter distances. Observed abundance changes in bird abundance are more likely to reflect local processes such as habitat modification.

# Résumé

La littérature suggère que les impacts des êtres humains sur l'environnement tels que la perte d'habitat, les invasions d'espèces exotiques et les changements climatiques peuvent engendrer des pertes de biodiversité. Cependant, l'importance relative de ces effets est peu connue. Le but de cette étude est de déterminer jusqu'à quel point les changements climatiques sont responsables des variations observées dans l'abondance des espèces aviaires. J'ai examiné la question en utilisant des données provenant du Relevé des oiseaux nicheurs (BBS) de l'Amérique du Nord, une des bases de données biologiques les plus importantes et les plus détaillées disponibles. J'ai trouvé que 40% des populations d'oiseaux étudiées montrent des variations linéaires en abondance entre 1970 et 1999. Au cours de la même période de temps, la température présente des changements linéaires significatifs pour 13% des routes du Relevé étudiées tandis que les précipitations ne présentent pas de tendances significatives. J'ai analysé les relations spatiales entre l'abondance et le climat et, j'ai trouvé qu'elles ne sont pas très fortes ($R^2$ médian = 0.119), mais généralement semblables dans le temps. Les tendances temporelles en abondance ne sont quasiment pas reliées aux tendances de la température ou de la température sub-optimale de 1970 à 1999. J'ai trouvé que les changements de température sont spatialement autocorrelés sur de très grandes distances, tandis que les changements en abondance sont autocorrelés sur de plus petites distances. Les variations en abondance observées reflètent fort probablement des processus locaux comme, par exemple, des modifications de l'habitat.

# Table of Contents

# Introduction

Species are currently disappearing at 50 – 100 times the natural rate, and this rate is expected to rise dramatically in the future (Secretariat of the Convention on Biodiversity 2000). Biodiversity is currently thought to be threatened by habitat fragmentation and loss, ozone depletion, climate change, toxic chemicals, and a variety of other threats (Secretariat of the Convention on Biodiversity 2000; Czech 2000). The Convention on Biological Diversity signatories commit to take steps to preserve their biodiversity, and a first step toward protecting biodiversity is to determine the relative magnitude of threats to it (Secretariat of the Convention on Biodiversity 2000). To accomplish this, one must test how biodiversity changes in response to changes in hypothesized threats in natural systems. One can then develop and test predictive models of the response of biodiversity to changes in threat levels. The purpose of this study is to determine what portion of the variance in avian abundance can be related to changing climate.

Climate has changed significantly over the past century and changes are accelerating. Global surface temperatures increased by 0.6 ± 0.2°C during the 20th century (IPCC 2001). Temperatures in the Northern Hemisphere increased more during the 20th century than during any other century in the last millennium. The 1990s were the warmest decade of the millenium (IPCC 2001). Although climate has generally warmed over the past century, climate change patterns have varied spatially across the globe. The largest increases in temperature occurred over mid- to high- latitudes of the Northern Hemisphere (IPCC 2001). Climate changes have also varied on a more regional basis, with some regions warming and others cooling. In Canada, the Mackenzie Basin warmed

1.8°C between 1895 and 1993, whereas the eastern Arctic Archipelago cooled 1.0°C between 1946 and 1993 (Minister of Public Works and Government Services 1996). However, including areas of regional cooling, global mean surface temperatures are projected to increase between 1990 and 2100, from 1.4 to 5.8°C (IPCC 2001).

This projected increase in global mean surface temperatures is predicted to lead to changes in precipitation, since temperature increase alters atmospheric circulation, activates the hydrologic cycle, and increases atmosphere moisture (IPCC 2001). Continental precipitation has already increased by 5-10% during the 20th century in the Northern Hemisphere. However, some parts of the Northern Hemisphere experienced a decrease in precipitation, and in the subtropics, rainfall appears to have decreased by 3% overall (IPCC 2001). Interestingly, projections for precipitation changes are less certain than projections for temperature changes. Regional precipitation projections vary from +20% to –20% during this century (IPCC 2001).

Species' responses to historical climate change have varied dramatically, from distribution changes to mass extinctions (Webb 1992). For example, severe climate changes between 12,000 and 10,000 years ago (temperature increased between 3°C and 6°C: Webb et. al 1987) coincide with the extinction of spruce parkland and several large mammal species in North America (Webb 1992). Holocene pollen records that show European trees spread from their glacial refugia at rates ranging from close to no movement for *Pinus* and *Larix* to rates of 2 km/year for *Alnus* (Huntley and Birks 1983), in response to atmospheric warming.

Recent biological effects of climate change have also been documented. Changes in phenology, physiology, range and distribution have been related to temperature change since the 1970s (Korner and Walther 2001). Root et al. (2003) performed a meta-analysis of 143 studies that span at least ten years and show changes in both species trait and temperature over time. According to a table of a subset of these studies in Schneider and Root (2002), these studies show changes in mammals, birds, invertebrates, amphibians, reptiles, fish, vascular plants, mountain plants, reptiles, trees, shrubs, grasses, and forbs. For each species included in the analysis, a qualitative expected response to temperature change was established, including changes in density, range (shifts poleward or to higher elevation), phenology, morphology, or genetic frequencies were considered. Of over 1,473 species that showed a change in a given trait over time, 81% changed in the expected direction given the temperature change observed.

There are many other examples of species changes coinciding with climate changes. Parmesan et al. (1999) found that many European butterfly species have moved northward and up mountains concomitant with warming over the last 30 – 100 years. Also in Britain, mobile butterflies that are habitat generalists were shown to have increased their ranges between 1970 and 1999 in response to warming (Warren et al. 2001). European bird species richness was found to be changing in response to climate change, with warmer winters likely providing an advantage to resident species over migrants (Lemoine and Böhning-Gaese 2003). In temperate regions, some birds have been laying their eggs earlier in the spring in response to warming climate (Both and Visser 2001, Brown et al. 1999, Forchhammer et al. 1998). A set of British bird species moved north by an average of 18.9 km between 1968-72 and 1988-91 time periods (Thomas and Lennon 1999). Thus, there is ample evidence that shifts in populations related to climate can be detected.

The purpose of this study was to determine to what extent directional changes in North American bird abundances can be related to changes in regional climate, relative to the set of other variables that may influence abundance. In other words, given that many variables can potentially lead to directional change in species' abundance, is climate change a major factor, or a relatively minor one? To address this, I asked a series of subsidiary questions. First, to what extent have local bird abundances changed in a directional manner (i.e., long-term change in average abundance, as opposed to year-to-year variance) in North America? To what extent did local temperature and precipitation also change directionally? In addition to simple climate trends, I calculated climate trends relative to each species' optimum temperature and precipitation, and I determined whether these trends are significant. Next, I asked how much of the spatial variation in abundance can be related to the spatial variation in climate, and given predictable spatial relationships between abundance and climate, I expected these relationships to remain unchanged through time. Furthermore, I expected species whose spatial variation in abundance is strongly related in climate also to show strong abundance – climate relationships through time. Finally, I asked how much of the variation in temporal abundance trends can be related to climate or climate sub-optimality trends between 1970 and 1999, and whether those trends are spatially autocorrelated over similar spatial scales. This study is designed to document the empirical relationships between abundance and climate that could be used to predict changes in abundance.

## Methods

### *Data*

Bird abundance data were obtained from the North American Breeding Bird Survey (BBS) (Patuxent Wildlife Research Center 2002). This annual survey was started in 1966 to track the status and trends of North American bird populations. Carried out by skilled volunteers, the BBS surveys over 4100 routes in the US and Canada. Each route is ~40 kilometers in length and located along secondary roads. Between May and July, surveyors of a route make 50 three-minute stops at ~0.8 kilometer intervals and record the total number of individual birds heard or seen at each stop (Patuxent Wildlife Research Center 2002). The data are one of the most comprehensive biodiversity databases available today.

From this dataset, I extracted species identification numbers, route numbers, route starting point latitudes and longitudes, and the number of individuals of each species detected at each route, from 1970 through 1999. Data prior to 1970 were eliminated because the survey was not geographically widespread during its first years. Data after 1999 were eliminated because appropriately mapped climate data were not yet available. I included all routes (n=1071) that had been censused for at least 24 of the 30 years in the study period (Fig.1).

Of the ~680 species of birds represented in the BBS database, I included only species within the Order Passeriformes (passerines, mostly songbirds) because these are the species most reliably censused with BBS protocols. I further restricted analysis to those Passeriformes with relatively broad spatial ranges – present on at least 20% of the 1071 routes included in the analysis – since these species are likely to be found over a wide enough range of climatic conditions to establish climate-abundance relationships. Consequently, a total of 89 species of Passeriformes (out of 327) were retained in the study (Appendix A).

Temperature and precipitation data were taken from *Terrestrial Air Temperature and Precipitation: Monthly and Annual Time Series (1950 – 1999) Version 1.02* (Willmott and Matsuura 2001), downloaded from the Center for Climatic Research, Department of Geography, University of Delaware website. This data set provides spatially-interpolated climate data corrected for elevation differences on a 0.5° by 0.5° grid, and it is cross-validated for interpolation accuracy at each weather station. Using ArcMap, each BBS route was assigned a temperature and precipitation value for each year included in the study, based on the gridded climate data at the start of the BBS route.

I estimated the linear temporal trends in temperature, precipitation, and abundance based on mean spring (May – July) values from 1970 through 1999. Abundance trends were calculated for each species at each BBS route on which it was observed. Temperature and precipitation trends were calculated for each BBS route.

For each of the 89 species included in the study, I also calculated temperature and precipitation optima based on data from 1970 to 1984 (the first 15 of 30 years included in the study). Optima were calculated as the mean temperature and precipitation at which the species occurred, weighted by the species' abundance at each site. I then calculated, for each species on each BBS route on which it was observed, the absolute (unsigned) difference between the species' optimum temperature and the observed temperature. I refer to this difference as temperature sub-optimality. Precipitation sub-optimality was calculated similarly. I then estimated the linear temporal trends in temperature and precipitation sub-optimality for each species on each route over the entire study period. Thus, a positive slope for the relationship between temperature sub-optimality and time indicates that conditions on a route are moving away from the optimum temperature for a given species (Fig. 2).

Data were transformed as necessary to yield approximately symmetrical distributions. I transformed BBS abundance data as $x' = \log_{10}(x+0.5)$. Although temperature data are not normally distributed, no transformation significantly improves their distribution. Precipitation data were transformed as $x' = x^{0.75}$.

The magnitude of spatial autocorrelation was measured with Moran's I, using Rookcase, a GIS add-on program (Sawada 2002).

## Results

### *Abundance and Climate Trends*

I first tested whether local bird abundances changed detectably on BBS routes between 1970 and 1999. Nearly 40% of the 56,425 species observations on a given BBS route showed statistically significant linear trends in abundance through time ($p \leq 0.05$). The slopes of the abundance changes over time range from -0.0941 to +0.128 individuals per route per year (Fig. 3). Thus, local bird abundances clearly have been changing over the study period.

Has climate also changed detectably over the same period? I found that 13.4% of the 1071 linear relationships between temperature and time are statistically significant (at $p \leq 0.05$) even over this relatively short time period. Slopes of regressions of temperature as a function of time range from -0.0651 to +0.131 °C/year (Fig. 4a). Significant temperature trends are found mainly on coastal routes (Fig. 5). Warming trends are predominant on northwest coastal and eastern routes, whereas cooling trends are predominant on western and central routes (Fig. 5).

A total of 8.65% of the 56,425 linear relationships between temperature sub-optimality and time are statistically significant at $p \leq 0.05$. The slopes of the regression lines for temperature sub-optimality changes over time range from -0.163 to +0.163 °C/year (Fig. 6a). Temperature is becoming more favourable (approaching optimal value) for about half the populations in North America.

Directional precipitation changes detectable over this time period are rare. Only 6.44% of the 1071 linear relationships between precipitation and time are statistically significant ($p<0.05$). The slopes of the regression lines for precipitation changes over time range from -0.768 to +0.538 $mm^{0.75}$/year (Fig. 4b). Significant precipitation trends are found predominantly on small pockets of eastern and western coastal routes (Fig. 7). Spatial patterns among routes generally becoming wetter and drier are weak, however western routes are predominantly becoming wetter (Fig. 7).

Only 4.75% of the 56,425 linear relationships between precipitation sub-optimality and time are statistically significant ($p<0.05$). The slopes of the regression lines for precipitation sub-optimality changes over time range from -0.821 to +0.871 $mm^{0.75}$/year (Fig. 6b).

Since 5% of the trends are expected to be statistically significant due to chance alone, the observed precipitation and precipitation suitability trends that are significant may be due to chance alone. Although the distribution of precipitation change is non-random, this study does not consider precipitation further.

### *Spatial Relationship between Abundance and Temperature*

If climate change were a main driver of change in bird abundance, then one would expect the spatial variation in the abundances of individual species among routes to depend strongly upon temperature. To test this possibility, I fitted a second-degree polynomial model of the average species' abundances on a route (1970 – 1974) as a function of the average temperature (1970 – 1974). Not surprisingly, these species-level relationships between pooled abundance and temperature are generally either peaked or monotonic positive (Fig. 8). $R^2$ values range from 0.00361 to 0.568, with a median of 0.119 (Fig.9); 96.6% of the models are significant at $p<0.05$. Such low $R^2$ values indicate that relatively little of the spatial variation in abundance for individual species is related to the spatial variation in temperature.

One would also expect that abundance-temperature relationships through space remain unchanged through time. To test this, I pooled abundance and temperature data based on the last five years of the study period, 1995 – 1999, and again fitted abundance to a second-degree polynomial function of temperature. These $R^2$ values range from 0.0115 to 0.567, with a median of 0.114. The correlation between the $R^2$ values obtained in each of the two time periods at the start and end of the study period was strong ($r = 0.803$, $n = 89$, $p < 10^{-5}$; Appendix B provides values for each species and each time period). Thus, the relationships between abundance and temperature are weak but generally consistent in form through the study period.

To test whether the parameters of the abundance – temperature relationship are consistent through time, I added a dummy variable to represent the two time periods (0 for 1970 – 1974, 1 for 1995 – 1999) to the second-degree polynomial model:

$$\begin{aligned}\text{Abundance} &= c_0 + c_1{*}\text{Temperature} + c_2{*}\text{Temperature}^2 + c_3{*}\text{Dummy} + \\ &\quad c_4{*}\text{Dummy}{*}\text{Temperature} + c_5{*}\text{Dummy}{*}\text{Temperature}^2\end{aligned} \tag{1}$$

I ran this model stepwise backward to obtain the best model fit for each species. According to the significance of the $c_3$, $c_4$, and $c_5$ coefficients in the models, the y-intercept ($c_3$) changed for 39% of the species, the slope at the y-intercept ($c_4$) changed for 70% of the species, and the point of inflection (often temperature at maximum abundance) ($c_5$) changed for 50% of the species. Changes were evenly split between increases and decreases. Overall, subtle but statistically significant changes in the relationship between abundance and temperature were detected between the two time periods for eighty-nine percent of the species studied.

Finally, if climate change were a main driver of changing species abundance, then species whose abundances covaried strongly with temperature through space should also show changes in abundance related to temperature change over time. For each species, I correlated the explained variance (Pearson $r^2$) in the relationship between abundance and temperature over time (1970 – 1999) with the explained variance in the relationship through space ($R^2$). I did this using both the 1970 – 1974 and 1995 – 1999 periods, with similar results: there is little correlation between the strength of spatial and temporal abundance – temperature relationships. Which variables do predict whether a given species responds to change in temperature? I found no obvious reasons for differences between species, based on migratory status, diet, number of broods, nest location, family, or ecoregion (analyses not shown).

### ***Relationships between Abundance and Temperature Trends***

With approximately 40% of species-routes showing significant changes in abundance, 13% of routes showing significant changes in temperature, and 9% of routes showing significant changes in temperature sub-optimality over time, are these changes related?

Trends in bird abundance are apparently largely unrelated to climate trends (Fig. 10). Considering all species on all routes, I found only a very weak linear relationship between the magnitude of abundance trends and temperature trends ($r = -0.020$, $p < 10^{-5}$, $n = 56{,}425$: Fig. 11a). Nor did I find a linear relationship with temperature sub-optimality trends ($r = 0.061$, $p < 10^{-5}$, $n = 56{,}425$: Fig. 11b).

However, the relationship between temporal abundance and temperature/temperature sub-optimality trends may differ among species. I therefore examined the correlation between the abundance trends and the temperature trends, species by species, considering all BBS routes each species was observed. In no case did the rate of climate change account for >2.4% of the variation in the rate of abundance change (Fig. 11a). Change in temperature sub-optimality explained similarly little variance in the abundance trend (Fig. 11b).

There is, nonetheless, a signature of climate change on bird abundance: many more of the temperature change – abundance change correlations are significant than would be expected by chance in a set of 89 comparisons (one per species). The distribution of p values from a set of correlations based on randomly generated data is expected to be uniform. Observed p values for the Pearson correlations between abundance slopes (as functions of time) and both temperature slopes (Fig. 12a) and temperature sub-optimality slopes (Fig. 12b) deviate from uniform distributions, with disproportionately many p values below 0.1 (Komolgorov-Smirnov test for uniform distribution, $p < 10^{-5}$) for both temperature and temperature sub-optimality)

Even though significant correlations are abundant, they are not stronger than one would expect by chance. I first Fisher transformed the r values as $r' = \ln[(1+r)/(1-r)]$ (Zar 1984) to approximate a normal distribution. I then tested the difference between the observed distribution of r′ and an expected normal distribution of r′ with a mean of zero (Fig. 11). Correlations between slopes of abundance trends and temperature trends (Fig. 11a) are slightly more negative than one would expect by chance (mean $r = -0.0294$, $t = -3.15$, $p = 0.002$, $n = 89$). This suggests that there was a slight tendency, among species, for abundance to decrease as temperature increased (or vice-versa) between 1970 and 1999. Correlations between slopes of abundance trends and temperature sub-optimality trends (Fig. 11b) do not differ significantly from the expected distribution (mean r = 0.0150, t = 1.46, p = 0.147, n = 89). This result, along with a non-significant Lilliefors test (p = 0.212) suggests that there was no tendency, among species, for abundance to increase or decrease as temperature tended away from or toward each species' optimum temperature, between 1970 and 1999.

Furthermore, if climate change were a main driver of change in bird abundance, then one would expect the two variables to show similar spatial autocorrelation through space. Both the rates of climate change and abundance change are spatially structured (Fig. 13). However, of the 89 species included in this study, only seven have temporal trends in abundance that are spatially autocorrelated at a similar or larger scale than temperature. Most are spatially autocorrelated on a much smaller scale (Fig. 14).

## Discussion

Bird abundances and temperature are both changing, and species clearly do respond to temperature. Much evidence exists for shifts in species' phenology, physiology, range and distribution, and even extinctions, coinciding with temperature change (Root et al. 2003; Webb 1992; Parmesan et al. 1999). As in earlier work, we could detect a response to climate change in many species' abundance trends (39% with temperature and 37% with temperature sub-optimality).

However, if the question is not whether climate change effects are detectable, but whether they account for a biologically significant amount of the variation in species' abundances, then the answer appears to be no. Changes in North American passerine abundances over broad spatial scales are only very weakly related to temperature changes between 1970 and 1999, and this is the period during which most climatic changes due to human activities have been observed. This suggests that other factors affect avian abundances more strongly. For example, habitat loss and modification, competition with exotic species, sensitivity to pesticides or atmospheric pollutants, etc. could all be more important causes of abundance changes (Vitousek 1994, Ceballos and Ehrlich 2002).

This does not mean that climate change may not become a major environmental concern. Climate change has the potential to greatly affect terrestrial and aquatic ecosystems, forestry, agriculture, and global economics. For example, global warming has caused polar ice caps to melt and sea levels to rise 10 – 15 cm since 1900 (Claussen et al. 2001). Increased frequency and intensity of storms, hurricanes, droughts, and floods have been attributed to global climate change, and future climate changes are predicted to be greater than those in the recent past (IPCC 2001). Adverse effects of natural and human-induced climate change are even recognized as important threats to global geopolitical stability (United Nations Environment Programme 2001).

These results do suggest, however, that global warming to date has been responsible for little of the observed changes in avian abundances in recent decades, either as a direct relationship, or relative to each species' preferred temperature. Based on the spatial autocorrelation of changes in bird abundance, these changes are more likely to be due to local processes such as habitat modification than temperature change.

These results also suggest that models using temperature projections and species temperature preferences (e.g. Pounds and Puschendorf 2004) to predict species extinctions would be weak at best. Abundance – temperature relationships through space are weak and change subtly but significantly through time. Projections based on individual species' past abundance – temperature relationships could therefore be biased. Temporal trends in abundance are weakly but significantly related to temporal trends in temperature, with at most 2.4% of the variation in abundance attributed to temperature trends during the study period. An increasing rate of temperature change in future years may lead to a stronger abundance – temperature relationship, but there is no reason to expect that the substantial residual variation unrelated to climate effects would be reduced.

Climate change could be indirectly impacting avian abundances by amplifying effects of other ecological changes such as habitat loss. Increased precipitation variability worsened the impact of habitat loss on the Bay checkerspot butterfly, resulting in extinction of two of its populations (McLaughlin et al. 2002). British butterfly distribution changes in response to climate change are limited by habitat (Warren et al.

2001). Landscape-scale land use change could impede species' dispersal and migration and reduce species' ability to track changing locations of favourable climate conditions. In such cases managing habitat changes would have been more important than managing effects of climate change.

If conservation plans are based on 25- to 100- year projections, then ideally they should be based on studies using similar temporal scales. For example, studies based on paleontological records spanning millennia that show a link between biodiversity and climate may not be relevant for predicting species extinctions over the next century. The thirty-year period studied here seems to be an appropriate time scale for conservation purposes. It is possible that passerine abundances respond to climate trends with a time lag, such that a relationship was not detected here. However, since I used 30-year linear trends in temperature and abundance in this study, lags would have to be very long to have been missed with this method.

It is also possible that the abundance – temperature relationships observed in this study were weak because passerine abundances may have responded to climate trends in different ways in different ecosystems. Since similar biological communities have been found to respond to climate changes differently in different geographical areas (Bohning-Gaese et al. 1994), similar climate change trends may be affecting bird abundances differently across space. My data show no obvious differences in temporal abundance – temperature trend relationships across space according to geographic location (ecoregion). This does not rule out the possibility that birds are responding to climate change in different ways in different local ecosystems, at a grain finer than that studied here.

I also tested whether guilds of species respond to climate change in similar ways. It is possible that the total abundance of birds in particular guilds may respond predictably to temperature change but that, within guilds, individual species' changes are unpredictable. For example, sedentary butterflies with specialized habitats were found to respond differently to habitat and climate change than mobile butterflies occupying various habitats (Warren et al. 2001). Migratory birds benefit from cold winters, whereas resident birds suffer from cold winters (Lemoine and Bohning-Gaese 2003). Although some species' abundances responded more strongly to temperature change than others, I found no evidence that differences among species were related to factors such as migratory status or diet.

It is possible that breeding season temperature is not the climatic factor most relevant to avian abundance. For example, minimum winter temperature or potential evapotranspiration may be better indicators than mean spring temperature. However, these climate variables tend to be very strongly collinear, so it is unlikely that dramatically different results would be observed with other climate variables. The mean spring temperature data I used were obtained at a coarser resolution than the BBS data. Microclimatic trends at some survey routes may differ from the regional climate trends from which the climate data were interpolated. However, BBS routes, being 40km long, are likely to include numerous microhabitats, and thus sample the regional macroclimate. Since I studied migratory and resident species, mean spring temperatures interpolated from regional data are appropriate indicators of temperatures which would have been experienced by all birds included in this study.

The largest source of error in this study is likely to be the BBS data. Observer bias is thought to have the most significant potential impact and is therefore often addressed in studies using BBS data (Link and Sauer 1998; Kendall et al. 1996). Observer bias may occur in two ways: surveyors may be generally improving over time, and differences between observers may exist, affecting counts between routes and within routes when observers change over time. I assume in this study that observer biases are independent of climate change trends. The BBS data do not contain sufficient information with which to calculate observer bias correction factors on a route-by-route basis.

Finally, it should be said that other groups of organisms are likely to be more sensitive to climate change than birds. Birds' mobility could enable them to select more favourable microhabitats within a given region where small climatic changes occur. For example, birds could remain at the same breeding site each year, and yet forage in different nearby microhabitats each year. Other less mobile species are probably less able to buffer themselves from climate changes.

## *Conclusion*

This study investigated the extent to which climate change may be responsible for observed changes in avian species' abundances between 1970 and 1999. Spatial relationships between abundance and temperature are not strong and they change subtly but significantly through time. Temporal trends in abundance were only very weakly related to trends in temperature and temperature sub-optimality from 1970 to 1999. In general, temperature change was spatially autocorrelated over much greater distances than abundance changes. Changes in bird abundance observed over this period are more likely to reflect local processes such as habitat modification. Therefore, models based on temperature projections are unlikely to accurately predict future biodiversity losses on these time scales.

## Literature Cited

Bohning-Gaese, K., Taper M. L., and J. H. Brown. 1994. Avian community dynamics are discordant in space and time. OIKOS. 70: 121 – 126.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature. 411: 296 – 298.

Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science. 296: 904 – 907.

Claussen, E., Cochran, V. A., and D. P. Davis. 2001. Climate Change: Science, Strategies & Solutions. Pew Center on Global Climate Change, Arlington, Virginia.

Czech, B., Krausman, P. R., and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience. 50(7): 593 – 601.

Forchhammer, M. C., Post, E., and N. C. Stenseth. Breeding phenology and climate. Nature. 391: 29 – 30.

Huntley, B., and H. J. B. Birks. 1983. An atlas of past and present pollen maps for Europe: 0-13000 years ago. Cambridge University Press, Cambridge, UK.

IPCC, 2001. *Climate Change 2001. Synthesis Report*. Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kendall, W. L., Peterjohn, B. G., and J. R. Sauer. First-time observer effects in the North American Breeding Bird Survey. The Auk. 113(4): 823 – 829.

Korner, C. and G. –R. Walther. 2001. Fingerprints of climate change – concluding remarks. In Walther, G. -R., Burga, C. A., and P. J. Edwards (eds.) *"Fingerprints" of Climate Change. Adapted Behaviour and Shifting Species Ranges*. Kluwer Academic / Plenum Publishers, New York. Pp. 305 – 316.

Lemoine, N., and K. Böhning-Gaese. 2003. Potential impact of global climate change on species richness of long-distance migrants. Conservation Biology. 17(2): 577 – 586.

Link, W. A., and J. R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. Ecological Applications. 8(2): 258 – 268.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L., and P. R. Ehrlich. 2002. Climate change hastens population extinctions. PNAS. 99(9): 6070 – 6074.

Parmesan, C. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature. 399: 579 – 583.

Patuxent Wildlife Research Center. North American Breeding Bird Survey. Oct.31, 2001. Nov.7, 2003.

http://www.mp2-pwrc.usgs.gov/bbs/about/.

Pounds, J. A., and R. Puschendorf. 2004. Clouded futures. Nature. 427: 107 – 109.

Pounds, J. A., Fogden, M. P. L., and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature. 398: 611 – 615.

Root, T. L., Price, J. R., Hall, K. R., Schneider, S. H., Rosenzweig, C., and J. A. Pounds. 2003. Fingerprings of global warming on wild animals and plants. Nature. 421: 57 – 60.

Sawada, M. 2002. Rookcase SA. Department of Geography, University of Ottawa. Unpublished.

Schneider, S. H. and T. L. Root. 2002. Climate Changes: Overview and Implications for Wildlife. In Schneider, S. H. and T. L. Root (eds.) *Wildlife Responses to Climate Change. North American Case Studies*. Island Press, Washington, *D.C.*

Secretariat of the Convention on Biodiversity. 2000. *Sustaining Life on Earth. How the Convention on Biological Diversity promotes nature and human well-being.* Secretariat of the Convention on Biodiversity.

Thomas, C. D. and J. J. Lennon. 1999. Birds extend their ranges northward. Nature. 399: 213.

United Nations Environment Programme. 2001. Military cooperation emphasized to tackle ozone and climate issues. June 1, 2001. May 12, 2004. http://www.uneptie.org/ozonaction/library/pressrel/military.html

Vitousek, P. M. 1994. Beyond global warming: Ecology and global change. Ecology. 75(7): 1861 – 1876.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature. 414: 65 – 69.

Webb, T. III, Bartlein, P. J., and J. E. Kutzbach. 1987. Climatic change in eastern North America during the past 18,000 years: Comparisons of pollen data with model results. In Ruddiman, W. F. and H. E. Wright, Jr. (eds.) *North America and Adjacent Oceans during the Last Deglaciation. The Geology of North America.* K-3. Pp. 447 – 462. Boulder, Colorado: Geological Society of America.

Webb, T. III. 1992. Past Changes in Vegetation and Climate: Lessons for the Future. In Peters, R. L. and T. E. Lovejoy (eds.) *Global Warming and Biological Diversity*. Hamilton Printing Company, New York. Pp. 59 – 75.

Willmott, C. J. and K. Matsuura. 2001. Terrestrial Air Temperature and Precipitation: Monthly and Annual Time Series (1950 – 1999). July 1, 2001. Aug. 7, 2002. http://climate.geog.udel.edu/~climate/html_pages/download.html#ghcn_T_P_clim

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., New Jersey.

Table 1. The shapes of relationships between abundance and temperature (as they vary spatially), for 89 species included in the study, for two five-year periods at the start and end of the study.

| shape of spatial relationship | 1970 – 1974 | 1995 – 1999* |
|---|---|---|
| not significant | 18 | 7 |
| positive linear | 3 | 1 |
| negative linear | 3 | 2 |
| peaked | 59 | 72 |
| U-shaped | 6 | 6 |

*Total number of observations = 88. One species was not categorized, with significant positive $c_1$ and $c_2$ values.

Figure 1. Locations of the 1071 BBS routes included in the study. Each route was surveyed a minimum of 80% of the years between 1970 and 1999 (24 years).

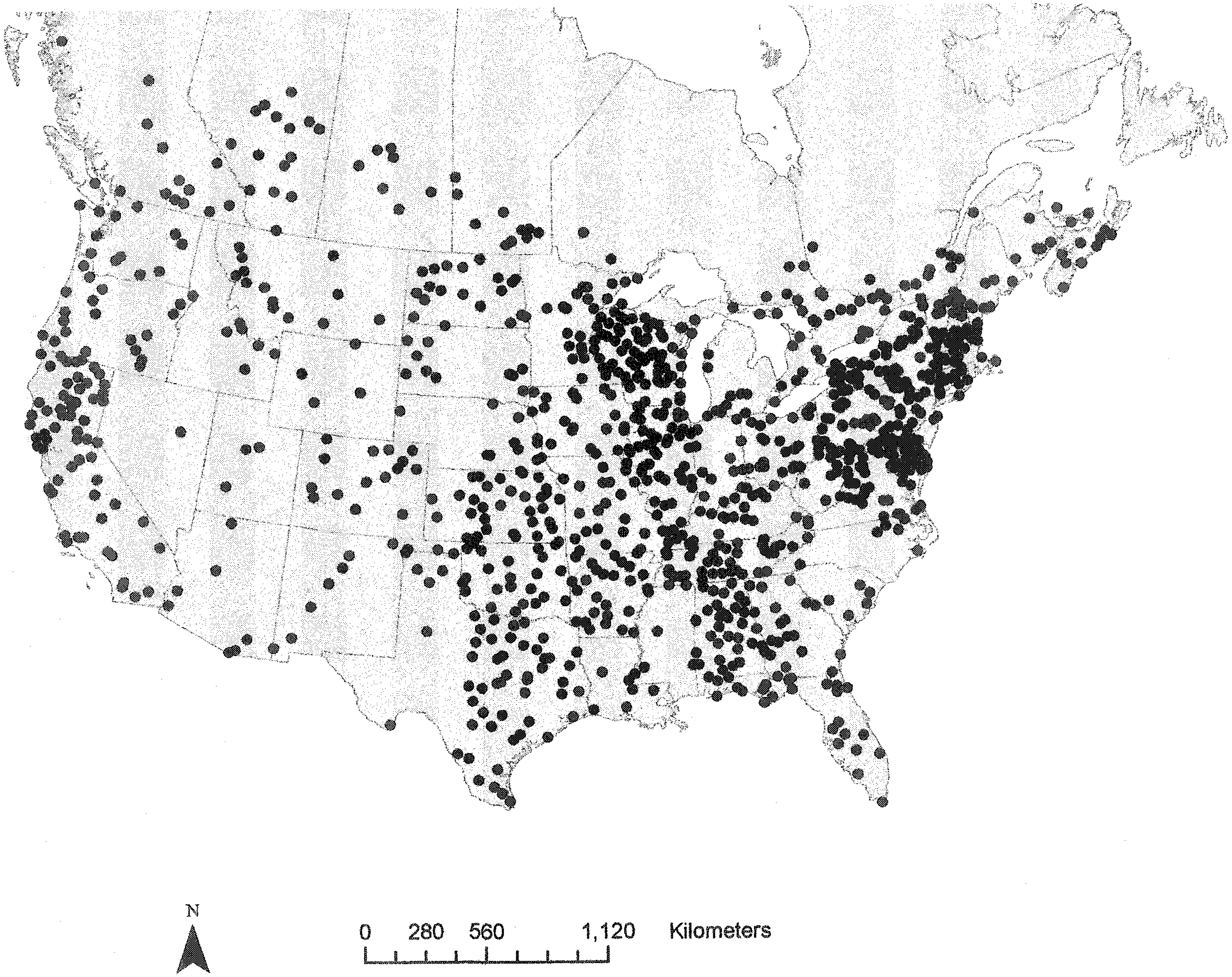

N
0
280
560
1,120
Kilometers

Figure 2. Climate sub-optimality method. First, temperature and precipitation optima were calculated for each of the 89 species included in the study, based on data from 1970 to 1984 (first 15 of 30 years included in the study). To do this for temperature, the mean temperature at all sites where each species was observed, weighted by the species' abundance at each site, was calculated (shown as horizontal line in both (a) and (b), which show a hypothetical example of the first 5 years at one site). For each site and year, the difference between the observed temperature (shown as grey squares) and each species' optimum temperature is calculated (a). Finally, the absolute difference between the species' optimum temperature and each year's observed temperature (shown as grey circles) is calculated (b) for each site and year. In the study this is done for each year 1970 through 1999. Linear temporal trends are then estimated for each species on each site where it occurs (b; dashed line).

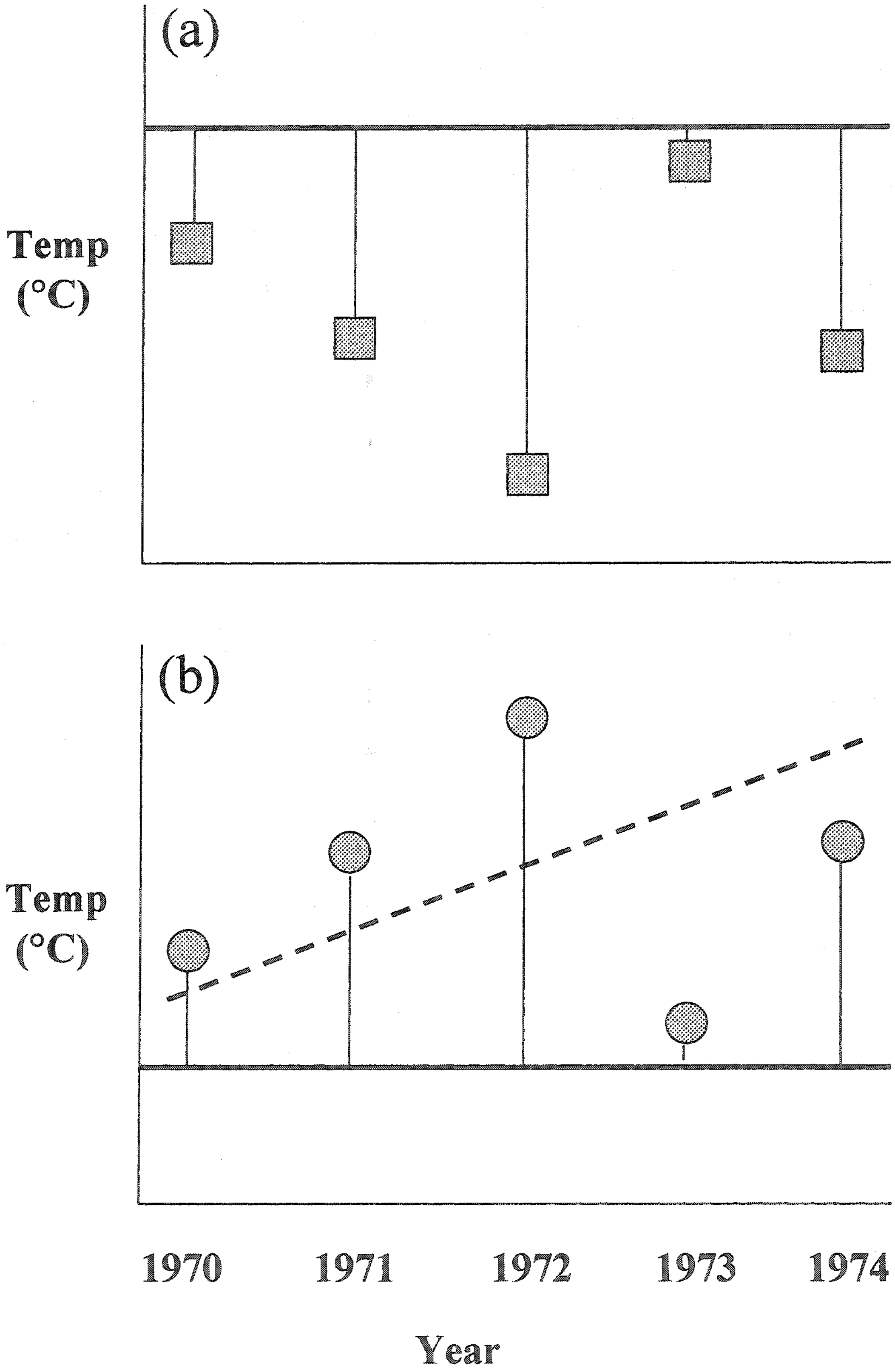

(a)
Temp (°C)
(b)
Temp (°C)
1970
1971
1972
1973
1974
Year

Figure 3. Distribution of slopes of abundance as a function of time. n = 56,425 slopes, one for each species on each route it was surveyed between 1970 and 1999. Approximately 40% of these slopes are significantly different from zero ($p \leq 0.05$).

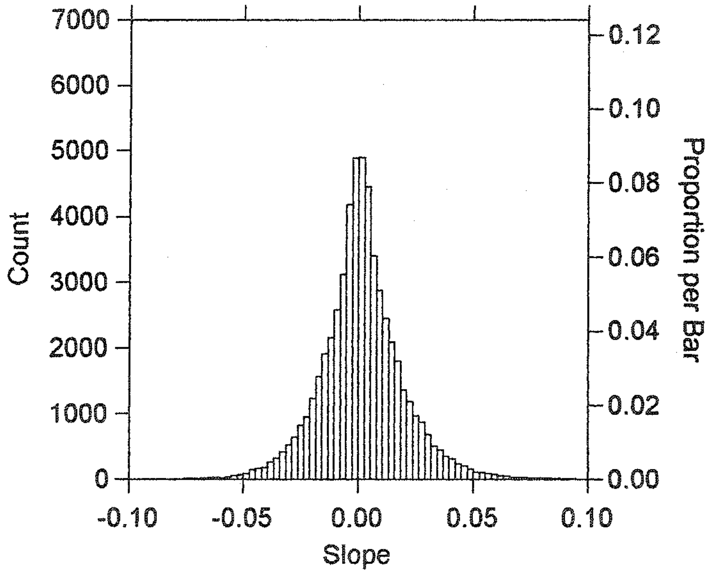
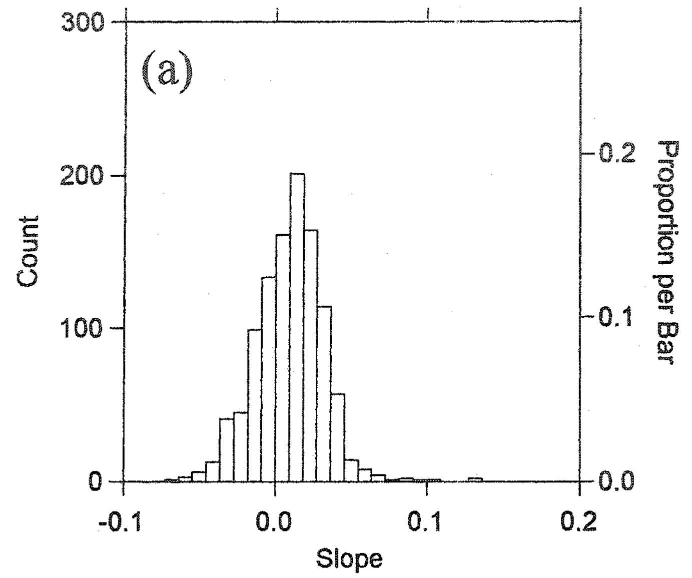

7000
6000
5000
4000
3000
2000
1000
0
Count
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion per Bar
-0.10
-0.05
0.00
0.05
0.10
Slope

Figure 4. Distribution of the slopes of (a) temperature (°C) and (b) precipitation $(\text{mm})^{0.75}$ as functions of time on 1,071 BBS routes included in the study.


(a)
300
200
100
0
Count
0.2
0.1
0.0
Proportion per Bar
-0.1
0.0
0.1
0.2
Slope

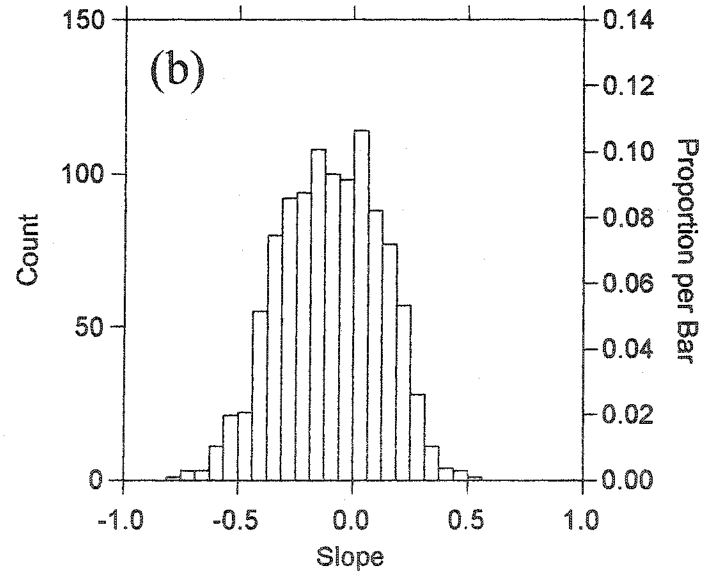

(b)
150
100
50
0
Count
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion per Bar
-1.0
-0.5
0.0
0.5
1.0
Slope

Figure 5. BBS study routes where average spring (May to July) temperature measurements (°C) over the years 1970 –1999 indicate warming or cooling trends. Significant trends ($p \leq 0.05$) are distinguished.

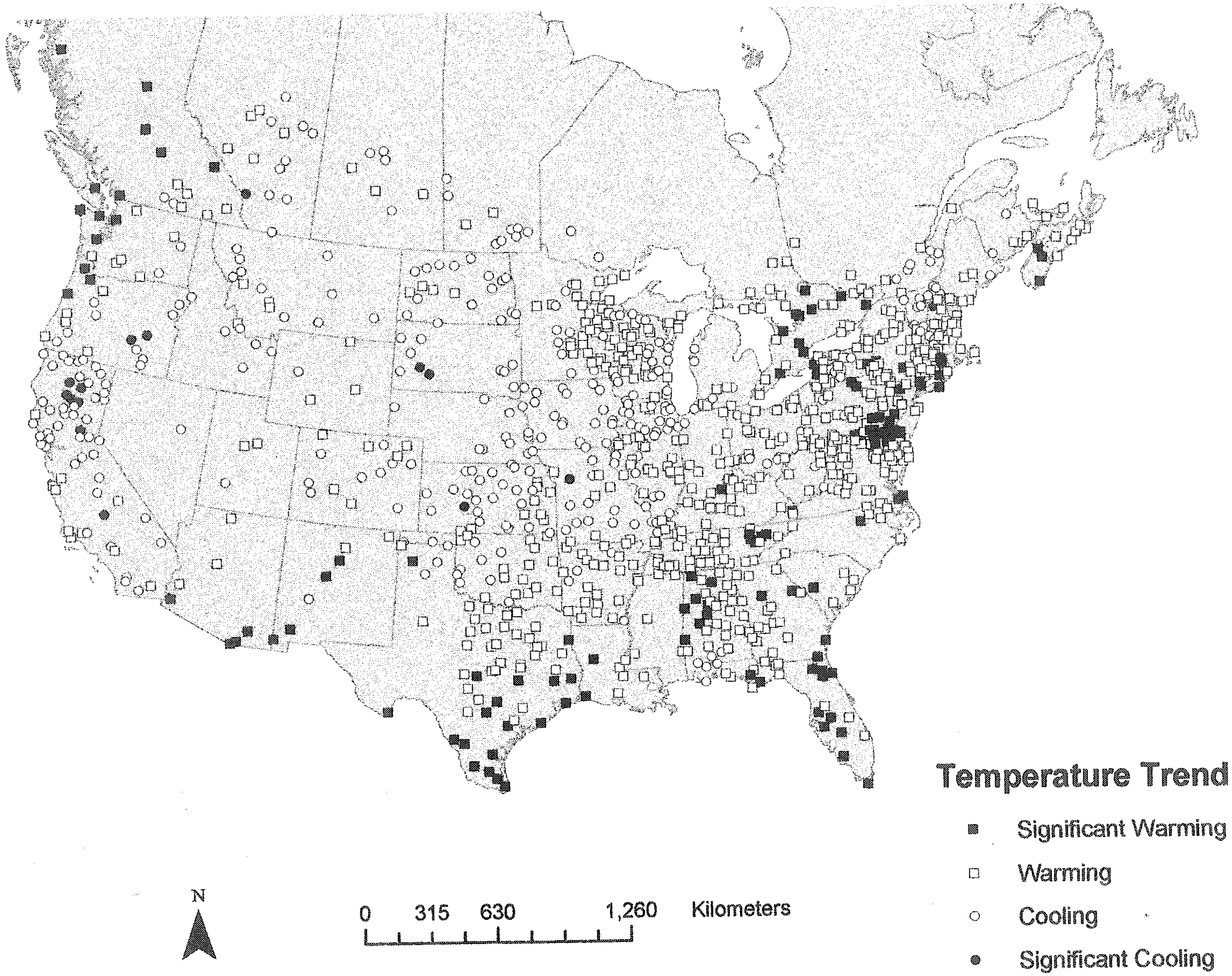
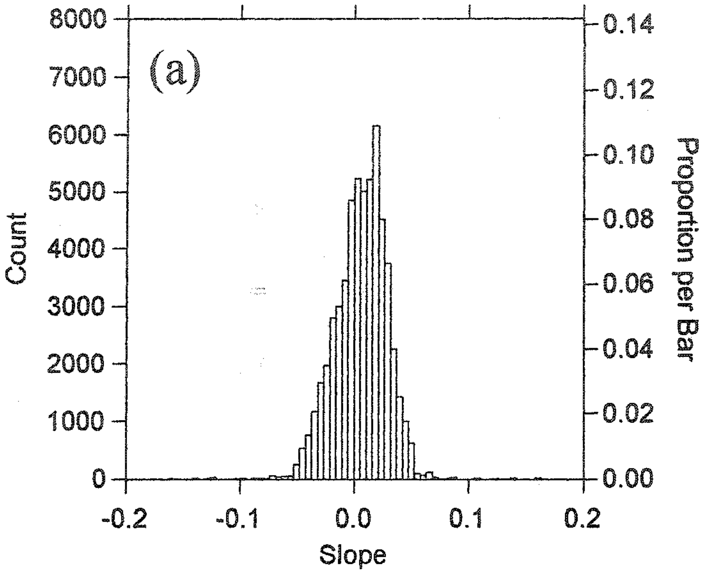

Temperature Trend
■ Significant Warming
□ Warming
○ Cooling
● Significant Cooling
0
315
630
1,260
Kilometers
N

Figure 6. Distribution of slopes of (a) temperature (°C) and (b) precipitation sub-optimality $(\text{mm})^{0.75}$ as functions of time. $n = 56{,}425$ slopes, one for each species on each route it was surveyed between 1970 and 1999.


(a)
Count
8000
7000
6000
5000
4000
3000
2000
1000
0
Proportion per Bar
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
-0.2
-0.1
0.0
0.1
0.2
Slope

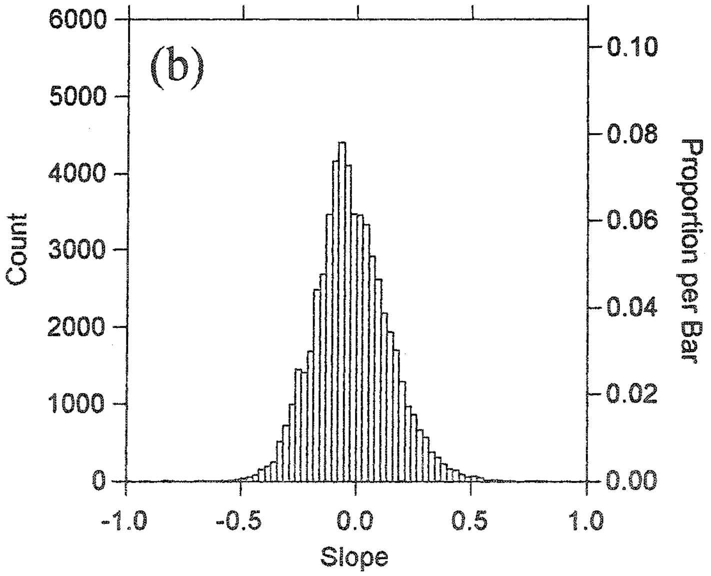

(b)
Count
6000
5000
4000
3000
2000
1000
0
Proportion per Bar
0.10
0.08
0.06
0.04
0.02
0.00
-1.0
-0.5
0.0
0.5
1.0
Slope

Figure 7. BBS study routes where average spring (May to July) precipitation measurements $(\mathrm{mm})^{0.75}$ over the years 1970 –1999 indicate trends toward wetter or drier conditions. Significant trends ($p \leq 0.05$) are distinguished.

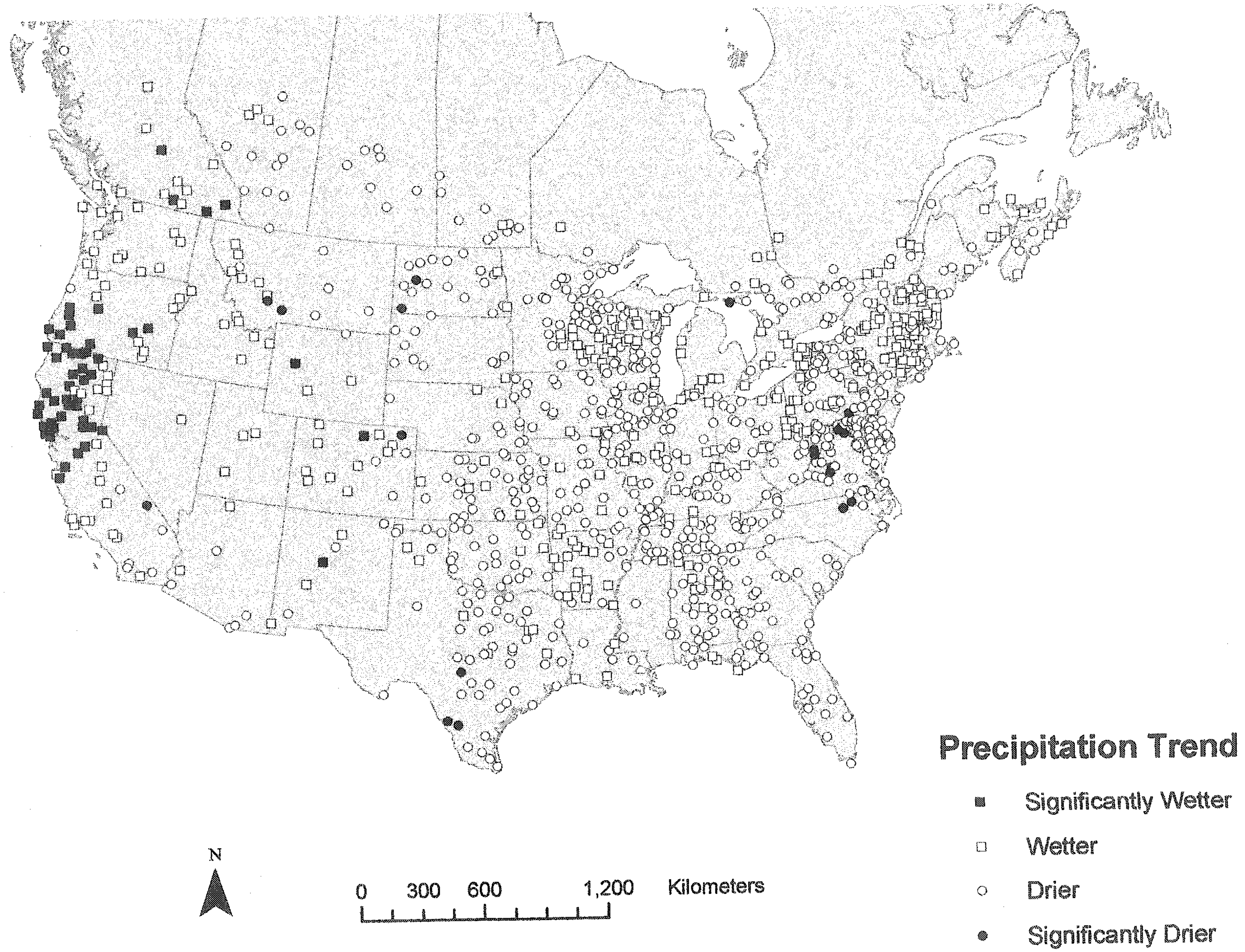

Precipitation Trend
■ Significantly Wetter
□ Wetter
○ Drier
● Significantly Drier
N
0
300
600
1,200
Kilometers

Figure 8. Average abundance plotted as a function of average spring (May – July) temperature (°C) for four representative species; European Starling (a), Brown-headed Cowbird (b), American Robin (c), and the Northern Mockingbird (d). Average abundance and temperature measurements over a five-year period, 1970 – 1974 are plotted. LOESS curves have been added to indicate shape of relationship.

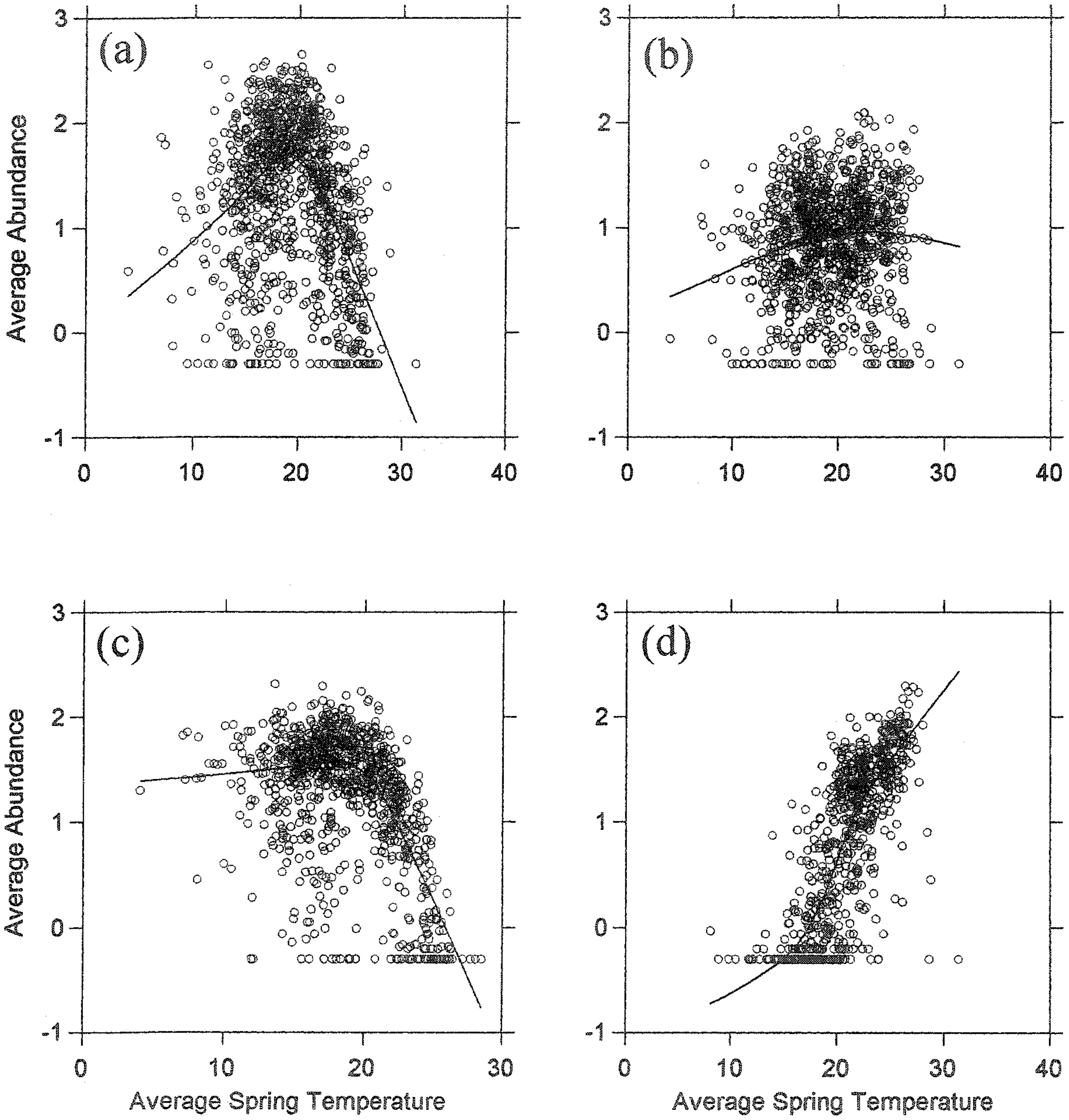

(a)
(b)
(c)
(d)
Average Abundance
Average Abundance
Average Spring Temperature
Average Spring Temperature
3
2
1
0
-1
0
10
20
30
40

Figure 9. Distribution of $R^2$ values between the spatial variation in abundance and temperature for the 89 species included in the study. $R^2$ values are obtained from fitting the following model for each species:

abundance = $c_0$ + $c_1$temperature + $c_2$temperature$^2$, where *temperature* is average spring (May – July) temperature (°C) and both *abundance* and *temperature* are averaged over the period 1970 – 1974. Dashed line indicates the expected distribution of $R^2$ values, given random associations between abundance and temperature.

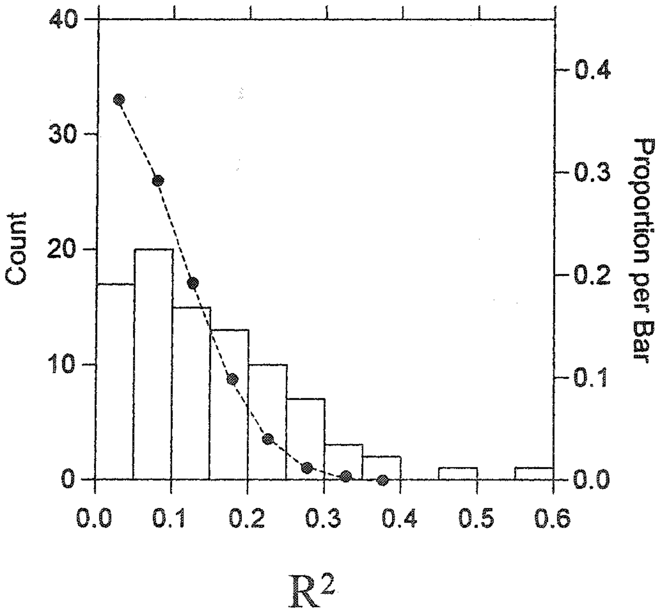

Count
Proportion per Bar
R²
0
10
20
30
40
0.0
0.1
0.2
0.3
0.4
0.0
0.1
0.2
0.3
0.4
0.5
0.6

Figure 10. Magnitude of slopes of bird abundance trends plotted as a function of magnitude of slopes of (a) temperature and (b) temperature sub-optimality trends (n=56,425). Slopes are obtained from linear regressions of temperature and temperature sub-optimality over time (1970 – 1999).

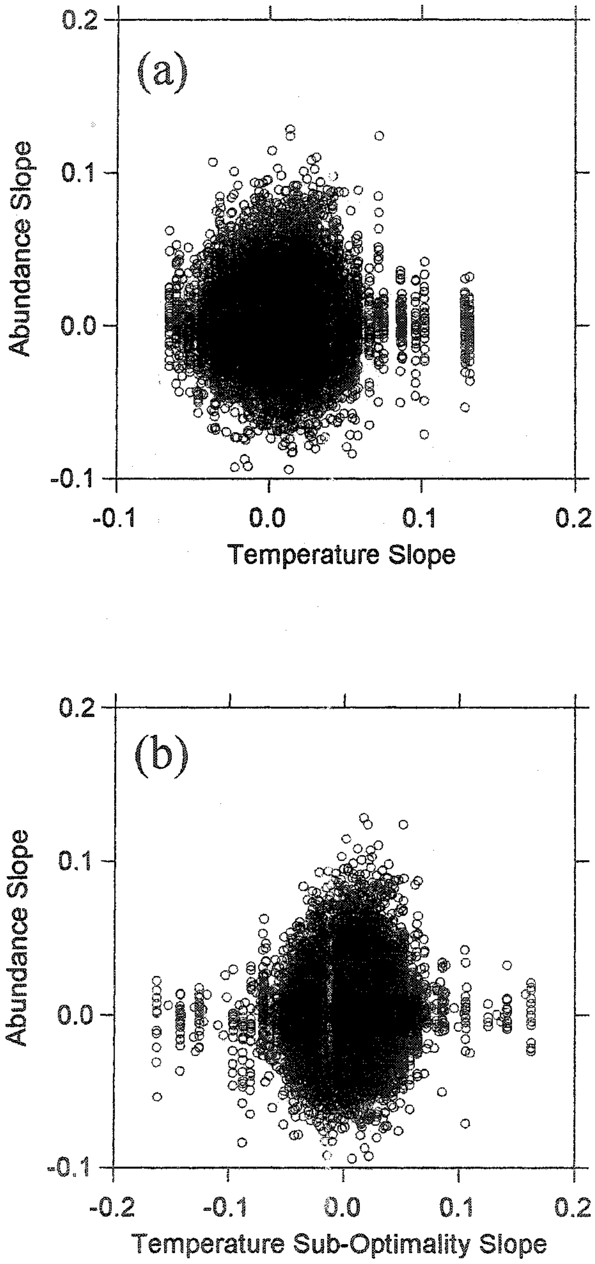
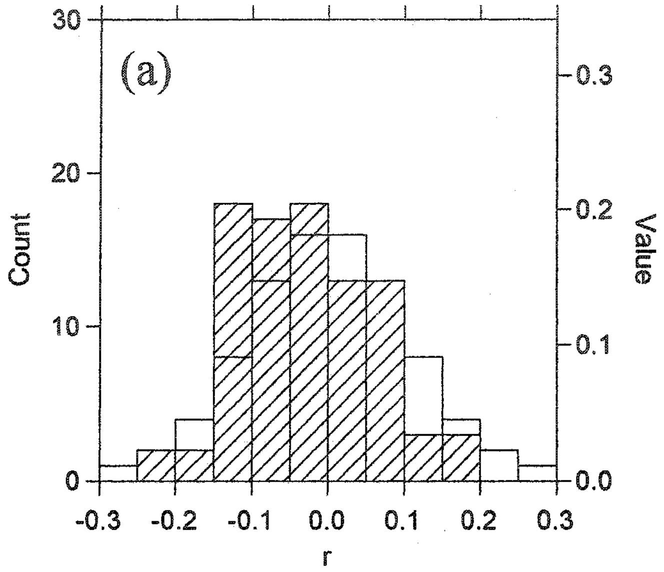

(a)
Abundance Slope
0.2
0.1
0.0
-0.1
-0.1
0.0
0.1
0.2
Temperature Slope
(b)
Abundance Slope
0.2
0.1
0.0
-0.1
-0.2
-0.1
0.0
0.1
0.2
Temperature Sub-Optimality Slope

Figure 11. Distribution of expected r values (white) are compared to the observed distribution of r values (shaded) from correlations between regression slopes of change in abundance over time and regression slopes of change in temperature (a) and temperature sub-optimality (b) over the time period 1970 – 1999. n = 89 species.


(a)
Count
Value
r
30
20
10
0
0.3
0.2
0.1
0.0
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3

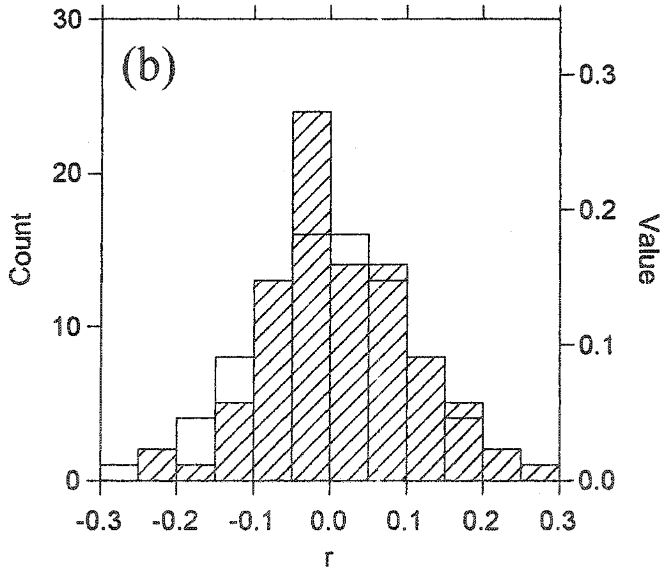
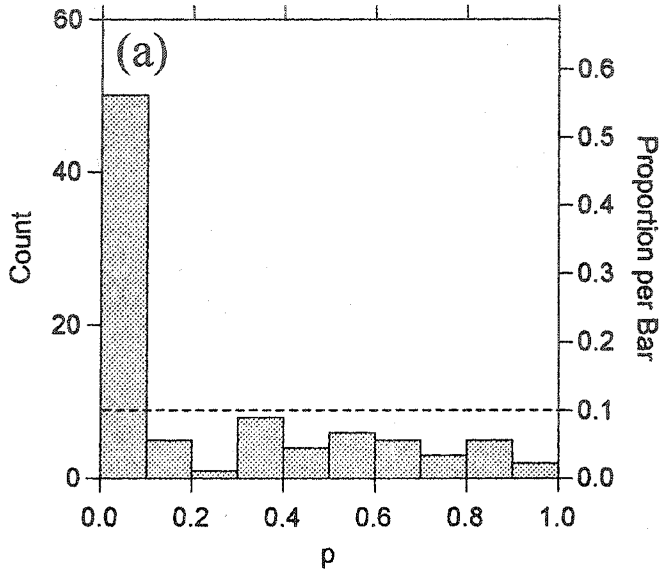
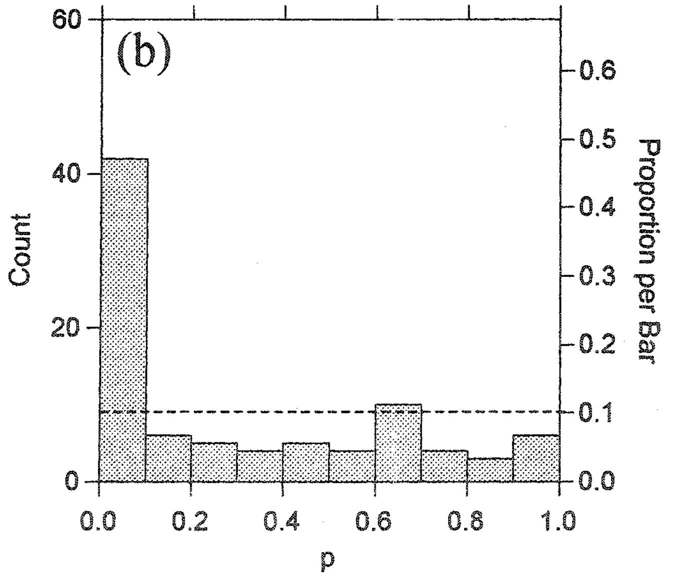

(b)
Count
Value
r
30
20
10
0
0.3
0.2
0.1
0.0
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3

Figure 12. Distribution of observed p values from correlations between regression slopes of change in abundance over time and regression slopes of change in temperature (a) and temperature sub-optimality (b) over the time period 1970 – 1999. n = 89 species. Dashed line indicates expected frequency of 0.1 for each categorical p value.



(a)
Count
60
40
20
0
Proportion per Bar
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.2
0.4
0.6
0.8
1.0
p



(b)
Count
60
40
20
0
Proportion per Bar
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.2
0.4
0.6
0.8
1.0
p

Figure 13. Moran's I plotted as a function of lag distance calculated at 25 km intervals. Moran's I was calculated as a measure of spatial autocorrelation for temperature slopes on all BBS routes, as well as for abundance slopes of all 89 species included in the study, based on all BBS routes on which each species was observed. Shown here are Moran's I values for temperature and 6 randomly selected species.

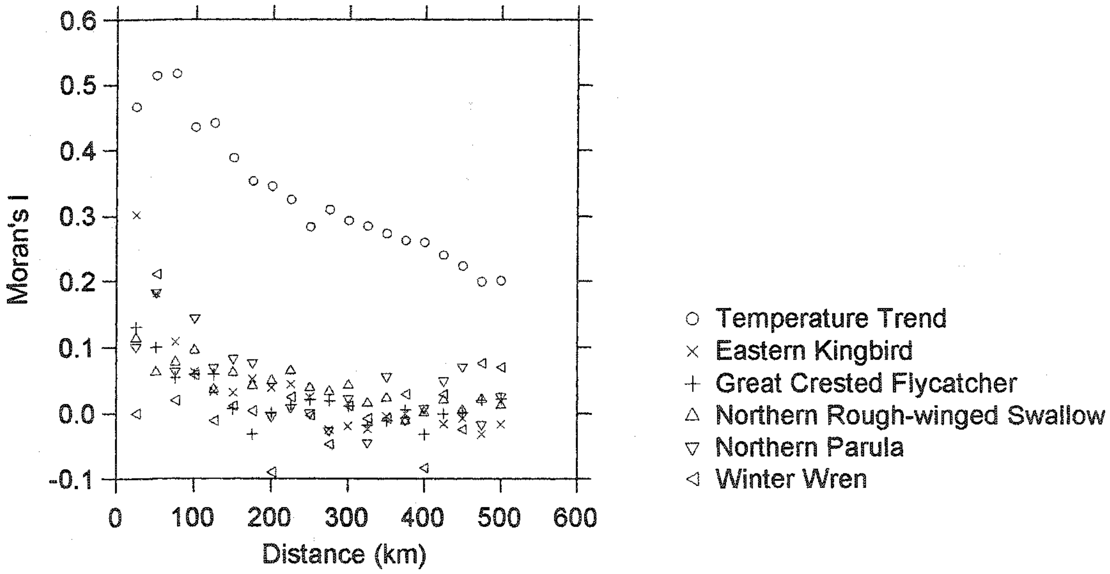
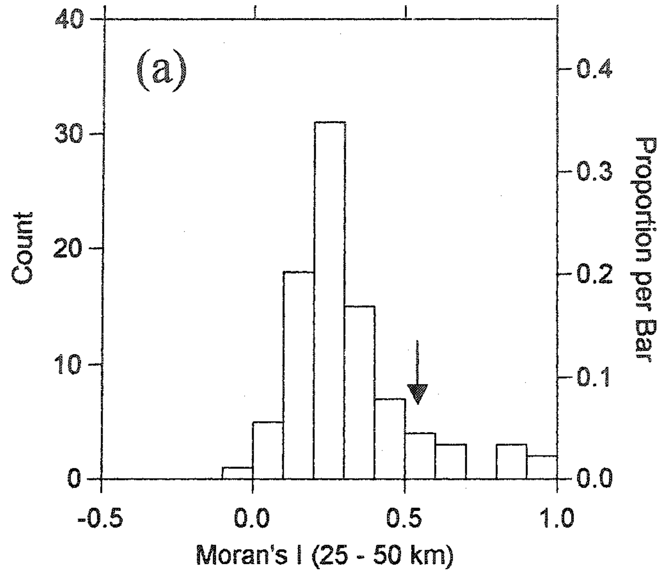
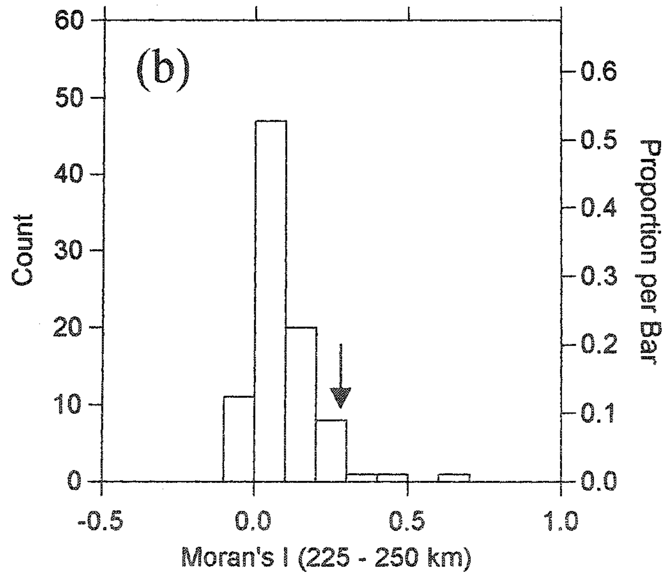

Moran's I
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
0
100
200
300
400
500
600
Distance (km)
○ Temperature Trend
× Eastern Kingbird
+ Great Crested Flycatcher
△ Northern Rough-winged Swallow
▽ Northern Parula
◁ Winter Wren

Figure 14. Moran's I calculated at (a) 25 – 50 km and (b) 225 – 250 km lag distance intervals. Moran's I was calculated as a measure of spatial autocorrelation for temperature slopes on all BBS routes, as well as for abundance slopes of all 89 species included in the study. Temperature trends (indicated by arrow) are spatially autocorrelated at a much larger spatial scale than most species' abundance trends. This is consistent at small (a) and large (b) lag distances.


(a)
Count
Proportion per Bar
40
30
20
10
0
0.4
0.3
0.2
0.1
0.0
-0.5
0.0
0.5
1.0
Moran's I (25 - 50 km)


(b)
Count
Proportion per Bar
60
50
40
30
20
10
0
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.5
0.0
0.5
1.0
Moran's I (225 - 250 km)

Appendix A. The 89 North American passerine species included in the study. Common names and family names (including generic) are provided.

| Species Name (Common) | Family Name |
|---|---|
| Horned Lark | Alaudidae (Larks) |
| Cedar Waxwing | Bombycillidae (Waxwings) |
| Dickcissel | Cardinalidae (Cardinals) |
| Indigo Bunting | Cardinalidae (Cardinals) |
| Blue Grosbeak | Cardinalidae (Cardinals) |
| Rose-breasted Grosbeak | Cardinalidae (Cardinals) |
| Northern Cardinal | Cardinalidae (Cardinals) |
| Blue Jay | Corvidae (Crows/Jays) |
| Common Raven | Corvidae (Crows/Jays) |
| American Crow | Corvidae (Crows/Jays) |
| Chipping Sparrow | Emberizidae (Emberizids) |
| Eastern Towhee | Emberizidae (Emberizids) |
| Swamp Sparrow | Emberizidae (Emberizids) |
| Field Sparrow | Emberizidae (Emberizids) |
| White-throated Sparrow | Emberizidae (Emberizids) |
| Lark Sparrow | Emberizidae (Emberizids) |
| Grasshopper Sparrow | Emberizidae (Emberizids) |
| Savannah Sparrow | Emberizidae (Emberizids) |
| Vesper Sparrow | Emberizidae (Emberizids) |
| Song Sparrow | Emberizidae (Emberizids) |
| American Goldfinch | Fringillidae (Finches) |
| House Finch | Fringillidae (Finches) |
| Purple Finch | Fringillidae (Finches) |
| Barn Swallow | Hirundinidae (Swallows) |
| Cliff Swallow | Hirundinidae (Swallows) |
| Tree Swallow | Hirundinidae (Swallows) |
| Bank Swallow | Hirundinidae (Swallows) |
| Northern Rough-winged Swallow | Hirundinidae (Swallows) |
| Purple Martin | Hirundinidae (Swallows) |
| Orchard Oriole | Icteridae (Blackbirds) |
| Brewer's Blackbird | Icteridae (Blackbirds) |
| Common Grackle | Icteridae (Blackbirds) |

| | |
|---|---|
| Western Meadowlark | Icteridae (Blackbirds) |
| Eastern Meadowlark | Icteridae (Blackbirds) |
| Baltimore Oriole | Icteridae (Blackbirds) |
| Bobolink | Icteridae (Blackbirds) |
| Brown-headed Cowbird | Icteridae (Blackbirds) |
| Red-winged Blackbird | Icteridae (Blackbirds) |
| Loggerhead Shrike | Lanidae (Shrikes) |
| Brown Thrasher | Mimidae (Mockingbirds) |
| Gray Catbird | Mimidae (Mockingbirds) |
| Northern Mockingbird | Mimidae (Mockingbirds) |
| Tufted Titmouse | Paridae (Chickadees/Titmice) |
| Black-capped Chickadee | Paridae (Chickadees/Titmice) |
| Carolina Chickadee | Paridae (Chickadees/Titmice) |
| Kentucky Warbler | Parulidae (Wood-Warblers) |
| American Redstart | Parulidae (Wood-Warblers) |
| Hooded Warbler | Parulidae (Wood-Warblers) |
| Yellow-breasted Chat | Parulidae (Wood-Warblers) |
| Chestnut-sided Warbler | Parulidae (Wood-Warblers) |
| Black-throated Green Warbler | Parulidae (Wood-Warblers) |
| Yellow Warbler | Parulidae (Wood-Warblers) |
| Northern Parula | Parulidae (Wood-Warblers) |
| Louisiana Waterthrush | Parulidae (Wood-Warblers) |
| Ovenbird | Parulidae (Wood-Warblers) |
| Prairie Warbler | Parulidae (Wood-Warblers) |
| Pine Warbler | Parulidae (Wood-Warblers) |
| Common Yellowthroat | Parulidae (Wood-Warblers) |
| Nashville Warbler | Parulidae (Wood-Warblers) |
| Blue-winged Warbler | Parulidae (Wood-Warblers) |
| Black-and-white Warbler | Parulidae (Wood-Warblers) |
| House Sparrow | Passeridae (OldWorldSparrows) |
| Red-breasted Nuthatch | Sittidae (Nuthatches) |
| White-breasted Nuthatch | Sittidae (Nuthatches) |
| European Starling | Sturnidae (Starlings) |
| Blue-gray Gnatcatcher | Sylviidae (OldWorldWarblers/Gnatcatchers) |
| Scarlet Tanager | Thraupidae (Tanagers) |
| Summer Tanager | Thraupidae (Tanagers) |
| Carolina Wren | Troglodytidae (Wrens) |

|  |  |
|---|---|
| Winter Wren | Troglodytidae (Wrens) |
| House Wren | Troglodytidae (Wrens) |
| Hermit Thrush | Turdidae (Thrushes) |
| American Robin | Turdidae (Thrushes) |
| Veery | Turdidae (Thrushes) |
| Wood Thrush | Turdidae (Thrushes) |
| Eastern Bluebird | Turdidae (Thrushes) |
| Eastern Kingbird | Tyrannidae (TyrantFlycatchers) |
| Alder Flycatcher | Tyrannidae (TyrantFlycatchers) |
| Willow Flycatcher | Tyrannidae (TyrantFlycatchers) |
| Acadian Flycatcher | Tyrannidae (TyrantFlycatchers) |
| Eastern Wood-Pewee | Tyrannidae (TyrantFlycatchers) |
| Eastern Phoebe | Tyrannidae (TyrantFlycatchers) |
| Great Crested Flycatcher | Tyrannidae (TyrantFlycatchers) |
| Western Kingbird | Tyrannidae (TyrantFlycatchers) |
| Least Flycatcher | Tyrannidae (TyrantFlycatchers) |
| White-eyed Vireo | Vireonidae (Vireos) |
| Yellow-throated Vireo | Vireonidae (Vireos) |
| Warbling Vireo | Vireonidae (Vireos) |
| Red-eyed Vireo | Vireonidae (Vireos) |

Appendix B. Shown below are the $R^2$ values from fitting a second-degree polynomial model to individual species' abundances, and Pearson $r^2$ values from fitting linear models for each species. $R^2$ values are based on pooled abundance and temperature data from 1970 – 1974 (1970s) and 1995 – 1999 (1990s). Pearson $r^2$ values are based on linear slopes of abundance and temperature/temperature sub-optimality over the time period 1970 – 1999 for each species route. To investigate whether species with strong spatial relationships are the same species with strong temporal relationships between abundance and temperature, the $R^2$ and $r^2$ values for each species are later correlated.

| **Species Name (Common)** | $R^2_{space}$ **1970s** | $R^2_{space}$ **1990s** | $r^2_{time}$ | $r^2_{time}$ **sub-opt** |
|---|---|---|---|---|
| Horned Lark | 0.021 | 0.019 | 0.000 | 0.000 |
| Cedar Waxwing | 0.287 | 0.219 | 0.010 | 0.019 |
| Dickcissel | 0.159 | 0.222 | 0.008 | 0.001 |
| Indigo Bunting | 0.199 | 0.189 | 0.001 | 0.001 |
| Blue Grosbeak | 0.088 | 0.105 | 0.000 | 0.000 |
| Rose-breasted Grosbeak | 0.163 | 0.189 | 0.006 | 0.003 |
| Northern Cardinal | 0.487 | 0.455 | 0.020 | 0.011 |
| Blue Jay | 0.112 | 0.098 | 0.013 | 0.041 |
| Common Raven | 0.084 | 0.083 | 0.007 | 0.008 |
| American Crow | 0.053 | 0.075 | 0.003 | 0.000 |
| Chipping Sparrow | 0.162 | 0.191 | 0.012 | 0.000 |
| Eastern Towhee | 0.073 | 0.282 | 0.005 | 0.006 |
| Swamp Sparrow | 0.074 | 0.084 | 0.003 | 0.005 |
| Field Sparrow | 0.205 | 0.200 | 0.019 | 0.006 |
| White-throated Sparrow | 0.352 | 0.407 | 0.001 | 0.012 |
| Lark Sparrow | 0.204 | 0.097 | 0.009 | 0.012 |
| Grasshopper Sparrow | 0.065 | 0.053 | 0.001 | 0.002 |
| Savannah Sparrow | 0.139 | 0.120 | 0.022 | 0.000 |
| Vesper Sparrow | 0.034 | 0.053 | 0.041 | 0.021 |
| Song Sparrow | 0.223 | 0.130 | 0.014 | 0.019 |

|  |  |  |  |  |
|---|---|---|---|---|
| American Goldfinch | 0.264 | 0.231 | 0.003 | 0.011 |
| House Finch | 0.011 | 0.052 | 0.035 | 0.051 |
| Purple Finch | 0.040 | 0.057 | 0.001 | 0.000 |
| Barn Swallow | 0.195 | 0.077 | 0.005 | 0.057 |
| Cliff Swallow | 0.058 | 0.033 | 0.011 | 0.035 |
| Tree Swallow | 0.288 | 0.186 | 0.004 | 0.005 |
| Bank Swallow | 0.084 | 0.030 | 0.007 | 0.001 |
| Northern Rough-winged Swallow | 0.004 | 0.012 | 0.001 | 0.000 |
| Purple Martin | 0.082 | 0.320 | 0.030 | 0.028 |
| Orchard Oriole | 0.335 | 0.121 | 0.009 | 0.009 |
| Brewer's Blackbird | 0.067 | 0.094 | 0.007 | 0.006 |
| Common Grackle | 0.248 | 0.224 | 0.017 | 0.015 |
| Western Meadowlark | 0.056 | 0.020 | 0.008 | 0.009 |
| Eastern Meadowlark | 0.156 | 0.175 | 0.014 | 0.015 |
| Baltimore Oriole | 0.107 | 0.234 | 0.012 | 0.012 |
| Bobolink | 0.143 | 0.211 | 0.007 | 0.003 |
| Brown-headed Cowbird | 0.029 | 0.035 | 0.016 | 0.036 |
| Red-winged Blackbird | 0.107 | 0.085 | 0.026 | 0.022 |
| Loggerhead Shrike | 0.168 | 0.097 | 0.010 | 0.009 |
| Brown Thrasher | 0.211 | 0.217 | 0.004 | 0.003 |
| Gray Catbird | 0.283 | 0.246 | 0.020 | 0.009 |
| Northern Mockingbird | 0.568 | 0.567 | 0.000 | 0.001 |
| Tufted Titmouse | 0.268 | 0.154 | 0.006 | 0.001 |
| Black-capped Chickadee | 0.022 | 0.110 | 0.019 | 0.029 |
| Carolina Chickadee | 0.043 | 0.053 | 0.002 | 0.000 |
| Kentucky Warbler | 0.020 | 0.051 | 0.059 | 0.044 |
| American Redstart | 0.212 | 0.256 | 0.000 | 0.000 |
| Hooded Warbler | 0.094 | 0.043 | 0.013 | 0.001 |
| Yellow-breasted Chat | 0.119 | 0.179 | 0.005 | 0.000 |
| Chestnut-sided Warbler | 0.270 | 0.258 | 0.000 | 0.007 |
| Black-throated Green Warbler | 0.151 | 0.225 | 0.000 | 0.000 |
| Yellow Warbler | 0.300 | 0.268 | 0.000 | 0.000 |
| Northern Parula | 0.122 | 0.092 | 0.002 | 0.000 |
| Louisiana Waterthrush | 0.011 | 0.015 | 0.001 | 0.000 |
| Ovenbird | 0.184 | 0.200 | 0.001 | 0.002 |
| Prairie Warbler | 0.111 | 0.062 | 0.011 | 0.004 |
| Pine Warbler | 0.330 | 0.220 | 0.000 | 0.000 |

| | | | | |
|---|---|---|---|---|
| Common Yellowthroat | 0.089 | 0.111 | 0.000 | 0.017 |
| Nashville Warbler | 0.049 | 0.146 | 0.014 | 0.003 |
| Blue-winged Warbler | 0.030 | 0.087 | 0.011 | 0.010 |
| Black-and-white Warbler | 0.151 | 0.201 | 0.005 | 0.002 |
| House Sparrow | 0.197 | 0.114 | 0.006 | 0.003 |
| Red-breasted Nuthatch | 0.047 | 0.090 | 0.001 | 0.000 |
| White-breasted Nuthatch | 0.066 | 0.074 | 0.007 | 0.007 |
| European Starling | 0.212 | 0.147 | 0.001 | 0.010 |
| Blue-gray Gnatcatcher | 0.103 | 0.104 | 0.003 | 0.002 |
| Scarlet Tanager | 0.139 | 0.090 | 0.002 | 0.005 |
| Summer Tanager | 0.073 | 0.156 | 0.024 | 0.031 |
| Carolina Wren | 0.229 | 0.355 | 0.000 | 0.002 |
| Winter Wren | 0.192 | 0.232 | 0.004 | 0.003 |
| House Wren | 0.120 | 0.107 | 0.008 | 0.000 |
| Hermit Thrush | 0.089 | 0.095 | 0.003 | 0.000 |
| American Robin | 0.378 | 0.324 | 0.001 | 0.000 |
| Veery | 0.219 | 0.144 | 0.011 | 0.007 |
| Wood Thrush | 0.009 | 0.012 | 0.003 | 0.012 |
| Eastern Bluebird | 0.108 | 0.240 | 0.011 | 0.007 |
| Eastern Kingbird | 0.085 | 0.075 | 0.000 | 0.000 |
| Alder Flycatcher | 0.247 | 0.294 | 0.001 | 0.001 |
| Willow Flycatcher | 0.052 | 0.055 | 0.000 | 0.000 |
| Acadian Flycatcher | 0.035 | 0.023 | 0.001 | 0.000 |
| Eastern Wood-Pewee | 0.062 | 0.118 | 0.004 | 0.004 |
| Eastern Phoebe | 0.121 | 0.035 | 0.008 | 0.004 |
| Great Crested Flycatcher | 0.031 | 0.078 | 0.000 | 0.000 |
| Western Kingbird | 0.103 | 0.056 | 0.037 | 0.074 |
| Least Flycatcher | 0.273 | 0.299 | 0.016 | 0.015 |
| White-eyed Vireo | 0.174 | 0.227 | 0.000 | 0.001 |
| Yellow-throated Vireo | 0.013 | 0.034 | 0.005 | 0.007 |
| Warbling Vireo | 0.076 | 0.086 | 0.000 | 0.000 |
| Red-eyed Vireo | 0.143 | 0.117 | 0.001 | 0.002 |