CLIMATE CHANGE, RANGE SHIFTS, AND DIFFERENTIAL GUILD RESPONSES OF MICHIGAN BREEDING BIRDS

By

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ABSTRACT

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There are few large-scale macroecological studies to date that use multi-species data to evaluate the influence of climate change on range shifts in wildlife. In part, this deficiency relates to the lack of suitable data. Recent completion of consecutive Breeding Bird Atlases in 12 states offers a valuable opportunity to explore the influence of climate change on avian communities. My objectives were to test for poleward range shifts among diverse avian species across broad temporal and geographic scales, and if I found systematic shifts, to further evaluate species among foraging guilds and migratory strategies for differential shifts. I analyzed Michigan Breeding Bird Atlas data, which provided 2 statewide surveys at a 20-year interval, (1983 to 1988 and 2001 to 2008), and represented over 1,000,000 occurrence records for more than 200 species of breeding birds. Analyses showed systematic shifts in the distribution of bird species with wide-ranging life histories, suggesting that a fundamental ecological change is occurring. In species with measurable range shifts, I further observed greater shifts in the northern boundary of southerly species. This work is among the first empirical studies in the Midwestern United States to quantify systematic range shifts for a diverse taxon at sufficient temporal and spatial scales for compelling inference.

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CHAPTER 1

INTRODUCTION

The ecological consequences of climate change include altered habitats, mismatched phenological relationships, and range shifts in terrestrial species (Parmesan 1996; Parmesan and Yohe 2003; Root et al. 2003). As temperatures warm, species are shifting northwards towards cooler climes (Thomas and Lennon 1999; Hitch and Leberg 2007; La Sorte and Thompson 2007). Range shifts are predicted in response to climate change for many taxonomic groups including mammals, amphibians, and birds (e.g. Huntley et al. 2006; Pounds et al. 2006; Davies et al. 2009). An implication of climate-induced range expansion and contraction are novel species assemblages, which may alter competition and predator-prey community dynamics, and may drive higher local extirpation rates among species less likely to adapt (Charmantier et al. 2008; Stralberg et al. 2009). The challenge is finding suitable data to evaluate these predictions.

Birds are an excellent group for large-scale research because of their diverse life histories, ease of detection relative to other classes of organisms, and extensive data regarding distribution, habitat selection, and abundance (Gibbons et al. 2007; Gill 2007; Niven et al. 2009). Of particular importance are statewide breeding bird atlas (BBA) projects that yield large-scale data sets with multi-species observations across many years. The large geographic scale of BBA projects and the complex relationships birds maintain in trophic and phenological hierarchies allow inference on large-scale phenomena such as climate change. A powerful advantage of repeated BBA projects, now completed in 12 states, is the opportunity to test for measurable changes in occupancy and range shifts for individual species and among guilds (Gaston 1996; Gaston et al. 2000). This approach may elicit important findings about northward and elevational

shifts as potential responses to climate change (e.g. Araujo et al. 2005; Thomas et al. 2006; La Sorte and Thompson 2007). Li et al. (2010) predicted climate change induced range shifts with large-scale occurrence records for a family of widespread avian species in China. They further described an association between species occurrence and six environmental variables of temperature and precipitation. Jimenez-Valverde et al. (2011) demonstrated a positive relationship between climatic factors and avian distribution structure. Additional predictive models have identified potential impacts of climate on species distribution, and regional studies, primarily focused on European species, have documented range shifts (Thomas and Lennon 1999; Lemoine et al. 2007; Hickling et al. 2006; Thomas et al. 2006).

Many studies to date have limited inference about distribution changes due to location, small geographical extent, elevation, and narrow species breadth. Physical geography limits poleward distribution changes in a number of studies; these limitations include physical boundaries imposed by large bodies of water, elevational variation, absence of an adjacent land mass, and highly fragmented landscapes. There is also a deficit in current literature about the specific mechanism or fundamental ecological variables driving systematic population-level changes across heterogeneous landscapes and disparate species (Walther et al. 2002; Parmesan 2006; Thomas et al. 2006). The need remains for studies using multi-species data to quantify changes that allow us to describe the influence of climate change on observed range shifts. Further, we need to reduce the ambiguity imposed by elevational variation, and replicate studies that elucidate a correlative relationship between climate change and range shifts.

While the evaluation of a correlative relationship between climate change and range shifts is complex, advancing research at large scales in different regions is necessary for making robust inference about the influence of this relationship on wildlife (Parmesan and Yohe 2003;

Walther et al. 2005; Zuckerberg et al. 2009b). These research needs are specifically relevant in central North America in the context of extreme weather events, shifting climate patterns described by predictive models, and the need for case studies in the Great Lakes region (Christensen et al. 2007; Hellman et al. 2010; Hayoe et al. 2010). To date, two studies in New York and Ohio provide the only empirical research in the United States that quantified systematic range shifts for a taxonomic group at sufficiently broad temporal and fine spatial scales for compelling inference (Zuckerberg et al. 2009b; Batdorf 2012). With this in mind, choosing suitable species and scale for quantifying range changes related to climatic variables is essential for a better understanding of this dynamic, and the ecology influencing systematic patterns (Thomas and Lennon 1999; Melles et al. 2011).

As climate-driven ranges shift across heterogeneous landscapes, we are likely to see differential responses among avian species with varying resource selection, migratory behavior, and relative sensitivity to environmental changes (e.g. Cotton 2003; Sparks et al. 2005; Donnelly et al. 2009). Currently, there is no consensus regarding specific mechanisms driving diverse responses to environmental changes; one theory in current research suggests a genetic component to population-level responses (Balanyá et al. 2006; Bradshaw and Holapzfel 2006; Gienapp et al. 2007). Alternatively, the other major theory suggests that adaptive phenotypic plasticity among individual species allows for tracking environmental changes and resources at the population level (Przybylo et al. 2000; Réale et al. 2003; Charmantier et al. 2008). Adaptive plasticity is strongly correlated to reproductive fitness and timing, and may describe a specific mechanism underlying range shifts influenced by climate change (Both et al. 2006; Gienapp et al. 2007; Møller et al. 2010). As a result, we are then able to describe differential shifts among

migratory and foraging guilds, relative to the adaptive ability of species to track environmental changes and resources, as a change that may be indicative of the mechanism driving range shifts.

As an extension of resource selection adaptation and sensitivity to changes in climate, we are likely to observe greater range shifts among species with specialized resource niches, and lesser range shifts among species better adapted to exploit a range of resources. Differential responses may be intensified by the interacting effects of climate change and the altered timing of seasonal activities including migration, leaf out, and insect emergence (Root et al. 2003; Charmantier et al. 2008; Donnelly et al 2009). The timing of egg laying and emergence of invertebrate food resources is a crucial and synchronous seasonal event between insects and breeding birds (Visser et al. 1998; Visser et al. 2004; Charmantier et al. 2008). Any mismatched phenological and trophic relationships pose ecological consequences, especially for species less likely to adapt to changes in the environment (Both and Visser 2001; Both et al. 2006; Charmantier et al. 2008). In addition to specialized resource selection, complex annual life cycles and endogenous constraints on phenotypic plasticity further increase sensitivity to environmental changes among Neotropical migrant and insectivorous species (Visser et al. 1998; Cotton 2003; Jonzén et al. 2006). As a function of selecting for broader resources, resident and short-distance migrants are better adapted to exploit a range of habitats for resource selection, and may exhibit less of a response to changing ecological pressures (Turner et al. 1998; Sparks et al. 2005; Lindell et al. 2007).

In the Great Lakes region of the United States, models predict earlier insect emergence, increased annual fecundity, and invasion by southerly and pest species in the coming decades (Hayoe et al. 2010; Hellman et al. 2010). The historical climate data that inform model projections also illustrate the potential of corresponding ecological data. During the last century

in Michigan, there were broad trends of increasing average temperatures, greater precipitation rates, and advancing growing seasons. However, during the last thirty years there has been an abrupt escalation of temperature and precipitation changes (Hayoe et al. 2010). These abrupt changes correspond with the time interval of the Michigan Breeding Bird Atlas, which provided two statewide surveys at a 20-year interval, 1983 to 1988 (Atlas I) to 2001 to 2008 (Atlas II). These data consist of more than 1,000,000 statewide occurrence records for 233 breeding birds in approximately 7,000 sample units (Brewer et al. 1991; MDNR 2012a). The extensive study area, breadth of species occurrence and distribution, and total number of records provided exceptional data for robust evaluations of broad ecological changes across time.

I hypothesized that northward range shifts have occurred among distinct breeding bird species in Michigan for 1983 to 1988 and 2001 to 2008. I also hypothesized that because insectivorous and Neotropical species are more sensitive to climatic changes, they would demonstrate greater northward range shifts. To look at how diverse species may be responding similarly to external influences, my first objective was to evaluate changes in range boundaries, center of statewide occurrence, and occurrence status between atlas periods. If I found evidence of northward shifts overall, my second objective was to then determine if those shifts varied among species grouped by foraging guilds and migration strategies. Using life history variables within the same modeling framework for the first objective, I evaluated for differential range shifts among insectivorous species and Neotropical migrant species.

STUDY AREA

The study area included the entire state of Michigan, USA, (147,121 km²) divided into 3 regions: the Upper Peninsula (UP), southern Lower Peninsula (SLP), and northern Lower Peninsula (NLP) (Figure 1). The state has a gradual north-south landcover gradient, limited elevation variation (174 m to 603 m), and broad latitudinal range (41° N to 48° N). The contiguous nature of forest landcover in northern Michigan is characterized by 3 major vegetation types:

- 1. Early-succession northern forest (aspen [Populus spp], and paper birch [Betula papyrifera]);
- 2. Mesic mixed forest (sugar maple [Acer saccharum], birch [Betula spp], eastern hemlock [Tsuga canadensis], and American beech [Fagus grandifolia]); and
- 3. Mixed boreal/wet coniferous forest (balsam fir [Abies balsamea], spruce [Picea spp], tamarack [Larix laricina], and white cedar [Thuja occidentalis]).

Southern Michigan is dominated by a fragmented agriculture-forest matrix, with 3 major vegetation types that include:

- 1. Open land (farms, open wetlands, barrens, and other treeless areas);
- 2. Wet deciduous forest (maple [Acer spp], and ash [Fraxinus spp]); and
- 3. Dry deciduous forest (oak [*Quercus spp*]).

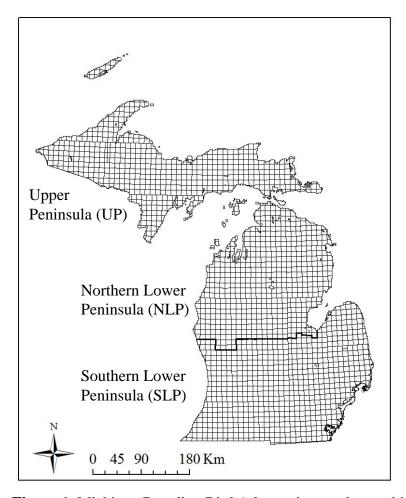


Figure 1. Michigan Breeding Bird Atlas regions and township delineations, 1983 to 2008.

Statewide climate is characterized by cold winters, temperate summers, and precipitation throughout the year. Annual precipitation rates have increased 10% to 15% over the period 1930 to 2010. For the period 1850 to 2010, mean temperature increased approximately 0.8° C (Christensen et al. 2007; Andresen et al. 2012). This increase is consistent with general global trends. Although regional temperatures vary considerably between years that temperature shifts have occurred, temperatures have changed much faster in recent decades. Mean average temperatures increased approximately 0.059° C per decade during the past century, 0.12° C per decade since 1950, and 0.26° C per decade since 1979, much of it concentrated during winter

months and at night (Brohan et al. 2006; Andresen et al. 2012) (Figure 2). In recent decades, more mild winter temperatures have led to less ice cover on the Great Lakes, and seasonal spring warm-up has occurred earlier than previously (Andresen 2009). Over the past 50 years, regional growing seasons have advanced 1 to 1.5 days, and in coming decades, vegetation hardiness zones are expected to shift northward, resulting in conditions similar to those currently found in northern Alabama by 2100 (Schwartz et al. 2006; Hellman et al. 2010).

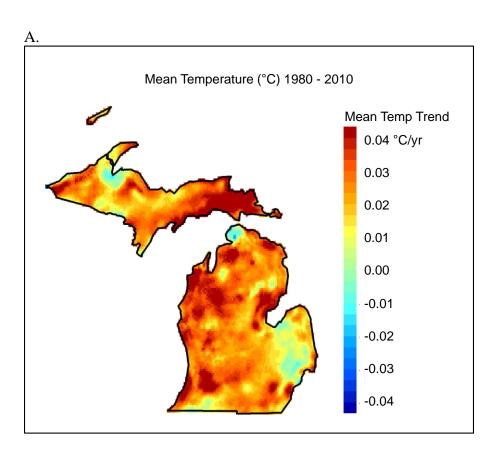
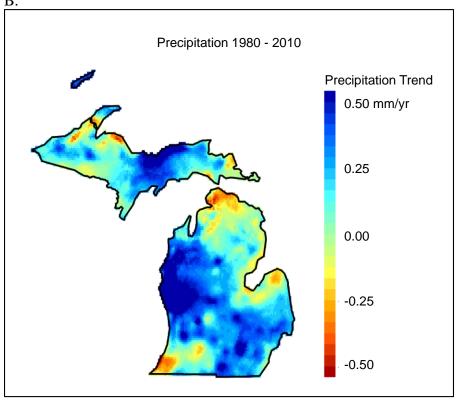


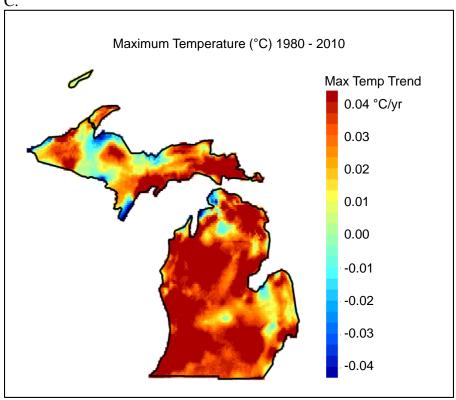
Figure 2. From 1980 to 2010 in Michigan, trend analyses for (A) the average rate of change in the annual mean temperature (°C), (B) the average rate of change in spring precipitation (mm) during March through May, and (C) the rate of change in maximum spring temperature (°C) during March through May. Maps produced by ClimateWizard[©], University of Washington, and The Nature Conservancy, 2013. Base climate data from the PRISM Group, Oregon State University. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

Figure 2 (cont'd)





C



METHODS

Breeding Bird Atlas Data

Long-term census data in the Michigan Breeding Bird Atlas documented the spatial occurrence of breeding birds across the state (Brewer et al. 1991; MDNR 2012a). Atlas I resulted from 6 years of fieldwork (1983 to 1988) by approximately 1,300 field observers and an estimated 100,000 observer hours statewide. Atlas I produced a database with over 506,000 records with breeding evidence for 233 species. Atlas II (2001 to 2008) involved approximately 1,600 field observers, and data comparable to Atlas I, with over 501,000 records and breeding evidence for 238 species. Insufficient effort data exists for Atlas II, precluding reliable effort comparison between the atlas surveys. In Atlas I and Atlas II, surveys utilized a grid system of townships (9.66 km X 9.66 km) and one-quarter townships identified as atlas blocks (4.83 km X 4.83 km) (Brewer et al. 1991; MDNR 2012a). The Michigan land survey grid system utilized for the BBA represented 1,896 townships and 7,080 blocks; 6,115 blocks were surveyed in Atlas I and 5,795 blocks were surveyed in Atlas II. Each atlas block centroid was associated with spatial bounding coordinates in standard geographic longitude and latitude decimal degree values in the Michigan GeoRef (MDNR 2012b).

Sampling intensity was based on identifying between 1 to 4 priority blocks for surveying in each township; a similar approach was applied in both atlas surveys. All 2,690 blocks in the SLP were assigned priority status. Sampling intensity was lower in the NLP and UP, where cover types were homogenous over large areas, and observer access was more limited. Two blocks in each township unit were randomly chosen in the NLP for 1,097 total priority blocks; one block in each township unit was randomly chosen in the UP for 514 total priority blocks. After surveys were completed in the identified priority block for a given township, observers

could elect to survey in neighboring blocks. Survey goals for blocks were based on standards established by the First Northeastern Breeding Bird Atlas Conference (Laughlin et al. 1982; Brewer et al. 1991; MDNR 2012a). Minimum survey goals per block included 50 breeding species and 10 to 20 hours of effort. Past research has shown that counts of 50 to 75 species represent > 75% of the breeding birds present in most blocks, a normally accepted level of survey effort in North America (Robbins and Geissler, 1990). The presence of unique species was determined at the block level using visual and auditory surveys of breeding bird evidence (MDNR 2012a). Field observers recorded species observations on a classification gradient of increasing support for breeding behavior. The lowest class of breeding evidence was the observation of a bird during the breeding season, and depending on evidence increased to possible, probable, or confirmed, with each class including levels of support to identify breeding behavior (Table B1). Regional and project coordinators reviewed, edited, and verified data before including records in the project database (Brewer et al. 1991). The Michigan Department of Natural Resources (MDNR), Wildlife Division, subsequently reviewed all data to ensure accuracy in the final BBA project (MDNR 2012b).

Range Shifts among Northerly and Southerly Species Groups

To accomplish the first objective of testing for range shifts in Michigan breeding birds, I analyzed BBA data for measurable changes in distribution. In my analyses, I evaluated 3 groupings representing all species, northerly distributed species, and southerly distributed species (Table C1). For each species, I measured changes in the center of statewide occurrence, statewide range boundaries, and localized colonization and extinction between atlas surveys

(Figure 3). The results from each of these steps informed further analysis of range dynamics among foraging and migratory groupings.

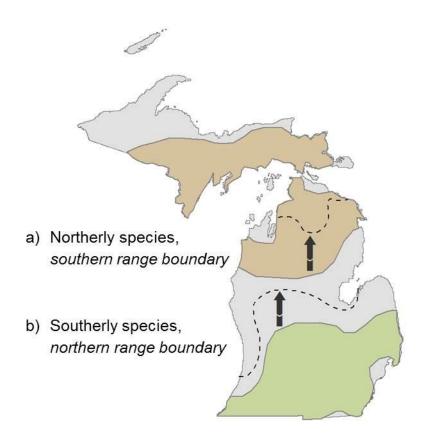


Figure 3. Theoretical northward shifts from Atlas I (1983-1998) to Atlas II (2001-2008) in (a) the southern range boundary of northerly species, and (b) the northern range boundary of southerly species. The dashed line represents the shifted range boundary location in Atlas II.

Species selection and classification—The first step in evaluating range dynamics was selecting species using criteria that helps account for potential bias in the data (Thomas and Lennon 1999, Zuckerberg et al. 2009b). I selected species that had previously been shown to demonstrate poleward range shifts in New York State (Zuckerberg et al. 2009b), and occurred in Michigan during the breeding season. I eliminated uncommon species (occurrence in less than 37 atlas

blocks), because they represented endangered species or species with restricted detection probability, to minimize bias from false absences in the data set. I excluded ubiquitous species (occurrence in more than 3775 atlas blocks), because they did not exhibit a distribution with a clear statewide range boundary. Hybrid, introduced, and game species were excluded because their population dynamics are directly influenced by intentional human involvement. Eruptive species with irregular seasonal or annual movements were also excluded.

Species with identifiable statewide range boundaries were classified according to northerly or southerly breeding range distribution. To classify each species, I first delineated a latitudinal boundary 100 km north and south of Michigan's boundary to define the study area extent (Zuckerberg et al. 2009b). A boundary extending beyond the state accommodated discontinuous geographic ranges that confound precise range margin identification (Reif 2010). I then used continental species accounts and avian range maps from Birds of North America (BNA) (Poole 2005) to classify high-latitude temperate species as northerly if the southern range boundary was within Michigan, and low-latitude temperate species as southerly if the northern boundary range was within Michigan.

I further classified individual species by life history strategies (DeGraaf et al. 1985; Sauer et al. 1999; DeGraaf and Yamasaki 2001; Poole 2005; BirdLife 2012) and reviewed these with avian biologists (K. Cleveland, Michigan Department of Natural Resources, personal communication; J. Owen, Michigan State University, personal communication). Each northerly and southerly species was assigned a breeding season foraging guild (insectivore, carnivore, piscivore, or omnivore), migratory strategy (Neotropical, short-distance, or resident), and breeding habitat guild (grassland, scrub/shrub, wetland, and wooded). I assigned foraging guilds by primary behavior during the breeding season and migratory strategies by behavior specific to

Michigan. Classification steps resulted in a final set of 41 species. These species displayed life history traits among 3 migratory strategies, 4 foraging guilds, and 5 breeding habitats (Table 1).

Species	Scientific Name	Dist. ^a	Foraging	Migratory	Habitat ^d
_			Guild ^b	Strategy	
Acadian Flycatcher	Empidonax virescens	S	Insect	Neo	Wood
Blue-gray Gnatcatcher	Polioptila caerulea	S	Insect	Neo	Wood
Blue-headed Vireo	Vireo solitaries	N	Insect	Neo	Wood
Blackburnian Warbler	Dendroica fusca	N	Insect	Neo	Wood
Boreal Chickadee	Poecile hudsonica	N	Omni	Short	Wood
Brown Creeper	Certhia americana	N	Insect	Short	Wood
Black-throated Blue Warbler	Dendroica caerulescens	N	Insect	Neo	Wood
Black-throated Green Warbler	Dendroica virens	N	Insect	Neo	Wood
Blue-winged Warbler	Vermivora pinus	S	Insect	Neo	Scrub
Carolina Wren	Thryothorus ludovicianus	S	Insect	Res	Scrub
Canada Warbler	Wilsonia canadensis	N	Insect	Neo	Wood
Common Loon	Gavia immer	N	Pisc	Short	Wet
Chestnut-sided Warbler	Dendroica pensylvanica	N	Insect	Neo	Scrub
Eastern Screech-Owl	Megascops asio	S	Omni	Res	Wood
Eastern Towhee	Pipilo erythrophthalmus	S	Omni	Short	Scrub
Field Sparrow	Spizella pusilla	S	Omni	Short	Scrub
Gray Jay	Perisoreus canadensis	N	Omni	Res	Wood
Great Egret	Ardea alba	S	Carn	Neo	Wet
Green Heron	Butorides virescens	S	Pisc	Neo	Wet
Grasshopper Sparrow	Ammodramus savannarum	S	Insect	Neo	Grass

^aStatewide distribution: northerly (*N*) and southerly (*S*)

^bBreeding season foraging guilds: carnivore (*Carn*), insectivore (*Insect*), omnivore (*Omni*), and piscivore (*Pisc*)

^cMigratory strategies: resident species (*Res*), short-distance migrants (*Short*), and long-distance Neotropical migrants (*Neo*)

^dBreeding habitats: grassland (*Grass*), scrub/shrub (*Scrub*), wetland (*Wet*), and wooded (*Wood*)

Table 1 (cont'd)

Table I (cont u)					
Henslow's Sparrow	Ammodramus henslowii	S	Insect	Short	Grass
Hermit Thrush	Catharus guttatus	N	Insect	Short	Wood
Hooded Warbler	Wilsonia citrine	S	Insect	Neo	Wood
Least Bittern	Ixobrychus exilis	S	Pisc	Neo	Wet
Lincoln's Sparrow	Melospiza lincolnii	N	Omni	Neo	Scrub
Louisiana Waterthrush	Seiurus motacilla	S	Insect	Neo	Wood
Magnolia Warbler	Dendroica magnolia	N	Insect	Neo	Wood
Nashville Warbler	Vermivora ruficapilla	N	Insect	Neo	Scrub
Northern Cardinal	Cardinalis cardinalis	S	Omni	Res	Scrub
Northern Waterthrush	Seiurus	N	Insect	Neo	Wood
	noveboracensis				
Orchard Oriole	Icterus spurius	S	Insect	Neo	Gen
Olive-sided Flycatcher	Contopus cooperi	N	Insect	Neo	Wood
Red-bellied Woodpecker	Melanerpes carolinus	S	Omni	Res	Wood
Ruby-crowned Kinglet	Regulus calendula	N	Insect	Short	Wood
Red-shouldered Hawk	Buteo lineatus	S	Carn	Short	Wood
Swainson's Thrush	Catharus ustulatus	N	Omni	Neo	Wood
Tufted Titmouse	Baeolophus bicolor	S	Insect	Res	Wood
Willow Flycatcher	Empidonax traillii	S	Insect	Neo	Scrub
Yellow-bellied	Empidonax	N	Insect	Neo	Wood
Flycatcher	flaviventris				
Yellow-bellied Sapsucker	Sphyrapicus varius	N	Omni	Short	Wood
Yellow-throated Vireo	Vireo flavifrons	S	Insect	Neo	Wood

To analyze dynamics of range centroids and boundaries, I generated observation histories for each species for all blocks where they were observed. It was necessary to take this extra step prior to analysis because the structure of the Atlas II dataset differed from the data structure in Atlas I. Using Atlas II observation data (for each species, in all blocks, and each atlas year) I selected records with the highest breeding evidence; this approach paralleled Atlas I records and eliminated additional observations for lower breeding evidence that were included in the larger Atlas II data set. I then amended the observation histories by identifying blocks with no records, the highest breeding evidence per block by year, unique blocks with records in each atlas, and

unique blocks without records for each atlas (Table A1). I tested the final observation histories for accurate representation of data class and format.

Center of statewide occurrence—To test for range changes I evaluated observation histories for each northerly and southerly species, in all atlas blocks, for all years in both atlas surveys. I used only the single greatest breeding observation records for a species in each block and each year. From the unweighted mean of block centroids with observation records, I found the center of statewide occurrence (by longitude and latitude) for each species in Atlas I and Atlas II. This identified the center of statewide distributions based on the mean location of observed occurrences. I then calculated the difference in center of occurrence between Atlas I and Atlas II.

I used an information-theoretic approach as an alternative to means testing to evaluate if including a spatial variable was meaningful when calculating changes in mean latitude and longitude. This approach quantified the strength of support for each of the hypotheses evaluated, and allowed for comparison of results with earlier research (Anderson 2008; Zuckerberg et al. 2009b). The alternative hypothesis for northerly and southerly species assumed a change in the mean latitude between Atlas I and II and a nonzero effect size. I calculated the second order Akaike's Information Criterion statistic (AIC_c) to compare support for models under the null and alternative hypotheses, following Anderson (2008):

$$\log_n\left\{\frac{\text{RSS}}{n}\right\} + 2K + \frac{2K(K+1)}{n-K-1},$$

(where n = sample size, RSS = residual sum of squares, K = number of parameters). The null hypothesis in the paired design does not have a term for differences between observations and consequently has an effect size of zero (K = 1). RSS for the null hypothesis was calculated as:

$$\sum_{i=1}^n (d_i)^2,$$

(where d_i = difference between the 2 sample distributions of mean observations). Assuming a nonzero effect size, the value for the alternative hypothesis was calculated as:

$$\sum_{i=1}^n (d_i - \bar{d})^2,$$

(with a term for an assumed difference between the two sample distributions, K = 2). The alternative hypothesis quantified model support for distinct latitudinal shifts between the two sample observations; the null hypothesis calculated the probability of no changes in latitude between observations (Zuckerberg et al. 2009b). I reported the probability of the null and alternative hypotheses, effect size, RSS values, the number of parameters (K), AIC_c, Δ AIC_c, and weight of evidence in support of the hypotheses (Anderson 2008) for northerly, southerly, and ungrouped species between both atlas surveys.

Range boundary shifts—The range boundary analysis quantified shifts in northern range boundaries of southerly species, and shifts in southern range boundaries of northerly species. Zuckerberg et al. (2009b) explored whether or not their boundary analysis was sensitive to increasing the number of blocks used in the calculation (ranging from 10 to 50); for northerly species, recalculations had little effect and showed no support for the null model, and among southerly species there was a small increase of support in model probabilities for a true intercept

value. They further suggested that using too many blocks for calculating statewide range boundaries may not actually represent range boundaries, and diminished the signal of the *y*-intercept. In my analysis, (having previously ruled out species with occurrence in less than 37 atlas blocks), I used data from 10 and 25 blocks for each species in the range boundary analysis. I evaluated the *n*-most southern blocks for northerly species, and the *n*-most northern blocks for southerly species. The mean statewide latitude and latitudinal range limits were calculated as the mean, minimum, and maximum block centroid location for each species (Anderson et al. 2009). The next step in evaluating for range shifts was comparison of range boundary shifts between Atlas I and II against overall changes in occupancy between atlas periods. Following Zuckerberg et al. (2009b) and Thomas and Lennon (1999), I calculated and plotted the change in occupancy for each species by statewide distribution,

$\log_{10}[occupied\ blocks\ Atlas\ II] - \log_{10}[occupied\ blocks\ Atlas\ I],$

against the change in northern and southern range boundaries between Atlas I and Atlas II using the ordinary least squares (OLS) approach. Using a regression model where parameters that can take any real number, and a model with a forced zero y-intercept value, I evaluated the AIC_c for proportional fit. I found the evidence ratio, which indicated the more probable model, using the likelihood of each model, given the data, and the overall model likelihood. Support for northern range shifts was demonstrated by greater evidence for the regression model and significantly positive y-intercept values, (Zuckerberg et al. 2009b), while controlling for changes in overall geographic distribution by incorporating the change in occupancy.

States of occurrence-To evaluate for changes in states of occurrence, I identified areas of atlas block gains and losses for northerly and southerly species between both atlas surveys (Thomas and Lennon 1999; Brommer 2004; Zuckerberg et al. 2009b, Bradbury 2011). Controlling for overall changes demonstrated by expanding or contracting distribution helped account for the variable nature of ranges, and allowed for stronger inference on the center of statewide occurrence and range boundary analyses. Species with expanding distributions are more likely to colonize towards the range margins and beyond, and those with contracting distributions are likely to move towards distributional centers (Brommer 2004). In the states of occurrence analysis, presence or absence was determined by observation records, (as opposed to presence as it relates to occurrence probability specific to other types of analysis), for each species in Atlas I and Atlas II. The absence or presence of species was assigned to each block in Atlas I and Atlas II. Each atlas block was also identified by the spatial bounding coordinates of the block centroid. Then, I quantified *losses* as the mean latitude and longitude of atlas blocks with species occurrence in Atlas I but not Atlas II. Gains were the mean latitude and longitude in atlas blocks with no detection in Atlas I and detection in Atlas II. Retention was identified by atlas blocks with occurrence in both Atlas I and II, and absence represented blocks with no occurrence (Zuckerberg et al. 2009b). I then incorporated distribution changes as the change in occupancy between Atlas I and Atlas II (previously calculated in the range boundary analysis). Values from the change in occupancy that were distributed around zero suggested no overall changes in distribution, while directional changes in distribution were suggested as values moved toward 1.0. For expanding distributions, I would expect to see positive values toward 1.0, and for contracting distributions, negative values are expected toward -1.0 (Brommer 2004). By conducting a regression of range margin changes on distribution changes, I also quantified the

expected changes in range margins without overall changes in distribution (Thomas and Lennon 1999; Brommer 2004).

Differential Range Shifts among Foraging and Migratory Groups

To accomplish the second objective to evaluate species groups for differential changes as a way of exploring the underlying ecology, I further analyzed species that demonstrated range shifts. First, I evaluated species organized into foraging groups as either insectivorous or noninsectivorous, and then evaluated species in migratory groups as either Neotropical or non-Neotropical), (Table C2 and Table C3). I followed the same analysis as above for the center of occurrence, range boundary, and states of occurrence for foraging groups then migratory groups. In the evaluation of changes in the center of statewide distributions, the alternative hypothesis for the insectivorous guild (and subsequently Neotropical migrants) among the other groupings supported a change in the mean latitude between the observations and a nonzero effect size. The null hypothesis suggested no differences between observations and an effect size of zero. For migratory groups and foraging groups, the range boundary analysis quantified shifts in northern range boundaries of southerly species, and shifts in southern range boundaries of northerly species. Finally, the states of occurrence analysis identified areas of atlas block gains and losses for species in each group between Atlas I and II (Thomas and Lennon 1999; Brommer 2004; Zuckerberg et al. 2009b; Bradbury 2011). I conducted all analyses in R 2.13.1 (R Development Core Team, R; A language and environment for statistical computing, Vienna, Austria, R Foundation for Statistical Computing, 2006).

Animal use and care exemption—The Michigan State University Institutional Animal Care and Use Committee (IACUC) exempted this research from review, effective 28 December 2010.

RESULTS

Center of Occurrence

Shifts in the center of statewide occurrence ranged from a southward movement of 81.7 km for the yellow-bellied flycatcher (*Empidonax flaviventris*) to a northward movement of 52.0 km for the Henslow's sparrow (*Ammodramus henslowii*). Results provided greater support for the hypothesis for a change in the center of statewide occurrence between Atlas I and Atlas II (Prob (H_A|data) = 0.99) (Table 2). The overall model showed changes in latitude, as demonstrated by a large evidence ratio in favor of the alternative hypothesis (156.1), and Δ AIC_c value of 10.1. A difference greater than 3.0 in the Δ AIC_c value further suggested a change in the overall model for changes in mean latitude.

Table 2. Center of statewide occurrence analysis quantifying changes in mean latitude for 41 birds. Michigan Breeding Bird Atlas I and II. 1983 to 2008.

Model	RSS	K	Δ AIC $_{c}$	$L(\mathbf{h} \mathbf{data})$	Prob(h data)	Evidence Ratio
Alternative ^a	3.73E+10	2	0.0000	1.0000	0.9936	156.0915
Null ^b	5.04E+10	1	10.1009	0.0064	0.0064	

^aAlternative hypothesis quantifies support for latitudinal shifts between sample observations ^bNull hypothesis quantifies support for no significant changes in latitude between observations

Compared with all species, the southerly species group demonstrated similar shifts in their statewide occurrence. However, a greater percentage of southerly species shifted polewards than overall, and shifts were in the opposite direction than overall; while 39.0% of all species demonstrated northward movement in their center of occurrence, I found that 38.1% of 21 southerly species showed southward movement, and 61.9% of southerly species showed northward movement. Among northerly species, I found greater differences in the magnitude of

species that demonstrated shifts in the center of their statewide occurrence. For 20 northerly species, only 15% showed a northerly shift in center of occurrence compared with 39.0% of all species with northward movement. Eighty-five percent of northerly species demonstrated a southerly shift, while 61.0% of all species had a southerly shift.

Among changes in center of occurrence for foraging guilds, I found greater support for a shift in 26 insectivorous species (Prob ($H_A|data$) = 0.99), relative to the lack of support for a best model for the 15 non-insectivorous species (Prob ($H_0|data$) = 0.60) (Table 3). The insectivore model indicated changes in latitude, as demonstrated by a ΔAIC_c value of 8.5 and large evidence ratio (69.9) in favor of the alternative hypothesis for distinct shifts between observations. Shifts in the center of statewide occurrence for the insectivore guild ranged from southward movements of 81.7 km for the yellow-bellied flycatcher and 79.9 km for the brown creeper ($Certhia\ americana$), to northward movements of 52.0 km for the Henslow's sparrow and 11.0 km for the willow flycatcher ($Empidonax\ traillii$). I found that 70.8% of insectivorous species demonstrated northward movement in their center of occurrence, and 53.3% of non-insectivorous species shifted northward. Among changes in center of occurrence for migratory groups, I found greater support for a shift in 25 Neotropical species ($Prob\ (H_A|data) = 0.99$), relative to the lack of support for a best model for the 16 non-Neotropical species ($Prob\ (H_O|data) = 0.63$)

Table 3. Center of statewide occurrence analysis quantifying changes in mean latitude by life history strategies. Michigan Breeding Bird Atlas I and II. 1983 to 2008.

Group	Model	RSS	K	Δ AIC _c	$L(\mathbf{h} \mathbf{data})$	Prob(h/data)	Evid. Ratio
Insectivore	Alt ^a	2.69E+10	2	0.000	1	0.986	69.882
	Null ^b	4.09E+10	1	8.494	0.014	0.014	
Non-insectivore	Null	9.52+10	1	0	1	0.599	1.494
	Alt	8.39+10	2	0.802	0.670	0.401	
Neotropical	Alt	1.91+10	2	0	1	0.99	178.361
	Null	3.19+10	1	10.368	0.006	0.006	
Non-neotropical	Null	1.9+10	1	0	1	0.626	1.676
	Alt	1.7 + 10	2	1.032	0.597	0.374	

^aAlternative hypothesis quantifies support for latitudinal shifts between sample observations

Range Boundary Analysis

In the analysis on range boundary changes and overall changes in occupancy, I found stronger support for the hypothesis that birds are shifting their ranges northwards. Results from the range boundary analysis suggest a change in the mean latitude between observations and a nonzero effect size, and the importance of including a spatial component in the evaluation. I found strongest model support for northward changes in range boundaries for the southerly species group, while accounting for overall changes in occurrence (Table 4). Twenty-eight species (68.3%) demonstrated a northward shift their range boundary (mean 41.7 km), and 13 species (31.7%) had southward range boundary shifts (mean 25.2 km) (Table D1).

^bNull hypothesis quantifies support for no significant changes in latitude between observations

Table 4. Range boundary analysis for change in mean latitude between Michigan Breeding Bird Atlas I and II, 1983-2008.

Group	Model	K	Δ AIC $_{ m c}$	weight	
Northerly species	Alternative	3	0.0	0.567	
	Null	2	0.5	0.433	
Southerly species	Alternative	3	0	0.738	
	Null	2	2.1	0.262	
All species	Alternative	3	0	0.721	
	Null	2	1.9	0.279	

For all 41 species I estimated a northward range boundary shift from a positive y-intercept value of 13.2 km (SE = 6.41 km, P = 0.04) (Table 5). Species that demonstrated positive changes in occupancy generally shifted their range boundaries northward (Figure 4c). Results that suggested a northward shift has occurred using an OLS approach were corroborated by an Information-Theoretic approach of comparing two competing models for all species while controlling for overall changes in states of occurrence. Although I found that the null model remains a possible model given the data ($\Delta AIC_c = 1.9$, Prob (H₀|data) = 0.28), the alternative model for poleward range shifts is more than twice as likely (Prob (H_A|data) = 0.72) (Table 4).

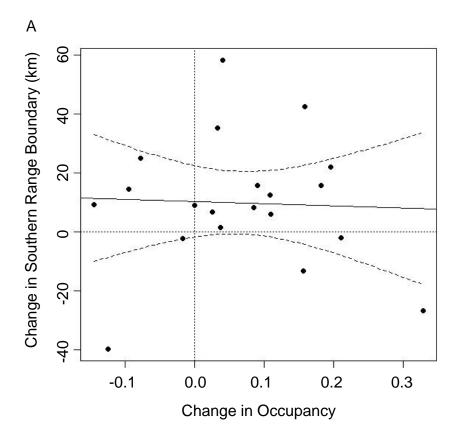
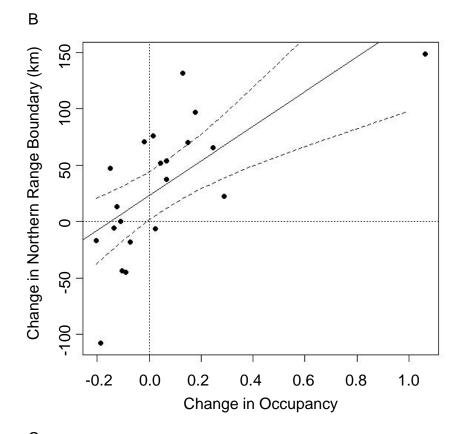


Figure 4. Latitudinal change in range boundaries (km) plotted against the change in occupancy for (A) 20 northerly, (B) 21 southerly, (C) all 41, D) 26 insectivore, and E) 25 Neotropical species in Michigan between Atlas I (1983-1998) and Atlas II (2001-2008). Northerly species demonstrated a northward shift in southern range boundaries of 10.4 km (SE = 5.8 km) (P = 0.09). Southerly species demonstrated a northward shift in northern range boundaries of 22.7 km (SE = 10.3 km) (P = 0.04). All species demonstrated a northward shift in range boundaries of 13.2 km (SE = 6.4 km) (P = 0.05). Insectivore species demonstrated a northward range shift in range boundaries of 6.8 km (SE = 8.0 km) (P = 0.41). Neotropical species demonstrated a northward range shift in range boundaries of 16.0 km (SE = 8.7 km) (P = 0.08).

Figure 4 (cont'd)



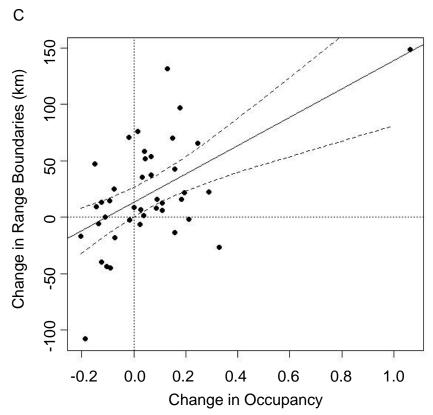
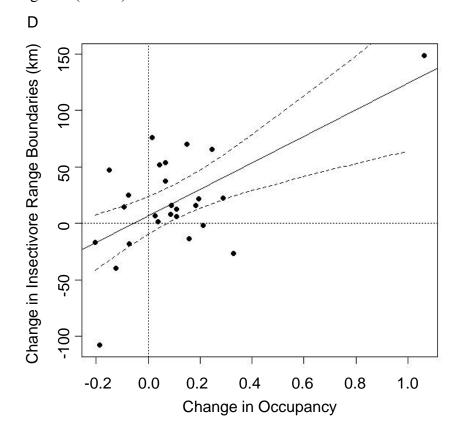
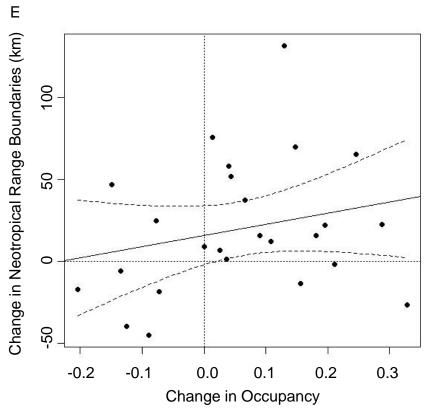


Figure 4 (cont'd)





For 20 northerly species in the range boundary analysis, 75% expressed southern range boundary shifts northward, while 25% showed southern range boundary shifts southward. When northerly species had positive occupancy change values, 94% demonstrated southern range boundary shifts northward (mean 19.4 km) (Figure 4a). When species had negative occupancy change values, they tended to have southern range boundary shifts northward (mean 16.3 km). I estimated a northward range boundary shift from a positive *y*-intercept value of 10.4 km (SE = 5.8 km, P = 0.08) (Table 5). However, I did not find strong evidence supporting probabilities for either hypothesis when comparing the two competing models for northerly species (Prob (H_A|data) = 0.57), and (Δ AIC₆ = 0.5, Prob (H_O|data) = 0.43) (Table 4).

Table 5. Estimating shift distances from the ordinary least squares regression in the range boundary analysis, Michigan Breeding Bird Atlas, 1983 to 2008.

Group	Shift distance (km)	Std. Error (km)	Pr(> t)
Northerly Species	10.41	5.76	0.088
Southerly Species	22.67	10.25	0.039
All Species	13.19	6.41	0.046

For 21 southerly species in the range boundary analysis, 61.9% expressed northern range boundary shifts northward (mean 68.0 km), while 38.1% showed northern range boundary shifts southward (mean 30.4 km). When southerly species had positive occupancy change values, most demonstrated northern range boundary shifts northward (mean 74.9 km) (Figure 4b). If species demonstrated a negative occupancy change value, they tended to have northern range boundary shifts southward (mean 33.9 km). I estimated a northward range boundary shift from a positive y-intercept value of 22.7 km (SE = 10.3 km, P = 0.04) (Table 5). Model probabilities support the

alternative hypothesis for northward range shifts while controlling for overall changes in occupancy (Prob (H_A |data) = 0.74), and ($\Delta AIC_c = 2.1, Prob$ (H_O |data) = 0.26) (Table 4).

Results from evaluating foraging guilds in the range boundary analysis indicated that for 26 insectivore species 73.1% showed northward shifts in their northern or southern range boundaries (mean 36.8 km). While this was less than changes seen among all non-insectivore species, of which 60% showed northward range boundary shifts (mean 51.8 km), more species in the insectivore guild demonstrated changes and had greater shifts than other individual guilds. When insectivore species demonstrated positive changes in occupancy, they generally shifted their range boundaries northward (Figure 4d). Fourteen northerly insectivore species demonstrated a mean northward shift in southerly range boundaries of 33.1 km. Among 12 southerly insectivore species, I found a mean northward shift of 35.8 km in northerly range boundaries. Among Neotropical species, those with positive changes in occupancy tended to shift their range boundaries northward (Figure 4e).

States of Occurrence

The states of occurrence analysis controlled for overall changes in distribution in the analyses for center of statewide occurrence and range boundary results. In the states of occurrence results for change in occupancy (Table D1), negative values indicated contracting distributions, and positive values indicated expanding distributions. Values distributed around zero indicated little to no changes in distribution and provided support toward the hypothesis for range shifts (Figure 5). After controlling for overall changes in distribution in the range boundary analysis, stronger evidence for the regression model indicated ranges have shifted poleward. Results from the evaluation of block status between Atlas I and II suggested consistency with changes in center of

occurrence and range boundaries, indicating range shifts have occurred; this consistency in results lends further support for overall range shifts among diverse species.

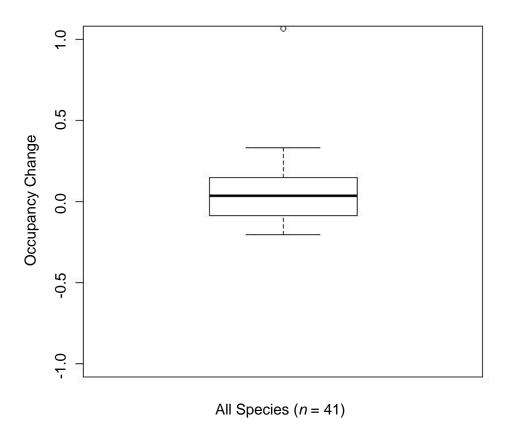


Figure 5. In the states of occurrence analysis, values for the change in occupancy distributed around zero suggest no overall changes in distribution. The change in occupancy is represented for all species. Expanding distributions have positive values toward 1.0, and contracting distributions have negative values moving to -1.0.

States of occurrence results for northerly species suggested northward trends in movement; at the most southerly latitudes in Michigan, species were absent from blocks, and as latitude increased, species exhibited block loss, block gain, and continued block presence, the expected pattern as species shift northward (Figure 6a-c). I found a similar pattern in the states of occurrence results among southerly species, which demonstrated a northward movement trend. Here, species remained present at the most southerly latitudes, and as latitude increased, demonstrated block loss, block gain, and remained absent at northerly latitudes. Similar to the results for northerly species, block loss and block gain occurred in the same pattern at the center of latitudinal occurrence. I found a third northward trend in the states of occurrence for both Neotropical and insectivore species groups, which is consistent with the other range characteristics indicating range shifts have occurred. Towards southerly latitudes, Neotropical and insectivorous species demonstrated block losses; as latitude became more northerly, species remained absent, experienced block gains, and then remained present.

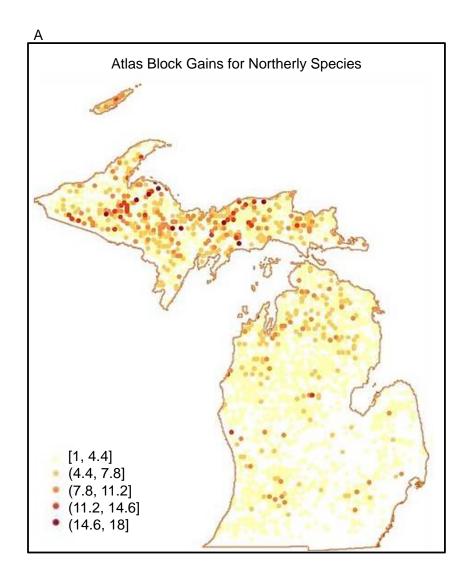


Figure 6a-c. Atlas block gains and losses for northerly and southerly species in the Michigan Breeding Bird Atlas I and II, 1983 to 2008. Each data point represents the number of species in each block that demonstrated a gain or loss. Gains represent blocks with no detection in Atlas I and detection in Atlas II. Losses represent blocks with species occurrence in Atlas I but not Atlas II.

Figure 6 (cont'd)

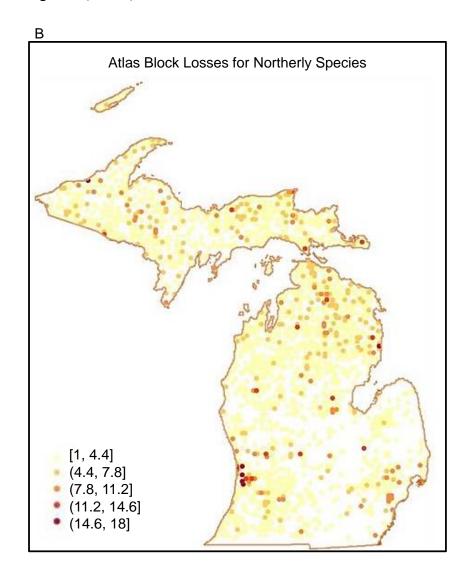
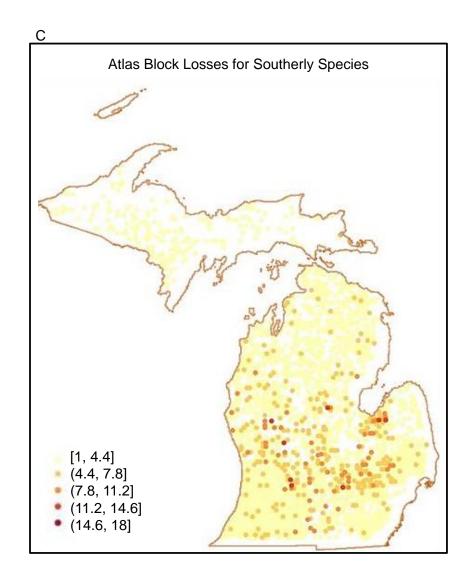


Figure 6 (cont'd)



DISCUSSION

My research may be among the first empirical studies in the Midwestern United States, and one of a small number in North America, to quantify systematic range shifts for a diverse taxonomic group at large scales. I found northward range shifts for the majority of species, with various breeding range distributions, foraging strategies, and migratory behaviors, (Figure 5, Table 2, Table 4, and Table 5). While the majority of species demonstrated range shifts, there was stronger support for northward shifts in the expanding ranges of southerly species, when compared with northerly species. My results also suggest that a nuanced pattern may exist among life history strategies within the larger context of range shifts.

I found consistent patterns within the results for the center of occurrence, range boundary, and states of occurrence, which indicate the majority of species have shifted their ranges polewards. After accounting for changes in occupancy, support for range shifts is demonstrated in results showing a similar magnitude and direction between poleward shifts in the center of occurrence, poleward shifts in range boundaries, and little change in states of occurrence between Atlas I and Atlas II. I found that when the ranges of southerly species were expanding, there were northward shifts in northern range boundaries, no change or a southward shift in the center of occurrence, and increased occurrence between Atlas I and Atlas II. When southerly species experienced range contractions, there were southward shifts in northern range boundaries, no change or a southward shift in the center of occurrence, and decreased occurrence between Atlas I and Atlas II. If the ranges of northerly species expanded, I found southward shifts in southern range boundaries, no change or a southward shift in the center of occurrence, and increased occurrence between Atlas I and Atlas II. When northerly species experienced range contractions, there were northward shifts in southern range boundaries, no change or a

northward shift in the center of occurrence, and decreased occurrence between Atlas I and Atlas II.

My findings elucidate trends in range shifts for Michigan, New York, and Ohio that appear to be unique to North America. These findings contribute to a growing body of evidence for climate-driven range shifts that represents heterogeneity in observable changes and regionspecific factors that influence long-term range trends (Chen et al. 2011; Tingley et al. 2012). European studies using coarse-scaled data on a limited number of species found northward shifts in northern range boundaries only (Thomas and Lennon 1999; Lemoine et al. 2007; Reif et 2010). In North America, Hitch and Leberg (2007) found evidence for northerly shifts in northern boundaries only, at an estimated rate of 2.35 km per year. A 2007 study that evaluated Christmas Bird Count data in the U.S. found similar northerly range shifts in northern boundaries only, at an estimated rate of 1.5 km per year (La Sorte and Thompson 2007). A recent metaanalysis across taxonomic groups and continents compared range shifts, and estimated that distributions were shifting to higher latitudes two to three times faster than previously reported, at a median rate of 16.9 km per decade (Chen et al. 2011). The same study also suggests that there is great variance in the rates of change for individual species, and that on average, about one-quarter of species groups shift in the opposite direction than predicted; these findings are consistent with those I identified for avian species in Michigan.

Of the few large-scale studies in North America that have quantified systematic range shifts for a diverse taxonomic group, two have analyzed breeding bird data for a similar group of species during a comparable period. Zuckerberg et al. (2009b) analyzed 129 species using the New York State Breeding Bird Atlas (1980-1985 and 2000-2005). They found that birds demonstrated northerly range shifts, with greater northerly shifts in southern range boundaries,

estimated at 11.4 km per year. Batdorf (2012) analyzed up to 67 species from Ohio Breeding Bird Atlas projects conducted during 1982-1987, and 2006-2011. Results indicated that birds in Ohio were demonstrating northerly shifts in northern boundaries, and stronger evidence for southerly shifts in southern boundaries. When evaluating my results along with those identified for a similar group of species in a different region of their North American breeding ranges, I found similarities in overall poleward trends for northerly range shifts in southerly species. In Michigan and Ohio, there was greater support for northerly range shifts in southerly species compared to northerly species. When comparing Michigan species based on their statewide distribution group, I also found greater support for northerly range shifts in southerly species.

In the center of occurrence analysis, I found a similar range of distances in southerly and northerly shifts in the center of occurrence between Michigan and New York. A smaller southerly shift for northerly species was the only trend in Ohio. While species in New York did not show systematic trends in the center of occurrence across differing life history traits, I found greater shifts among insectivorous species in Michigan. Although Zuckerberg et al. (2009b) found more species overall showed a northerly shift in the center of occurrence than in Michigan, I found a larger percentage of southerly species showed northerly shifts. Only a small percentage of the northerly species shifted their center of occurrence northward compared to species in New York State. In the range boundary analysis, I found that most northerly species expressed southern range boundary shifts northward, whereas in New York, there was no trend either way for the majority of northerly species moving northward or southward.

I found a similar distance in the estimated northward shift of southern range boundaries in Michigan (n = 20, 10.4 km, SE = 5.8) and New York (n = 43, 11.4 km, SE = 3.1); in Ohio there was a similar distance in the estimated shift for southern range boundaries (n = 68, 11.8)

km, SE = 6.1), but the shift was southward. Range boundary analysis for southerly species showed a comparable northward shift of northern boundaries in Michigan (n = 21, 22.7 km, SE = 10.3) and New York (n = 41, 15.9 km, SE = 8.5), and to a lesser magnitude in Ohio (n = 20, 6.8 km SE = 4.5). While Zuckerberg et al. (2009b) found support for a change in the mean latitude among groups of northerly and southerly species, my results provided support for southerly species, and to a lesser degree when grouped all together. This may be the result of the difference in the larger sample size between New York (n = 129), the smaller group of species common to Michigan (n = 41), and the influence this has in model probability results for the null or alternative hypotheses. Collectively, the results from Michigan, New York, and Ohio suggest that northward range shifts have occurred for many species across a large expanse of their continental ranges. The results also suggest that the northern boundary, or leading edge, may be more sensitive to climate change than the southern boundary, or trailing edge, of species.

While some degree of variation is expected along different regions in a continental range boundary, the consistency across Michigan, New York, and Ohio suggests the following:

- Across diverse species we can observe systemic trends in latitudinal range shifts, despite various regional factors;
- Despite a wide range in the magnitude and direction for individual species shifts, consistent trends emerge in northward range shifts for southerly species, and are suggested for insectivorous and Neotropical species; and
- Changes are not just regional or the result of fluid range boundaries, and collectively, allow for inference on large expanses of range boundaries.

There is a consistent direction and magnitude of shifts in center of occurrence for all species, and species common only to the three studies across Michigan, New York, and Ohio. For

example, among northerly species there was a mean shift southward in changes of the center of occurrence for all species (9.9 km) and species common in Michigan, New York, and Ohio (11.4 km). In general, all species evaluated versus only those common to Michigan, New York, and Ohio showed slightly greater values in the magnitude of shifts. When looking at the center of occurrence for northerly species by northward or southward shifts, the mean southward shifts were two to three times greater than the northward shifts, and ranged from 21.5 km to 23.4 km. While overall southerly species had a smaller magnitude in the change of center of occurrence in each of the three states, they showed a much stronger change when looking at northward or southward shifts only; southerly species also had greater northward shifts in center of occurrence than for northward shifts in center of occurrence for northerly species. This suggests southerly species (at their northern range boundaries), have been changing at a faster rate than northerly species (at their southern range boundaries). We may then expect to observe southerly species expand or shift distributions northward faster as populations colonize new areas. This may result in greater competition for resources as southerly species shift into areas where northerly species are slower to contract or shift their southern range boundaries.

Insectivorous and Neotropical species had bigger changes in the center of occurrence than other life history groupings; among northward shifts only, the mean distance for changes in the center of occurrence was between 8.3 km to 12.2 km, and for southward shifts only, the mean distance for changes was from 11.6 km to 17.6 km. Most southerly Neotropical species in Michigan, New York, and Ohio showed a much greater mean northward shift in northern range boundaries (28.8 km) and at greater distances (70.07 km, blue-gray gnatcatcher [*Polioptila caerulea*]) than mean southward shifts in northern boundaries (5.5 km) and distances (17.05 km, Louisiana waterthrush [*Seiurus motacilla*]). The majority of southerly species in Michigan, New

York, and Ohio showed greater mean northward shifts (45.8 km) in northern boundaries than southward shifts (4.3 km), and at greater distances northward (157.0 km, Carolina wren [Thryothorus ludovicianus]) than southward (17.05 km, Louisiana waterthrush). Most northerly Neotropical species demonstrated larger southern shifts in their southern boundary, and at greater distances southward (68.5 km in Ohio and 26.6 km in Michigan, blue-headed vireo [Vireo solitarius]), than northward (13.5 km in New York and 6.8 km in Michigan, chestnut-sided warbler [Dendroica pensylvanica]).

Although I predicted finding range shifts, I did not expect to find the same level of shifts relative to other studies. Not only do the Great Lakes play a significant role in shaping regional climate, their proximity also imposes barriers to species movements. Compared to geographical constraints in other studies, the broad north to south distance in Michigan was one factor that may have contributed to the range shifts I observed, even with the constraint of a smaller number of species analyzed. Michigan also lacks significant elevational variation, a factor that may have constrained species movement in other studies, and further contributed to the measurable changes I found in both northerly and southerly range boundaries in Michigan. For most species with southern range boundaries in Michigan, the core of their continental breeding ranges lays to the north in Canada. Despite this, I anticipated that the proximity of the Great Lakes would limit species movement, decreasing measurable shifts. Lake Superior creates a barrier north of the Upper Peninsula in Michigan, similar to the barriers imposed by Lake Erie to the north of Ohio, and Lake Ontario north of New York. Despite the barrier imposed by Lake Superior, I was able to identify contracting range shifts for northerly species, albeit to a lesser degree than shifts in southerly species. While I found northward shifts in southern range boundaries and consistent levels of occurrence, there were slightly dissimilar trends in changes of center of occurrence,

indicating less support for broad range shifts. In southern Michigan, the Lower Peninsula is bordered to the east by Lake Michigan and west by Lake Huron. These geographical features do not constrain poleward movement in a similar manner, and may be contributing factors in explaining why I found greater shifts in southerly species. Not only have southerly species demonstrated shifts in their northerly boundaries, they have also expanded their ranges northward into the state. There were nine new species, each with a historical range south of the state, that were observed in southern Michigan in Atlas II, further supporting my results for southerly species shifting northward.

My findings are in line with predictions of greater sensitivity for different foraging and migratory strategies, and support shifts in the center of occurrence and occupancy among insectivorous and Neotropical species. These species tend to be specialized in their feeding niches and resource selection, and may be limited in novel habitats and conditions (Lindell et al. 2007; Pineda-Diez de Bonilla et al. 2012). In addition to specialized resource selection, complex annual life cycles and endogenous constraints on adaptability further increase sensitivity to environmental changes among insectivorous and Neotropical migratory species (Visser et al. 1998; Pulido et al. 2001; Cotton 2003; Jonzén et al. 2006). My results in the center of occurrence analysis are also consistent with predictions of lesser sensitivity among resident, short-distance migratory, and omnivorous species, which demonstrated a lesser degree of shifts. As a function of selecting for broader resources, resident, short-distance migrants, and omnivorous species are better adapted to exploit a range of habitats for resource selection, and may exhibit less of a shift under changing ecological pressures (Turner et al. 1998; Thomas and Lennon 1999). While there was greater model support suggested for non-insectivorous and non-Neotropical species in range

boundary changes, I found greater support for northward shifts in the center of occurrence and the magnitude of shifts for insectivorous and Neotropical species.

Pervasive range shifts across diverse species and regions correspond with dramatic changes in climate, and provide compelling evidence for a correlative relationship between climate change and range shifts. During the last thirty years, there has been an abrupt escalation of temperature and precipitation changes in Michigan (Hayoe et al. 2010). Earlier timing of the last spring freezing date has caused the growing season to increase by seven days in the Midwest over the same time period. These abrupt changes correspond with the dramatic range shifts that have occurred during the same time interval, and parallel changes in New York and Ohio. Increasing average temperatures, greater precipitation rates, and advancing growing seasons closely influence the timing of insect emergence. We would then expect that species that maintain a close phenological relationship between the timing of insect emergence and breeding might be more sensitive to changing environmental conditions. As invertebrate species have shifted their phenology (Hodgson et al. 2011; Boggs and Inouye 2012; Ellwood et al. 2012), my results suggest that insectivorous and Neotropical species may have responded to these changes.

The results lending support for northward shifts for insectivorous species suggest that this foraging strategy may contribute to greater shifts under changing environmental conditions. As an extension of these trends, results from analyzing differential guild shifts provide a stronger link between insectivores, range shifts, and climate change, and help to describe specific ecological variables influencing range shifts. Differential shifts may be intensified by the interacting effects of climate change and the altered timing in seasonal activities including leaf out, egg laying, and insect emergence (Walther et al. 2002; Root et al. 2003; Charmantier et al. 2008; Kovacs et al. 2011). As a result, any mismatched phenological and trophic relationships

pose further ecological consequences, especially for species less likely to adapt to changes in the environment (Both and Visser 2001; Both et al. 2006; Stralberg et al. 2009).

While the BBA data analyzed here were not as complete or without error as was hoped for at the outset, they still represent an exceptionally useful resource that is likely to prove important to wildlife managers. Citizen science projects, including the BBA, pose challenges related to obtaining data, methodology, and data quality. Because of its nature as a large citizenscience project, certain aspects of the BBA may lack comprehensive data, such as observer effort. However, it is important to note that the extensive nature of the BBA provides a unique opportunity to evaluate for large-scale population trends. Through close collaboration with the professionals involved in the project and extensive exposure to data and background information, it is clear that the BBA is a valuable project for resource managers, the public, and research. Despite limitations or biases that may exist in the BBA data, extensive effort was directed at ensuring quality and limiting errors wherever possible. By recognizing this and incorporating important information and caveats within the project metadata, it is possible to utilize the BBA project as a resource for breeding bird information and ecological trends. It is important that future BBA projects implement consistent study design to allow for meaningful evaluation between projects. With this in mind, it is also of the highest importance to implement procedures to ensure accurate recording of observation data, as well as adequate collection of effort data. Future atlas projects stand to benefit greatly from increasingly available technology that allows observers to immediately and accurately record location, effort data, and observations. Future research using BBA projects may be strengthened by incorporating additional environmental variables, where available, that help describe the relationship between avian occurrence, potential sampling bias, coarse climate data, block-level land cover, and land use change over

time. Finally, given the increasing number of states with repeated atlas projects, there are significant opportunities to expand the scale of future research to evaluate for systematic shifts across large regions of the United States.

In conclusion, I found evidence for systematic northward range shifts in the northern boundary of southerly species and southern boundary of northerly species. These shifts have occurred in the breeding ranges of a diverse group of species. The similarity of my findings with those in New York and Ohio suggests that ecosystem changes in avian communities are pervasive at least across the Great Lakes region. Among species demonstrating range shifts, there are trends for greater changes in southerly species expanding north. Finally, consistency in systematic distribution changes that coincide with dramatic changes in climate suggest a correlative link between climate change and range shifts.

MANAGEMENT IMPLICATIONS

Faced with various ecological and economic consequences under climate change, my results provide needed quantification of large-scale changes in the Great Lakes Region. My results further provide an objective tool for monitoring large-scale ecological change. This is of great importance because finding objective measures of ecosystem change has been a core issue in the debate over climate change. Finding results indicating avian species have already shifted their statewide ranges builds a foundation to inform conservation policy, including habitat conservation plans, climate change adaption planning, and environmental reviews for managing state threatened and endangered species. Given the various consequences projected under climate models, it is important to understand how species have already responded under recent climate change. Hellman et al. (2010) modeled suitable bird habitat, weather data, and associated tree

species importance with global climate models to project positive and negative changes in habitat and distribution. They found that up to 76 of 147 avian species in the Great Lakes Region may lose habitat, and among these, up to 47 species will lose half. By evaluating these model predictions with my results for observable changes that have already occurred, we can identify species and associated habitats that are particularly vulnerable to habitat loss and climate change. Results for specific species, breeding habitats, and foraging resources are pertinent to the Michigan State Forest Management Plan (SFMP). Under the SFMP sections for special resource areas (Special Conservation Areas, High Conservation Value Areas, and Ecological Reference Areas), my results may help to identify species and associated habitats that are particularly vulnerable to ecological changes. As Michigan revisits its State Wildlife Action Plan, and planning for management of public lands, there will need to be accommodation for shifting species assemblages and attention paid to the longer-term affects of these changes. Incorporating species changes demonstrated in my results may provide a baseline for future assessments and identifying priority species for conservation. Between Atlas I and Atlas II, nine species with historic ranges south of the state shifted their ranges into southern Michigan. The expansion of southerly species may be an indicator that Michigan is likely to see expansion into the state by a larger array of taxa. Current populations may be stable, but as populations shift and new species create novel species assemblages, managers may need to revisit Vulnerability Assessments, plan for new species, and update adaptation master plans. The retreat of northerly species suggests that Michigan may be facing the loss of species that have long been native to the state, which may further reshape priorities for wildlife management. Management decisions will need to include accounting for invasive species shifting their ranges into Michigan, disease outbreak, forest management, decreased native taxa, and vulnerable species in marginal habitats. In setting

conservation priorities for native plants, animals, aquatic animals, and natural ecosystems, Michigan Natural Features Inventory (MNFI) now considers the influence of climate change and population trends. Incorporating my results for species that are demonstrating northward range shifts may be useful as MNFI updates their conservation priority rankings. The scope of management plans extends to Michigan's participation in the Upper Mississippi River and Great Lakes Region Joint Venture and implementation plans such as the Landbird Habitat Conservation Strategy and Waterbird Conservation Strategy. My results help identify species of conservation opportunity, and areas encompassed by current range shifts or in the direction of expected shifts. This research also addresses the near-term goal to increase knowledge of the potential impacts of climate change on priority bird species.

APPENDICES

APPENDIX A

Supplementary tables for BBA data, species groups used in analyses, and results for individual species

Table A1. Michigan Breeding Bird Atlas I (1983-1988) and Atlas II (2001-2008) observation
records and survey block summaries.

		Atlas I	Atlas I	Atlas II	Atlas I	Atlas II	Atlas I	Atlas II
Species	Atlas I &							
	Atlas II	& Atlas	blocks by	blocks	blocks	blocks	unique	unique
	total	II blocks	max	by max	with no	with no	blocks	blocks
	records	by max	breeding	breeding	records	records	with	with
		breeding	code	code			records	records
		code ^a						
BOBO	4880	4626	2335	2291	4738	5584	2335	1490
BRCR	2027	1875	745	1130	6328	6166	745	907
CSWA	4278	3955	1594	2361	5479	5381	1594	1692
GCKI	1695	1570	562	1008	6511	6303	562	770
NAWA	4837	4229	1393	2836	5680	5359	1393	1714
NOWA	1309	1285	562	723	6511	6461	562	612
PISI	897	868	482	386	6591	6715	482	359
PUFI	3033	2957	1400	1557	5673	5853	1400	1220
WTSP	4948	4452	1667	2785	5406	5408	1667	1665
ACFL	1347	1174	420	754	6653	6583	420	490
BWWA	2109	1849	729	1120	6344	6320	729	753
CERW	567	480	217	263	6856	6894	217	179
HOFI	5999	4519	682	3837	6391	4901	682	2172
NOCA	11355	8353	2804	5549	4269	4387	2804	2686
NOMO	373	354	161	193	6912	6911	161	162
YTVI	3607	3184	1188	1996	5885	5760	1188	1313
Total	53261	45730	16941	28789	96227	94986	16941	18184

^aAll references to "blocks by max breeding code" represent the observation records with the greatest breeding evidence for each species, per block, in each survey year.

Category	Code ^b	Behavior
Observed	О	Species (male or female) observed in a block during its breeding season, but no evidence of breeding. Not in suitable nesting habitat. Includes a wide range of species such as vultures or raptors, or a colonial nesting species not at the nesting colony.
Possible	РО	Species (male or female) observed in suitable nesting habitat during its breeding season.
	#	Species observed in suitable nesting habitat during its breeding season.
	X	Singing male present in suitable nesting habitat during its breeding season.
Probable	P	Pair observed in suitable habitat during its breeding season.
	S	Singing male present at the same location on at least two dates at least 7 days apart (5 or more) singing males on the same date during the breeding season.
	T	Permanent territory presumed through defense of territory (chasing individuals of the same species).
	C	Courtship behavior or copulation.
	N	Visiting probable nest-site.
	A	Agitated behavior or anxiety calls from adult.
	В	Nest building by wrens or excavation of holes by woodpeckers.
Confirmed	NB	Nest building by all except woodpeckers and wrens.
	PE	Physiological evidence of breeding (e.g. highly vascularized, edematous incubation [brood] patch or egg in oviduct based on bird in hand. To be used by experienced bird banders on local birds during the nesting season).
	DD	Distraction display or injury feigning.
	UN	Used nests or eggshells found. Caution: these must be carefully identified if they are to be accepted.
	FL	Recently fledged young (either precocial or altricial) incapable of sustained flight, restricted to natal area by dependence on adults or limited mobility.
	ON	Occupied nest: adults entering or leaving a nest site in circumstances indicating occupied nest. To be used for nests which are too high (e.g. the tops of trees) or enclosed (e.g. chimneys) for the contents to be seen.
	FY	Adults carrying food for young or feeding young.
	FS	Adult carrying fecal sac.
	NE	Nest with egg(s).
	NY	Nest with young seen or heard.

^aCourtesy of MDNR (2012b).
^bSimilar breeding codes were used in Atlas I and Atlas II and comply with NORAC standards.

Table C1. Northerly and s	southerly species groups	S.	
Northerly Species (n=20)		Southerly Species (n=	=21)
Common Name	Scientific Name	Common Name	Scientific Name
Blackburnian Warbler	Dendroica fusca	Acadian Flycatcher	Empidonax virescens
Black-throated Blue	Dendroica	Blue-gray	Polioptila caerulea
Warbler	caerulescens	Gnatcatcher	
Black-throated Green Warbler	Dendroica virens	Blue-winged Warbler	Vermivora pinus
Blue-headed Vireo	Vireo solitarius	Carolina Wren	Thryothorus ludovicianus
Boreal Chickadee	Poecile hudsonica	Eastern Screech-Owl	Megascops asio
Brown Creeper	Certhia americana	Eastern Towhee	Pipilo erythrophthalmus
Canada Warbler	Wilsonia canadensis	Field Sparrow	Spizella pusilla
Chestnut-sided Warbler	Dendroica pensylvanica	Grasshopper Sparrow	Ammodramus savannarum
Common Loon	Gavia immer	Great Egret	Ardea alba
Gray Jay	Perisoreus canadensis	Green Heron	Butorides virescens
Hermit Thrush	Catharus guttatus	Henslow's Sparrow	Ammodramus henslowii
Lincoln's Sparrow	Melospiza lincolnii	Hooded Warbler	Wilsonia citrine
Magnolia Warbler	Dendroica magnolia	Least Bittern	Ixobrychus exilis
Nashville Warbler	Vermivora ruficapilla	Louisiana Waterthrush	Seiurus motacilla
Northern Waterthrush	Seiurus noveboracensis	Northern Cardinal	Cardinalis cardinalis
Olive-sided Flycatcher	Contopus cooperi	Orchard Oriole	Icterus spurius
Ruby-crowned Kinglet	Regulus calendula	Red-bellied Woodpecker	Melanerpes carolinus
Swainson's Thrush	Catharus ustulatus	Red-shouldered Hawk	Buteo lineatus
Yellow-bellied Flycatcher	Empidonax flaviventris	Tufted Titmouse	Baeolophus bicolor
Yellow-bellied Sapsucker	Sphyrapicus varius	Willow Flycatcher	Empidonax traillii
•		Yellow-throated Vireo	Vireo flavifrons

Table C2. Insectivorous	and non-insectivorous spe	ecies groups.	
Insectivorous (n=26)		Non-insectivorous (n	=15)
Common Name	Scientific Name	Common Name	Scientific Name
Acadian Flycatcher	Empidonax virescens	Great Egret	Ardea alba
Blackburnian Warbler	Dendroica fusca	Red-shouldered Hawk	Buteo lineatus
Black-throated Blue Warbler	Dendroica caerulescens	Boreal Chickadee	Poecile hudsonica
Black-throated Green Warbler	Dendroica virens	Eastern Screech-Owl	Megascops asio
Blue-gray Gnatcatcher	Polioptila caerulea	Eastern Towhee	Pipilo erythrophthalmus
Blue-headed Vireo	Vireo solitarius	Field Sparrow	Spizella pusilla
Blue-winged Warbler	Vermivora pinus	Gray Jay	Perisoreus canadensis
Brown Creeper	Certhia americana	Lincoln's Sparrow	Melospiza lincolnii
Canada Warbler	Wilsonia canadensis	Northern Cardinal	Cardinalis cardinalis
Carolina Wren	Thryothorus ludovicianus	Red-bellied Woodpecker	Melanerpes carolinus
Chestnut-sided Warbler	Dendroica pensylvanica	Swainson's Thrush	Catharus ustulatus
Grasshopper Sparrow	Ammodramus savannarum	Yellow-bellied Sapsucker	Sphyrapicus varius
Henslow's Sparrow	Ammodramus henslowii	Common Loon	Gavia immer
Hermit Thrush	Catharus guttatus	Green Heron	Butorides virescens
Hooded Warbler	Wilsonia citrine	Least Bittern	Ixobrychus exilis
Louisiana Waterthrush	Seiurus motacilla		
Magnolia Warbler	Dendroica magnolia		
Nashville Warbler	Vermivora ruficapilla		
Northern Waterthrush	Seiurus noveboracensis		
Olive-sided Flycatcher	Contopus cooperi		
Orchard Oriole	Icterus spurius		
Ruby-crowned Kinglet	Regulus calendula		
Tufted Titmouse	Baeolophus bicolor		
Willow Flycatcher	Empidonax traillii		
Yellow-bellied	Empidonax		
Flycatcher	flaviventris		
Yellow-throated Vireo	Vireo flavifrons		

Table C3. Neotropical ar	nd non-neotropical specie	s groups.	
Neotropical (n=25)		Non-neotropical (n=1	16)
Common Name	Scientific Name	Common Name	Scientific Name
Acadian Flycatcher	Empidonax virescens	Carolina Wren	Thryothorus ludovicianus
Blackburnian Warbler	Dendroica fusca	Eastern Screech-Owl	Megascops asio
Black-throated Blue Warbler	Dendroica caerulescens	Gray Jay	Perisoreus canadensis
Black-throated Green Warbler	Dendroica virens	Northern Cardinal	Cardinalis cardinalis
Blue-gray Gnatcatcher	Polioptila caerulea	Red-bellied Woodpecker	Melanerpes carolinus
Blue-headed Vireo	Vireo solitarius	Tufted Titmouse	Baeolophus bicolor
Blue-winged Warbler	Vermivora pinus	Boreal Chickadee	Poecile hudsonica
Canada Warbler	Wilsonia canadensis	Brown Creeper	Certhia americana
Chestnut-sided Warbler	Dendroica pensylvanica	Common Loon	Gavia immer
Grasshopper Sparrow	Ammodramus savannarum	Eastern Towhee	Pipilo erythrophthalmus
Great Egret	Ardea alba	Field Sparrow	Spizella pusilla
Green Heron	Butorides virescens	Henslow's Sparrow	Ammodramus henslowii
Hooded Warbler	Wilsonia citrine	Hermit Thrush	Catharus guttatus
Least Bittern	Ixobrychus exilis	Red-shouldered Hawk	Buteo lineatus
Lincoln's Sparrow	Melospiza lincolnii	Ruby-crowned Kinglet	Regulus calendula
Louisiana Waterthrush	Seiurus motacilla	Yellow-bellied Sapsucker	Sphyrapicus varius
Magnolia Warbler	Dendroica magnolia	1	
Nashville Warbler	Vermivora ruficapilla		
Northern Waterthrush	Seiurus noveboracensis		
Olive-sided Flycatcher	Contopus cooperi		
Orchard Oriole	Icterus spurius		
Swainson's Thrush	Catharus ustulatus		
Willow Flycatcher	Empidonax traillii		
Yellow-bellied	Empidonax		
Flycatcher	flaviventris		
Yellow-throated Vireo	Vireo flavifrons		

Table D1. Results for each species in the center of occurrence, range boundary, and states of occurrence analyses.

Species	Scientific Name	D ^a	MS ^b	FG ^c	Center of Occurrence Shifts (km)	Range Boundary Shifts (km)	States of Occurrence Change
Acadian Flycatcher	Empidonax virescens	S	Neo	Insect	-1.27	37.32	0.07
Blue-gray Gnatcatcher	Polioptila caerulea	S	Neo	Insect	3.13	70.07	0.15
Blue-headed Vireo	Vireo solitaries	N	Neo	Insect	1.54	-26.64	0.33
Blackburnian Warbler	Dendroica fusca	N	Neo	Insect	-54.13	12.45	0.11
Boreal Chickadee	Poecile hudsonica	N	Short	Omni	5.54	9.36	-0.14
Brown Creeper	Certhia americana	N	Short	Insect	-79.87	8.26	0.09
Black-throated Blue Warbler	Dendroica caerulescens	N	Neo	Insect	-51.58	-1.89	0.21
Black-throated Green Warbler	Dendroica virens	N	Neo	Insect	-13.28	-13.25	0.16
Blue-winged Warbler	Vermivora pinus	S	Neo	Insect	-8.75	75.79	0.01
Carolina Wren	Thryothorus ludovicianus	S	Res	Insect	9.03	148.48	1.06
Canada Warbler	Wilsonia canadensis	N	Neo	Insect	-55.74	25.06	-0.08
Common Loon	Gavia immer	N	Short	Pisc	-34.05	35.30	0.03
Chestnut-sided Warbler	Dendroica pensylvanica	N	Neo	Insect	-19.37	6.82	0.03
Eastern Screech-Owl	Megascops asio	S	Res	Omni	3.76	-43.69	-0.10
Eastern Towhee	Pipilo erythro- phthalmus	S	Short	Omni	24.01	-0.07	-0.11
Field Sparrow	Spizella pusilla	S	Short	Omni	17.98	13.11	-0.12
Gray Jay	Perisoreus canadensis	N	Res	Omni	10.82	-2.28	-0.02

^aStatewide distribution: northerly (*N*) and southerly (*S*)

^bMigratory strategies: resident species (*Res*), short-distance migrants (*Short*), and long-distance Neotropical migrants (*Neo*)

^cBreeding season foraging guilds: carnivore (*Carn*), insectivore (*Insect*), omnivore (*Omni*), and piscivore (*Pisc*)

Table D1 (cont'd)

	Table D1 (cont'o	(h							
_	Great Egret	Ardea alba	S	Neo	Carn	-22.89	131.59	0.13	
	Green Heron	Butorides virescens	S	Neo	Pisc	8.88	-5.73	-0.13	
	Grasshopper Sparrow	Ammodramus savannarum	S	Neo	Insect	-49.91	46.98	-0.15	
	Henslow's Sparrow	Ammodramus henslowii	S	Short	Insect	52.01	-107.54	-0.19	
	Hermit Thrush	Catharus guttatus	N	Short	Insect	-29.94	6.08	0.11	
	Hooded Warbler	Wilsonia citrine	S	Neo	Insect	-6.00	65.44	0.25	
	Least Bittern	Ixobrychus exilis	S	Neo	Pisc	13.35	-44.90	-0.09	
	Lincoln's Sparrow	Melospiza lincolnii	N	Neo	Omni	-29.57	58.25	0.04	
	Louisiana Waterthrush	Seiurus motacilla	S	Neo	Insect	4.55	-17.05	-0.20	
	Magnolia Warbler	Dendroica magnolia	N	Neo	Insect	-68.73	15.64	0.18	
	Nashville Warbler	Vermivora ruficapilla	N	Neo	Insect	-45.04	15.69	0.09	
	Northern Cardinal	Cardinalis cardinalis	S	Res	Omni	5.11	70.52	-0.02	
	Northern Waterthrush	Seiurus noveboracensis	N	Neo	Insect	-19.68	1.42	0.04	
	Orchard Oriole	Icterus spurius	S	Neo	Insect	3.41	22.64	0.29	
	Olive-sided Flycatcher	Contopus cooperi	N	Neo	Insect	-26.47	-39.65	-0.12	
	Red-bellied Woodpecker	Melanerpes carolinus	S	Res	Omni	-13.91	96.80	0.18	
	Ruby-crowned Kinglet	Regulus calendula	N	Short	Insect	-62.82	14.45	-0.09	
	Red- shouldered Hawk	Buteo lineatus	S	Short	Carn	-34.83	-6.24	0.02	
	Swainson's Thrush	Catharus ustulatus	N	Neo	Omni	-60.28	8.97	0.00	
	Tufted Titmouse	Baeolophus bicolor	S	Res	Insect	-17.14	53.80	0.06	
	Willow Flycatcher	Empidonax traillii	S	Neo	Insect	10.97	-18.17	-0.07	

Table D1 (cont'd)

	<u> </u>						
Yellow-bellied	Empidonax	N	Neo	Insect	-81.74	21.96	0.20
Flycatcher	flaviventris						
Yellow-bellied	Sphyrapicus	N	Short	Omni	-23.89	42.50	0.16
Sapsucker	varius						
Yellow-	Vireo flavifrons	S	Neo	Insect	4.77	51.66	0.04
throated Vireo							

APPENDIX B

Vita

VITA

Name Jodi Ma	rie Kreuser
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Education		
Name and Location	<u>Dates</u>	<u>Diploma</u>
D.C. Everest High School Schofield, WI	1992-1996	Diploma
University of Wisconsin-Madison Madison, WI	2008-2010	B.S. Wildlife Ecology
Michigan State University East Lansing, MI	2010-2013	M.S. Fisheries and Wildlife Ecology
Employment		
Employer	<u>Dates</u>	Job Title
Michigan State University	2010-2013	Research Assistant
Michigan Department of Natural Resources	2011-2012	GIS Project Intern
University of Wisconsin-Madison	2009	Grassland Birds Field

Research Technician

LITERATURE CITED

LITERATURE CITED

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA.

Andresen, J., S. Hilberg, and K. Kunkel. 2012. Historical Climate and Climate Trends in the Midwestern USA. *In* U.S. National Climate Assessment Midwest Technical Input Report. J. Winkler, J. Andresen, J. Hatfield, D. Bidwell, and D. Brown, technical coordinators. Available from the Great Lakes Integrated Sciences and Assessments Center, http://glisa.msu.edu/docs/NCA/MTIT_Historical.pdf.

Araujo M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species-climate impact models under climate change. Global Change Biology 11:1504–1513.

Balanyá, J., J. M. Oller, R. B. Huey, G. W. Gilchrist, and L. Serra. 2006. Global genetic change tracks global warming in *Drosophila subobscura*. Science 313: 1773-1775.

Batdorf, K. E. 2012. Distributional changes in Ohio's breeding birds and the importance of climate and land cover change. Thesis, The Ohio State University, Columbus, USA.

BirdLife International. 2012. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 18/09/2012.

Boggs, C. L. and D. W. Inouye. 2012. A single climate driver has direct and indirect effects on insect population dynamics. Ecology Letters 15: 502-508.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441: 81-83.

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.

Bradbury, R. B., J. W. Pearce-Higgins, S. R. Wotton, G. J. Conway, and P. V. Grice. 2011. The influence of climate and topography in patterns of territory establishment in a range-expanding bird. Ibis 153: 336-344.

Bradshaw, W. E. and C. M. Holapzfel. 2006. Climate change – evolutionary response to rapid climate change. Science 312: 1477-1478.

Brewer, R., G. A. McPeek, and R. J. Adams. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing, USA.

Brohan, P., J. J. Kennedy, I. Harris, S. F. B. Tett, and P. D. Jones. 2006. Uncertainty estimates in regional and global observed temperature changes: A new data set from 1850. Journal of Geophysical Research, 111, D12106, doi:10.1029/2005JD006548, 2006.

Brommer, J. E. 2004. The range margins of northern birds shift polewards. Annales Zoologici Fennici 41: 391-397.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320: 800-803.

Chen, I. C., Jane K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024-1026.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr and P. Whetton. 2007: regional climate projections. *In:* Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences of the United States of America 100: 12219-12222.

Davies T.J., A. Purvis, and J. L. Gittleman. 2009. Quaternary climate change and the geographic ranges of mammals. American Naturalist 174: 297-307

DeGraaf, R.M., N. G. Tilghman, and S. H. Anderson. 1985. Foraging guilds of North American birds. Environmental Management 9: 493–536.

DeGraaf, R.M. and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Hanover, New Hampshire, USA.

Donnelly, A., T. Cooney, E. Jennings, E. Buscardo, and M. Jones. 2009. Response of birds to climatic variability-evidence from the western fringe of Europe. International Journal of Biometeorology 53: 211-220.

Ellwood, E. R., J. M. Diez, I. Ibanez, R. B. Primack, H. Kobori, H. Higuchi, and J. A. Silander. 2012. Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? Oecologia 168: 1161-1171.

Gaston, K. J. 1996. The multiple forms of the interspecific abundance-distribution relationship. Oikos 76: 211-220.

Gaston, K. J. and T. M. Blackburn. 2000. Pattern and Process in Macroecology. Blackwell Science, Malden, Massachusetts, USA.

Gibbons, D. W., P. F. Donald, H.G. Bauer, L. Fornasari, and I. K. Dawson. 2007. Mapping avian distributions: the evolution of bird atlases. Bird Study 54: 324-334.

Gienapp, P., R. Leimu, and J. Merila. 2007. Responses to climate change in avian migration time – microevolution versus phenotypic plasticity. Climate Research 35: 25-35.

Gill, F. B. 2007. Ornithology. W. H. Freeman. New York. USA.

Hayhoe, K., J. VanDorn, T. Corley II, N. Schlegal, and D. Wuebbles. 2010. Regional climate change projections for Chicago and the US Great Lakes. Journal of Great Lakes Research 36 (Supplement 2), 7–21.

Hellman, J. J., K. J. Nadelhoffer, L. R. Iverson, L. H. Ziska, S. N. Matthews, P. Meyers, A. M. Prasad, and M. P. Peters. 2010. Climate change impacts on terrestrial ecosystems in metropolitan Chicago and its surround, multi-state region. Journal of Great Lakes Research 36: 74-85.

Hickling R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12: 450–455.

Hitch, A. T. and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. Conservation Biology 21: 534-539.

Hodgson, J. A., C. D. Thomas, T. H. Oliver, B. J. Anderson, T. M. Brereton, and E. E. Crones. 2011. Predicting insect phenology across space and time. Global Change Biology 17: 1289-1300.

Huntley B., Y. C. Collingham, R. E. Green, G. M. Hilton, C. Rahbek, and S. G. Willis. 2006. Potential impacts of climatic change upon geographical distribution of birds. Ibis 148: 8-28.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, England.

Jiménez-Valverde, A., N. Barve, A. Lira-Noriega, S. Maher, Y. Nakazawa, M. Papeş, J. Soberón, J. Sukumaran, and A. Townsend Peterson. 2011. Dominant climate influences on North American bird distributions. Global Ecology and Biogeography 20: 114-118.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang, and N. C. Stenseth. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312: 1959-1961.

Kovacs, S. T. Csorgo, A. Harnos, P. Fehervari, and K. Nagy. 2011. Change in migration phenology and biometrics of two conspecific *Sylvia* species in Hungary. Journal of Ornithology 152: 365-373.

La Sorte, F. A., and F. R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. Ecology 88: 1803-1812.

Laughlin, S. B., D. P. Kibbe, and P. F. J. Eagles. 1982. Atlasing the distribution of breeding birds in North America. American Birds 36: 6-19.

Lemoine N., H. Bauer, M. Peintinger, and K. Boehning-Gaese. 2007. Effects of climate and land-use change on species abundance in a central European bird community. Conservation Biology 21: 495-503.

Li, R., H. Tian, and X. Li. 2010. Climate change induced range shifts of Galliformes in China. Integrative Zoology 5: 154-163.

Lindell, C. A., S. K. Riffell, S. A. Kaiser, A. L. Battin, M. L. Smith, and T. D. Sisk. 2007. Edge responses of tropical and temperate birds. The Wilson Journal of Ornithology 119: 205-220.

MDNR. 2012a. The Michigan Breeding Bird Atlas II Project Product Dataset. The Michigan Department of Natural Resources (MDNR), Wildlife Division, Lansing, Michigan; contract project coordinated by the Kalamazoo Nature Center, Kalamazoo, Michigan. Online connection to BBA2 Information: http://michigan.gov/dnr/0,1607,7-153-10370_35523---,00.html and http://www.michigandnr.com/ftp/requested_geospatial/wildlife_breeding-bird-atlas2.

MDNR. 2012b. The Michigan Breeding Bird Atlas II Project Documentation and Metadata. The Michigan Department of Natural Resources (MDNR), Wildlife Division, Lansing, Michigan; contract project coordinated by the Kalamazoo Nature Center, Kalamazoo, Michigan. Online connection to BBA2 Information: http://michigan.gov/dnr/0,1607,7-153-10370_35523---,00.html and http://www.michigandnr.com/ftp/requested_geospatial/wildlife_breeding-bird-atlas2.

Melles, S. J., M. J. Fortin, K. Lindsay, and D. Badzinski. 2011. Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. Global Change Biology 17: 17-31.

Møller, A. P., E. Flensted-Jensen, K. Klargor, W. Ardal, and J. T. Nielsen. 2010. Climate change affects the duration of the reproductive season. Journal of Animal Ecology 79: 777-784.

Niven, D. K., G. S. Butcher, and G. T. Bancroft. 2009. Christmas Bird Counts and climate change: northward shifts in early winter abundance. American Birds, 63: 10-15.

Parmesan, C. 1996. Climate and species' range. Nature 382: 765-766.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Parmesan, C., N. Ryrolm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullber, T. Tammaru, W. J. Tennett, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographic ranges of butterfly species associated with regional warming. Nature 399: 579-583.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42.

Pineda-Diez de Bonilla, E., J. L. Len-Cortes, and J. L. Rangel-Salazar. 2012. Diversity of bird feeding guilds in relation to habitat heterogeneity and land-use cover in a human-modified landscape in southern Mexico. Journal of Tropical Ecology 28: 369-376.

Poole, A. (Editor). 2005. The Birds of North America Online: http://bna.birds.cornell.edu.proxy2.cl.msu.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

Pounds, J. A., M. R. Bustamante, L. A. Coloma, J.A. Consuegra, M. P. L. Fodgen, P. N. Foster, E. La Marca, K. L. Master, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sanchez-Azofeifa, C. J. Still, and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161-167.

Przybylo, R., B. C. Sheldon, and J. Merilä. 2000. Climatic effects on breeding and morphology: evidence for phenotypic plasticity. Journal of Animal Ecology 69: 395-403.

Pulido, F. P. Berthold, G. Mohr, and U. Querner. 2001. Heritability of the timing of autumn migration in a natural bird population. Proceedings of the Royal Society B-Biological Sciences 268: 953-959.

Réale, D., A. G. MacAdam, S. Boutin, and D. Bertaux. 2003. Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society of London B-Biological Sciences 270: 591-596.

Reif, J., K. S. Astny, and V. Bejcek. 2010. Contrasting effects of climatic and habitat changes on birds with northern range limits in central Europe as revealed by an analysis of breeding bird distribution in the Czech Republic. Acta Ornithologica 45: 82-89.

Robbins, C. S. and P. H. Geissler. 1990. Survey methods and mapping grids. Pages 4.1-4.20 *in*: C. R. Smith, editor. Handbook for atlasing American breeding birds. Woodstock, Vermont Institute of Natural Science, USA.

Root T. L., J. T. Price, and K. R. Hall. 2003. 'Fingerprints' of global warming on animals and plants. Nature 421: 57-60.

Sauer J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 1999. The North American Breeding Bird Survey, results and analysis 1966-1998. Version 98.1. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schwartz, M.D., R. Ahas, and A. Aasa. 2006. Onset of spring starting earlier across the Northern Hemisphere. Global Change Biology 12: 343-351.

Sparks, T. H., F. Bairlein, J. G. Bojarinova, O. Huppop, E. A. Lehikoinen, K. Rainio, L. V. Sokolov, and D. Walker. 2005. Examining the total arrival distribution of migratory birds. Global Change Biology 11: 22-30.

Stralberg, D., D. Jongsomjit, C. A. Howell, M. A. Snyder, J. D. Alexander, J. A. Wiens, and T. L. Root. 2009. Re-shuffling of species with climate disruption: a no-analog future for California Birds? PLoS ONE 4(9): e6825. doi:10.1371/journal.pone.0006825.

Thomas, C.D., A. M. A. Franco, and J. K. Hill. 2006. Range retractions and extinction in the face of climate warming. Trends in Ecology and Evolution 21: 415–416.

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

Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology 18: 3279-3290.

Turner, J. R. G., J. J. Lennon, and J. A. Lawrenson. 1998. British bird species distributions and the energy theory. Nature 335: 539-541.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parsus major*). Proceedings of the Royal Society B-Biological Sciences 265: 1867-1870.

Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Advances in Ecological Research 35: 89-110.

Walther, G. R., S. Berger, M. T. Sykes. 2005. An ecological 'footprint' of climate change. Proceedings of the Royal Society B-Biological Sciences 272: 1427-1432.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

Zuckerberg, B., W. F. Porter, and K. Corwin. 2009a. The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. Journal of Animal Ecology 78: 172-181.

Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009b. Poleward shifts in breeding bird distributions in New York State. Global Change Biology 15:1866-1883.