

UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

PATTERNS IN HABITAT SELECTION BETWEEN BREEDING AND WINTERING
GROUNDS OF NEOTROPICAL MIGRANT PASSERINES

A THESIS
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
Degree of
MASTER OF SCIENCE

By
MARYANNE E. DANTZLER-KYER
Norman, Oklahoma
2017

PATTERNS IN HABITAT SELECTION BETWEEN BREEDING AND WINTERING
GROUNDS OF NEOTROPICAL MIGRANT PASSERINES

A THESIS APPROVED FOR THE
DEPARTMENT OF BIOLOGY

BY

Dr. Michael Patten, Chair

Dr. Jeffrey Kelly

Dr. Lara Souza

© Copyright by MARYANNE E. DANTZLER-KYER 2017
All Rights Reserved.

Acknowledgements

First, I would like to thank my advisor, Dr. Michael Patten. Thank you for providing me with never-ending guidance, reassurance, and support throughout my work on this project; your influence has greatly and permanently impacted my education and professional growth. To Dr. Lara Souza, thank you for helping me through some of the most difficult challenges I experienced with the fieldwork for this project and for always having an open door. Thank you to Dr. Jeffrey Kelly for helping me think through interpretations and for introducing me to new questions and ideas. To Wayne Stewart, thank you for helping me get all of the bugs worked out with my statistical models. I want to thank all of my lab mates for keeping things entertaining, challenging my perspectives, and encouraging me to be the best I can be. To Nate DeAngelis, thank you for being a constant support, making me laugh when I felt like crying, and for just being there anytime I needed someone. To Shelby Burrige, thank you for giving me confidence, keeping me motivated, and being a great friend and confidant. To Gwen Burgess, thank you for always being there for me, for keeping me positive, and for listening to me complain endlessly. To David Hille, thank you for showing me the ropes, offering me the best advice, and reassuring me constantly. Thank you to my mom, I could never thank you enough for all of the unconditional love and support you have provided me; I owe you so much. Jesse, thank you for your patience with me through all of this, for believing in me when I am unable to believe in myself, and for loving me despite my numerous flaws. I owe so much to so many others not mentioned here, as well. The love and support of those closest to me has allowed me to grow and succeed; for that, I will be forever grateful.

Table of Contents

Acknowledgements	iv
List of Tables	vi
List of Figures	vii
Abstract	ix
Chapter 1	1
Introduction	1
Methods	7
Data Analysis	9
Results	11
Discussion	16
References	22
Appendix A: Tables	28
Appendix B: Figure Legend	32
Appendix C: Figures	34

List of Tables

Chapter 1

Table 1. Summary of uninformed relationships between microclimate variables and the presence of migrants on the breeding and wintering grounds. ↑ indicates a positive relationship, while ↓ indicates a negative relationship. Percent value represents the percentage of posterior parameter values that were positive or negative (depending on arrow).....	29
Table 2. Summary of relationships between vegetation variables and the presence of migrants on the breeding and wintering grounds. ↑ indicates a positive relationship, while ↓ indicates a negative relationship. Percent value represents the percentage of posterior parameter values that were positive or negative (depending on arrow).....	30
Table 3. DIC scores for ‘uninformed’ and ‘informed’ breeding ground models. Uninformed and informed DIC scores for the microclimate and vegetation models of each species are compared. Bolded scores represent models that were more predictive	31
Table 4 . DIC scores for ‘uninformed’ and ‘informed’ wintering ground models. Uninformed and informed DIC scores for the microclimate and vegetation models of each species are compared. Bolded scores represent models that were more predictive.....	32

List of Figures

Chapter 1

- Figure 1.** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Hooded Warbler (HOWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....35
- Figure 2.** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Summer Tanager (SUTA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....36
- Figure 3.** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Black-and-white Warbler. (BAWA) Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....37
- Figure 4.** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the White-eyed Vireo (WEVI). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....38
- Figure 5.** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Kentucky Warbler (KEWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....39
- Figure 6.** Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Black-and-white Warbler (BAWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....40
- Figure 7.** Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Hooded Warbler (HOWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....41

Figure 8. Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the White-eyed Vireo (WEVI). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....42

Figure 9. Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Summer Tanager (SUTA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....43

Figure 10. Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Kentucky Warbler (KEWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.....44

Abstract

Migratory animals must select suitable habitat in different locations to take advantage of abundances of resources and escape harsh climates during seasonal changes. Niche tracking occurs when migratory animals fill the same niche space on the breeding and wintering grounds. Overlap of niche space is expected to occur because of physiological or behavioral needs, even though resources available on native and migratory ranges may differ. Neotropical birds migrate to breed where there is an abundance of potential mates and nesting sites and to winter where environmental conditions are less harsh. My objective was to assess whether Neotropical migrants tracked niche space between the breeding and wintering grounds. I measured microclimate and vegetation structure in the Ouachita National Forest (breeding) in southeastern Oklahoma and La Milpa Field Station in Orange Walk, Belize (wintering). I predicted that microclimate would be tracked by more species than vegetation structure. I did not find strong evidence that niche tracking occurred in Neotropical migrants for microclimatic conditions or vegetation structure, even though some patterns were apparent between microclimate and vegetation structure selection on the breeding and wintering grounds. Investigations of niche tracking at finer scales will help further our understanding of which physiological constraints and necessary resources contribute most to habitat selection in breeding and wintering grounds of migratory bird species, and how to predict future distributions in the face of major environmental changes.

Keywords: microclimate, vegetation structure, niche tracking, Bayesian analysis, habitat selection

Chapter 1

Patterns in habitat selection between breeding and wintering grounds of Neotropical migrant passerines

Authors: Maryanne E. Dantzler-Kyer

Introduction

Environmental conditions are dynamic across time and space. Therefore, animals must select habitat within their geographical range that offers suitable environmental conditions for their specific physiological and behavioral needs (Vandermeer 1972; Root 1988; Piper 2011; Bonebrake & Deutsch 2012; Carroll et al. 2015; Laube et al. 2015). Environmental conditions influence the availability of resources, which may help to determine where animals occupy space (Johnson 1980; Parrish 1995; Dawson et al. 2005; Patten et al. 2005; Champlain et al. 2009; Wiens et al. 2010; Hollander et al. 2011; Piper 2011; Sam et al. 2014). At times when resources are scarce, and environmental conditions are no longer favorable, some animals shift their geographical ranges (Gómez et al. 2016). Migratory animals must select suitable habitat in different locations to take advantage of abundances of resources and escape harsh climates during seasonal changes (Salewski & Bruderer 2007; Zink 2011; Gómez et al. 2016).

Neotropical birds migrate to breed and winter where environmental conditions are favorable (Joseph & Stockwell 2000; Gómez et al. 2016). Migration to the breeding

grounds is driven by the need to reproduce where there is an abundance of potential mates and nesting sites; however, escape from harsh winter conditions and low food availability on the breeding grounds drives migration to the wintering grounds (Salewski & Bruderer 2007; Zink 2011; Shaw & Couzin 2013). Because animals have specific physiological and behavioral constraints, niche overlap is expected to occur between the breeding and wintering grounds of Neotropical migrants, even though available resources may differ between breeding and wintering grounds (Laube et al. 2015). Overlap in climatic niche, or niche space defined by environmental conditions, occurs mainly because of the physiological limitations of these animals (Monahan & Tingley 2012; Laube et al. 2015). Temperature is considered to be a most important factor of climatic niche because so many biological functions are thermally regulated (Root 1988; Gómez et al. 2016). Migratory birds are expected to follow a set of climatic conditions and settle into a similar climatic niche to their breeding grounds when they select habitat in wintering grounds; this is called niche tracking. Neotropical migrant species track niche space more often than resident species (Gómez et al. 2016). This is probably explained by the wider climatic niche breadth of migrants and their exposure to more extreme changes in climate, which forces them to find favorable conditions in variable environments more often than resident species. Niche-tracking behavior in migrants also may be explained by physiological dependence on specific conditions or resources that are closely associated with a particular climate (Nakazawa et al. 2004; Monahan & Tingley 2012; Gómez et al. 2016). Current niche-tracking literature primarily focuses on broad-scale climate modeling to predict where migrant bird species will occur during seasonal shifts. These studies investigated the effects of

temperature, precipitation, and vapor pressure at large scales (Joseph & Stockwell, 2000; Nakazawa et al. 2004; Monahan & Tingley 2012; Laube et al. 2015; Gómez et al. 2016). It is important to understand niche space occupancy during seasonal movements at finer scales, too. Investigations of niche tracking at finer scales will help further our understanding of the physiological constraints and necessary resources that contribute most to habitat selection in breeding and wintering grounds of migratory bird species (Levey & Stiles 1992; Taylor & Norris 2007), and how to predict future distributions in the face of major environmental change (Whitbeck et al. 2016). Climate variables and vegetation characteristics are important predictors of habitat selection for birds at finer scales (Patten & Smith-Patten 2012; Sam et al. 2014; Zellweger et al. 2016).

Microclimate, or climate at small scales, allows animals to occupy space with favorable conditions within an otherwise highly variable environment (Ewers & Banks-Leite 2013; Carroll et al. 2015). Microclimate is distinctive within patches across a geographical landscape, and these differences in microclimate determine species distributions within any given habitat (Chen et al. 1999). In forest habitats, environmental gradients occur with the presence of forest edges or gaps. Edge effects, or the measurable differences in microclimate due to the creation of a forest edge, are detectable 15–184 m into forests worldwide, depending on which microclimate variable is being measured (Carmago & Kapos 1995; Chen et al. 1995; Murcia 1995; Didham & Lawton 1999; Davies-Colley et al. 2000; Gehlhausen et al. 2000; Ewers & Banks-Leite 2013). Based on the needs of individuals, microclimate selection allows for better survival because it offers climate buffers from extreme conditions (Francis 1968; Gloutney & Clark 1997; Patten & Smith-Patten 2012; Carroll et al. 2015; Pollock et al.

2015; González del Pliego et al. 2016). For example, shaded, cooler habitats are often selected for when ambient temperatures are extremely warm, while less shaded, warmer habitats are selected for when temperatures are cold (Bell et al. 2010; Krijgsveld et al. 2003; Larsson et al. 2013; Lee-Yaw et al. 2015). Selection of a specific microclimate reduces energetic costs of thermoregulation and foraging (Gloutney & Clark 1997; Chaplin et al. 2002; Krijgsveld et al. 2003; Dawson et al. 2005; Bell et al., 2010; du Plessis et al. 2012; Gruebler et al. 2014; Pollock et al. 2015). Birds are sensitive to changes in microclimate and experience unfavorable consequences due to these changes (Sam et al. 2014; Zellweger et al. 2016). Any change in temperature, humidity, or light intensity could be detrimental to fitness (Francis 1968; Root 1988; Dawson et al. 2005; Carroll et al. 2015). Temperature and humidity have especially important effects on nest success and nestling development (Francis 1968; Calder 1973; Rahn et al. 1977; Cooper 1999; Chaplin et al. 2002; Dawson et al. 2005). Tropical bird species usually prefer habitat that is under a closed canopy with low-light conditions (Patten & Smith-Patten 2012; Pollock et al. 2015). In fact, tropical residents may select habitat conditional on the light environment (Patten & Smith-Patten 2012). Although microclimate in forested areas is affected by edge orientation, time of day, and seasonal weather changes, microclimate depends primarily on vegetation and can become drastically altered with changes in vegetation structure (Francis 1968; Chazdon & Fetcher 1984; Swaine & Whitmore 1988; Matlack 1993; Chen et al. 1999; Gehlhausen et al. 2000; Champlin et al. 2009; Carroll et al. 2015).

Numerous studies have found that vegetation structure is the most important variable in determining habitat selection of birds, including Neotropical migrants (Karr

& Roth 1971; Karr & Freemark 1983; Parrish 1995; Kearney et al. 2007; Champlain et al. 2009; Seavy & Alexander 2011; Besnard et al. 2015; Zellweger et al. 2016).

Vegetation provides many resources including food, nest sites, and refuge from predators and extreme environmental conditions (Anderson & Shugart Jr. 1974; Levey & Stiles 1992; Parrish 1995; Haby et al. 2013; Besnard et al. 2015; Zellweger et al. 2016). Vegetation directly affects microclimate, which provides favorable environmental conditions for animal species (Adolph 1990; Chen et al. 1993; Chen et al. 1995; Chen et al. 1999; Dawson et al. 2005; Carroll et al. 2015). Forest plant species richness depends on macroclimate, and vegetation height and density are often related to successional stage. Available light contributes to the growth and maintenance of understory vegetation (Chazdon & Fetcher 1984; Chazdon & Pearcy 1991; Montgomery & Chazdon 2001; Zellweger et al. 2016). Canopy density directly affects light penetration into the canopy, which leads to a highly variable light environment throughout forests (Chazdon & Pearcy 1991).

Regardless of species composition, dense forest provides more stable temperatures than clear-cut forest (Chen et al. 1993; Ewers & Banks-Leite 2013). Temperatures, wind speeds, and light levels are higher at the forest edges and clear-cut areas than the interior forest. Temperature and light are inherently correlated, such that temperature increases with light (Matlack 1993; Chen et al. 1995; Chen et al. 1993; Chen et al. 1999; Didham & Lawton 1999; Davies-Colley, et al. 2000; Pollock et al. 2015; González del Pliego et al. 2016). Relative humidity and vapor pressure deficit are also dependent on light availability and temperature (Chen et al. 1993; Matlack 1993). During the day, when light availability and temperatures are high, interior forests

experience higher relative humidity than open areas; the opposite is true at night (Chen et al. 1993). Wind speed decreases with distance from forest edges (Chen et al. 1993; Chen et al. 1995; Patten & Smith Patten 2012). Vegetation provides climate-buffering zones that protect relatively stable interior forest microclimate from exposure to the variable climatic conditions of open areas surrounding forests (Matlack 1993; Ewers & Banks-Leite 2013; Pollock et al. 2015). Vegetation height may be an important factor for predicting bird species richness in forest habitats (Zellweger et al. 2016), yet vegetation structure is dynamic. Changes in vegetation can lead to decreased resource availability, fewer microhabitats, and altered microclimate, which ultimately leads to less suitable habitat and decreased animal species richness (Chazdon & Fetcher 1984; Chen et al. 1995; Murcia 1995; Gehlhausen et al. 2000; Champlain et al. 2009; González del Pliego et al. 2016).

The purpose of this study was to determine if niche-tracking behavior occurred in Neotropical migrant birds between their breeding and wintering grounds. I measured microclimate and vegetation structure at occupied sites to determine habitat characteristics of five migrant species. I predicted that niche tracking would occur in Neotropical migrants, and migrants would occur in habitats with the same microclimate and vegetation structure in both the breeding and wintering grounds. Specifically, I predicted that microclimate would be more predictive for migratory species occurrence than vegetation structure on the breeding and wintering grounds. The results of this study will provide insight to conservation managers on which environmental conditions and resources are most important for migratory bird species in breeding and wintering habitats.

Methods

Study sites

Breeding-ground habitat was studied at the Ouachita National Forest located in Le Flore and McCurtain Counties of southeastern Oklahoma (~34.7° N, 94.6° W). The forest is dominated by loblolly pine (*Pinus taeda*) and oak-hickory mixed hardwood forest and occupies approximately 10,702 ha. Elevations varies from 150 to 820 m. Common management practices include prescribed fire and timber harvest.

Wintering-ground habitat selection was studied at La Milpa Field Station, Orange Walk, Belize (~17.8° N, 89° W). The field station is located within the Rio Bravo Conservation and Management area and is managed by the Programme for Belize. The semi-moist, lowland forest has elevation upwards of 150 m. Forested area within this reserve is approximately 54,154 ha, and the surrounding land is primarily used for agriculture.

Field methods

Birds were surveyed on their breeding grounds in June–August 2016 and April 2017 (n = 60 points; 14–16 Jun, 24–26 Jun, 23–24 Jul, 30–31 Jul, 16–17 Aug, 8–9 Apr), while they were surveyed on their wintering grounds in January 2017 (n = 63 points; 4–18 Jan). No surveys took place on overly hot, windy, or wet days. Five species of migrants were used to represent the Neotropical migrant community present in both Oklahoma and Belize. These birds represented three families and occupied different parts of the forest canopy. Focal species included the Black-and-white Warbler

(*Mniotilta varia*), Kentucky Warbler (*Geothlypis formosa*), Hooded Warbler (*Setophaga citrina*), White-eyed Vireo (*Vireo griseus*), and Summer Tanager (*Piranga rubra*). Neotropical migrants were recorded if seen or heard while traveling along forest roads or trails in both forests. Data were collected at a center point, or the area within closest proximity to the focal bird. All focal Neotropical migrants were recorded if present within a 25-m radius of the center point, and all points were at least 50-m apart to avoid recounting any particular individual. A Garmin GPSMAP 64 unit was used to determine the location of each point.

Three environmental variables and five microclimate variables were measured at each point. Environmental variables included rainfall (none or light), ambient wind (Beaufort scale), and percent cloud cover (%). Microclimate variables included temperature (°C), heat index (°C), relative humidity (%), wind speed (m/s), and light intensity (kLux). All microclimate variables were measured at ground level using a Kestrel 3500 Pocket Weather Meter (temperature, heat index, wind speed, and humidity) and an Extech EasyView EA30 digital light meter (light).

Vegetation structure was measured at each point with a 1x1 m quadrat used to determine percent cover of live vegetation, leaf litter, and bare ground at each center point. Ground vegetation cover was estimated only at the center point. The vegetation cover at the center point was found to represent the entire 25-m radial plot by surveying random plots in all four cardinal directions of the center point in the breeding grounds; random plots did not differ significantly from vegetation cover found at the center point. Percent canopy cover was measured using a manual GRS densitometer. Canopy height was estimated from the center point, and digital photographs were taken of understory

vegetation in all four cardinal directions as a proxy for understory density. Photos of understory vegetation were later assigned a category to describe density, 1 – 5 (1 = very sparse, 0-10% cover; 2 = sparse, 10-30% cover; 3 = moderate, 30-60% cover; 4 = dense, 60-80% cover; 5 = very dense, 80-100% cover). To assign one density measurement to each point the harmonic mean was taken from all density scores. Harmonic mean was used to account for gaps in forest vegetation.

Data Analysis

To address the effects of microclimate and vegetation structure on the presence of Neotropical migrant birds on their breeding and wintering grounds, I built logistic regression models in the Bayesian framework. The effects of microclimate and vegetation structure on habitat selection were considered separately. The response variable was presence/absence of a given focal species. To assess effects of microclimate on habitat selection, I used temperature, light, and humidity as predictor variables. Although vapor pressure deficit (VPD) is a more biologically relevant variable (Anderson 1936), the correlation between temperature and VPD was high ($r = 0.92$) on the breeding grounds, which resulted in poor Markov Chain Monte Carlo sampling due to correlation between the two variables. To assess the effects of vegetation on habitat selection, I used percent canopy cover, canopy height, live vegetation cover, and understory density as predictor variables. Again, correlation between live and dead vegetation cover on the breeding grounds was high ($r = 0.89$), so only live vegetation cover was included as a predictor variable in the vegetation models. All variables were converted to z-scores to standardize and center the data, and

arithmetic means were assigned to missing data values (breeding $n = 19$; wintering $n = 13$).

Presence of Neotropical migrants, as influenced by microclimate and vegetation structure, was considered in both the breeding and wintering grounds. The Bayesian models were set as $y_i \sim \text{dbern}(\phi)$, where dbern is a Bernoulli distribution with parameter ϕ (the probability of occurrence). The probability of occurrence was modeled using a logit transformation, so that $\text{logit}(\phi) = \beta_0 + \beta_1 * x_1 \dots \beta_k * x_k$. I first assumed flat priors, set as $\beta \sim \text{dnorm}(0, 1.0\text{E-}8)$, where dnorm is a normal distribution with the parameters mean, μ , and precision, τ ($1/\sigma^2$). Posterior parameter estimates (β) and credibility intervals for each data set were generated for each species individually in OpenBUGS 3.2.3 rev. 2011 using three Markov chains and 100,000 iterations, thinned ten times, with a burn-in of 500,000 iterations to guarantee convergence at a stable point. All parameter initial values were set at zero. Estimates of the slope parameters were considered significant if the 95% Bayesian credibility intervals around the mean did not overlap zero. To draw inference from the classically non-significant slope parameters, the step function (1 if $e \geq 0$; 0 otherwise) was used.

Posterior parameter estimates generated from the breeding-ground models were then used as “informative” priors for the wintering microclimate and vegetation models, whereas posterior parameter estimates generated from the wintering ground models were used as “informative” priors for the breeding grounds. A Bayesian model comparison technique, Deviance Information Criterion (DIC), was used to compare the “uninformed” and “informed” models. DIC is a Bayesian likelihood-based model comparison method similar to Akaike’s Information Criterion (AIC). If the “informed”

models were more predictive (i.e., had a lower DIC score) of species occurrence than the “uninformed” models, then I inferred that niche tracking occurred between the breeding and wintering grounds. DIC scores were used to compare microclimate and vegetation models to determine which was more predictive of Neotropical migrant presence in the breeding and wintering grounds. Models were considered to be different when DIC scores differed by five or more points (Lunn et al. 2013).

Results

Microclimate

On the breeding grounds, microclimate significantly affected the presence of three species, the Hooded Warbler, Summer Tanager, and Black-and-white Warbler. All three microclimate variables, temperature, light, and relative humidity, were significant predictors for presence of Hooded Warblers. The relationships between temperature (mean = 27.75; SD = 30.02; 2.5% BCI = 27.39; 97.5% BCI = 28.48) light (mean = 6.2436; SD = 18.83; 2.5% BCI = 6.2435; 97.5% BCI = 6.99), and relative humidity (mean = 68.32; SD = 77.31; 2.5% BCI = 67.80; 97.5% BCI = 70.1549) and the presence of Hooded Warblers were negative (Figure 1). The relationship between light (mean = 7.68; SD = 16.33; 2.5% BCI = 6.30; 97.5% BCI = 12.49) and the presence of Summer Tanagers was also negative (Figure 2). Relative humidity (mean = 77.41; SD = 75.99; 2.5% BCI = 74.71; 97.5% = 79.49) significantly and positively affected the presence of Black-and-white Warblers (Figure 3). Although not classically significant, parameter estimates suggest that temperature was positively related to the presence of Summer Tanagers, and humidity was positively related to Summer Tanager presence (Figure 2).

The presence of Black-and-white Warblers was also negatively related to temperature, and negatively related to light (Figure 3). White-eyed vireo occurrence was positively related to light, and positively related to humidity. The effects of temperature on White-eyed Vireo occurrence were negligible (Figure 4). The presence of Kentucky Warblers was positively related to temperature, negatively related to light, and positively related to relative humidity (Figure 5) (Table 1).

On the wintering grounds, microclimate only significantly impacted the presence of White-eyed Vireos (Table 2). Temperature (mean = 25.33; SD = 26.46; 2.5% BCI = 24.94; 97.5% BCI = 25.84) had a significant negative effect on White-eyed Vireo occurrence. Although not classically significant, parameter estimates suggest that White-eyed Vireo occurrence was also negatively related to light and negatively related to humidity (Figure 4). Black-and-white Warbler presence was positively related to temperature, positively related to light, and positively related to relative humidity (Figure 3). Hooded Warbler occurrence was positively related to temperature and negatively related to light. Relative humidity had negligible effects on the presence of Hooded Warblers (Figure 1). Kentucky Warbler occurrence was positively related to temperature and negatively related to humidity. The effects of light on the occurrence of Kentucky Warblers were negligible (Figure 5). The presence of Summer Tanagers was positively related to temperature, negatively related to light, and positively related to humidity (Figure 2) (Table 1).

Vegetation

On the breeding grounds, three species were significantly affected by vegetation variables. The presence of Black-and-white warblers was significantly and positively affected by canopy height (mean = 23.09; SD = 22.59; 2.5% BCI = 22.0; 97.5% BCI = 23.94), the presence of Hooded Warblers was significantly and negatively affected by live ground vegetation cover (mean = 59.07; SD = 69.36; 2.5% BCI = 54.05; 97.5% BCI = 65.39), and the presence of White-eyed Vireos was significantly and positively affected by live ground vegetation cover (mean = 73.58; SD = 68.96; 2.5% BCI = 68.24; 97.5% BCI = 77.69). Although not classically significant, parameter estimates suggest that Black-and-white Warbler presence was also negatively related to canopy cover, negatively related to live ground vegetation cover, and positively related to vegetation density (Figure 6). The presence of Hooded Warblers was also positively related to canopy cover, negatively related to canopy height, and positively related to vegetation density (Figure 7). White-eyed Vireo occurrence was also positively affected by canopy cover, negatively related to canopy height, and negatively related to vegetation density (Figure 8). The presence of Summer Tanagers was negatively related to canopy cover, positively related to canopy height, negatively related to live vegetation cover, and negatively related to vegetation density (Figure 9). The presence of Kentucky Warblers was positively related to canopy cover, positively related to canopy height, positively related to live vegetation ground cover, and positively related to vegetation density (Figure 10) (Table 2).

On the wintering grounds, three species were significantly affected by vegetation variables. The presence of Hooded Warblers was significantly and positively

affected by canopy cover (mean = 91.76; SD = 85.62; 2.5% BCI = 85.32; 97.5% BCI = 94.81). Both Kentucky Warblers (mean = 3.29; SD = 3.20; 2.5% BCI = 3.06; 97.5% BCI = 3.42) and White-eyed Vireos (mean = 3.24; SD = 3.14; 2.5% BCI = 3.10; 97.5% = 3.35) were significantly and positively affected by vegetation density. Although not classically significant, posterior parameter estimates suggest that the presence of Hooded Warblers was negatively related to canopy height, negatively related to live ground cover, and positively related to vegetation density (Figure 7). The occurrence of Kentucky Warblers was negatively related to canopy cover, negatively related to canopy height, and negatively related to live ground cover (Figure 10). White-eyed vireo occurrence was negatively related to canopy cover, negatively related to canopy height, and negatively related to live vegetation ground cover (Figure 8). Presence of Black-and-white Warblers was positively related to canopy cover, positively related to canopy height, negatively related to live vegetation ground cover, and negatively related to vegetation density (Figure 6). Summer Tanager occurrence was negatively related to canopy cover, positively affected by canopy height, positively related to live vegetation ground cover, and negatively affected by vegetation density (Figure 9) (Table 2).

Model comparisons

When posterior estimates of breeding ground microclimate parameters were used to inform wintering ground microclimate models, the informed models were not more predictive of presence for any species, or the uninformed model was a better fit. Similarly, when posterior estimates of wintering ground microclimate parameters were used to inform the breeding ground microclimate models, the informed models were not

more predictive of presence for any species, or the uninformed model was a better fit (Table 3). When posterior estimates of breeding ground vegetation parameters were used to inform wintering ground vegetation models, the informed models were not more predictive of presence than the uninformed models for any species. When posterior estimates of wintering ground vegetation parameters were used to inform breeding ground vegetation models, the informed models were not more predictive of presence than uninformed models for any species (Table 4). DIC scores of informed vegetation models were slightly better than those of uninformed vegetation models for both the breeding and wintering grounds; however, the differences in scores were always less than five, so there is no strong support for either the uninformed or informed models being more predictive than the other (Lunn et al. 2013).

Because uninformed and informed models did not differ, or the uninformed model was more predictive of species presence, comparisons between microclimate and vegetation on the breeding and wintering grounds were made using DIC scores of the uninformed models. Microclimate models were more predictive of species presence than vegetation models for the Hooded Warbler and Summer Tanager on the breeding grounds. On the wintering grounds, however, neither microclimate or vegetation models were more predictive of species presence. Hooded Warblers were an exception to this; the vegetation model was more predictive than the microclimate model on the wintering grounds.

Discussion

The purpose of this study was to determine if overlap in niche space occurred between breeding and wintering grounds of migratory birds. Although, patterns between preferred microclimate and vegetation structure are apparent between the breeding and wintering grounds, the results of this study do not indicate that niche-tracking behavior at fine ecological scales occurs in Neotropical migrant passerines (Tables 1&2). This result was somewhat unexpected because other studies suggest that niche-tracking behavior does occur in Neotropical migrants (Monahan & Tingley 2012; Gómez et al. 2016). For example, Gómez et al. (2016) found that 49 species of Neotropical migrants consistently tracked broad-scale climate niche space. Instead, the results of this study indicate migratory birds probably choose habitat based on physiological and behavioral needs that are most important during each season.

Generally, microclimate seems to be most important to breeding birds, whereas vegetation and microclimate are equally important to wintering birds. The importance of microclimate in the breeding grounds is almost certainly related to reproductive and nesting behaviors that are necessary for species fitness. In a climatically heterogenic environment (i.e., temperate forests), birds must select habitat that provides conditions that promote reproductive success (Carroll et al. 2015). Light conditions affect the way that animals perceive visual signals within their environment, and mating behaviors are an important form of visual communication that is affected by light conditions. Female birds often choose mates that have bright feathers because they correspond with overall health. Ambient light conditions may be important to mate selection because males appear brighter when there is a greater amount of contrast between the environment and

their feathers. Some birds, such as the White-throated Manakin (*Corapipo gutturalis*), manipulate the light environment at the site of mating behaviors to appear more attractive to females (Endler & Théry 1996). The effects of light on migrant presence were important (i.e., at least 80% of posterior estimates suggested same relationship) probably because light has such an important effect on mate selection. The results of this study are in agreement with the results of a previous study that found that Neotropical residents select habitat conditional on the light environment (Patten & Smith-Patten 2012).

Temperature and relative humidity are especially important for nest success and chick growth and development. Chicks mature much faster in at optimal temperatures than they do in environments that are too warm or cool because the costs of thermoregulation are greatly reduced (Chaplin et al. 2002; Dawson et al. 2005). Temperature is important to survival of adult birds during the incubation period because females are constantly exposed to the environmental conditions present at the nest site for a long period of time, and optimal temperatures provide reduced thermoregulation costs, which is important because it is energetically costly to provision offspring (Gloutney & Clark 1997; Cooper 1999; Dawson et al. 2005). Not surprisingly, the effects of temperature on migrant presence were important at least 90% of the time for all focal species in this study, except White-eyed Vireos. Relative humidity has an affect on nest success, as well (Francis 1968; Rahn et al. 1977). Nest sites exposed to high temperatures and low relative humidity experience decreased egg viability (Francis 1968). Relative humidity is important for proper egg development because some water inside of the egg must be replaced with air for breathing before the chick is exposed to

the outside environment; if relative humidity conditions are not optimal, water transport systems are impaired and eggs are likely to fail (Rahn et al. 1977). Again the effects of humidity were important to migrant presence at least 88% of the time. Interestingly, relationships between microclimate and migrant presence were most often opposite in the wintering grounds for at least one microclimate variable; Summer Tanagers maintained the same relationships with microclimate variables on the wintering grounds. These results may suggest that habitat selection on the breeding and wintering grounds are driven by different physiological or behavioral needs.

In addition, microclimate also provides an important buffer from extreme environmental climatic conditions (Bell et al. 2010; Carroll et al. 2015). Bell et al. (2010) found that Lesser Prairie-Chickens select microclimate dependent on environmental conditions. For example, when temperatures were warmer, chickens preferred habitat with more shaded areas that provided thermal refuge. Daily ambient temperatures on the breeding grounds (Oklahoma) were often much warmer than ambient temperatures on the wintering grounds (Belize), while relative humidity was often higher on the wintering grounds than on the breeding grounds. Therefore, it is possible that Neotropical migrants also select microclimate dependent on environmental conditions, and select cooler, moister microclimate on the breeding grounds and warmer, dryer conditions on the wintering grounds. Future studies should also consider time of day as a source of variation in microclimate selection. Since microclimate conditions are dependent on time of day, understanding how microclimate of occupied space is affected by ambient conditions throughout the day will help us to better understand selection of specific microclimatic conditions.

Vegetation and microclimate were equally important for predicting migrant presence in the wintering grounds, suggesting microclimatic conditions are not as important on the wintering grounds as the breeding grounds. The Hooded Warbler was an exception, and vegetation structure did predict presence better than microclimate on the wintering grounds. This suggests that vegetation is more important to the Hooded Warbler on the wintering grounds than microclimate. Because of the relatedness between microclimate and vegetation structure, however, selection of vegetation structure on the wintering grounds probably also provides suitable microclimate conditions. Alternatively, Neotropical migrants may not track specific microclimate and vegetation structure on the wintering grounds, but instead may spend most of their time foraging wherever food is present. Insect abundance is often associated with warmer temperatures, and is higher at forest edges where vegetation is less dense. An abundance of food resources may partially explain why insectivorous birds spend time near such exposed areas (Champlain et al. 2009; Larsson et al. 2013; Jones et al. 2017). For example, Black-and-white Warblers were present more often in areas with less dense vegetation and warmer temperatures on the wintering grounds than on the breeding grounds. In fact, if food resources are the main factor in occurrence of Neotropical migrants, it is possible that the effects of microclimate and vegetation structure are indirect on the wintering grounds. In other words, migrants may occupy space that is characterized by microclimate and vegetation structure that is important to their prey items as long as they stay within their physiological limitations.

Although, the uninformed and informed vegetation models are not substantially different, it is worth mentioning that informed vegetation model DIC scores were lower

than uninformed vegetation models for every species in both the breeding and wintering grounds. This suggests that niche tracking for vegetation structure may actually occur; however, possibly due to small sample sizes, informed models were not substantially more predictive of species occurrence than uninformed models.

Climate change and anthropogenic land-use are major concerns for biodiversity. Because macroclimate and vegetation both significantly impact microclimate, breeding birds could experience significant loss of suitable nesting habitat (Pringle et al. 2003; Haby et al. 2013; Varner & Dearing 2014). The effects of climate change on microclimate stability will need to be continually monitored to understand how exactly climate change will alter microclimate and when changes in microclimate will occur, as some lag time between macroclimate and microclimate change is expected (Chen et al. 1999; Varner & Dearing 2014). Microhabitats may buffer the effects of climate change for some time, but continued loss of vegetation will lead to fewer of these (Varner & Dearing 2014). Land-use changes occur in forests by means of a variety of anthropogenic activities including clear-cutting, logging, hunting, burning, and abandoning land used for agriculture (Karr & Freemark 1983; Carmago & Kapos 1995; Asner et al. 2009). Natural disturbances, such as lightning, fire, windstorms, herbivory, and other animal activities, also contribute to changes in vegetation structure (Karr & Freemark 1983; Chazdon & Fetcher 1984; Meyer et al. 2011; Jones et al. 2017). These occurrences have already affected geographical ranges of many animals (Varner & Dearing 2014). Since vegetation provides an important buffer from extreme macroclimatic conditions, I suggest that conservation management focus on maintaining forest vegetation. Sustainable logging practices and replanting

native forest species after agricultural abandonment may be viable options for protecting microhabitats within temperate and tropical forests.

References

- Anderson, D.B. 1936. Relative humidity or vapor pressure deficit. *Ecology* 17: 277-282.
- Anderson, S.H., Shugart Jr., H.H. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55: 828-837.
- Asner, G.P., Rudel, T.K., Aide, M., Defries, R., Emerson, R. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23: 1386-1395.
- Bell, L.A., Fuhlendorf, S.D., Patten, M.A., Wolfe, D.H., Sherrod, S.K. 2010. Lesser Prairie-Chicken hen and brood habitat use on sand shinnery oak. *Rangeland Ecology and Management* 63: 478-486.
- Carmago, J.L.C., Kapos, V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology* 11: 205-221.
- Carroll, J.M., Davis, C.A., Elmore, R.D., Fuhlendorf, S.D. 2015. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. *PLoS ONE* 10: e0143676. doi:10.1371/journal.pone.0143676
- Champlin, T.B., Kilgo, J.C., Gumpertz, M.L., Moorman, C.E. 2009. Avian response to microclimate in canopy gaps in a bottomland hardwood forest. *Southeastern Naturalist* 8: 107-120.
- Chaplin, S.B., Cervenka, M.L., Mickelson, A.C. 2002. Thermal environment of the nest during development of Tree Swallow (*Tachycineta bicolor*) chicks. *Auk* 119: 845-851.
- Chazdon, R.L., Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72: 553-564.
- Chazdon, R.L., Pearcy, R.W. 1991. The importance of sunflecks for forest understory plants. *BioScience* 41: 760-766.
- Chen, J., Franklin, J.F., Spies, T.A. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63: 219-237.
- Chen, J., Franklin, J.F., Spies, T.A. 1995. Growing-season microclimate gradients from clearcut edges into old-growth Douglas-fir-forests. *Ecological Applications* 5: 74-86.

- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosfoske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F. 1999. Microclimate in forest ecosystem and landscape ecology variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* 49: 288-297.
- Cooper, S.J. 1999. The thermal and energetic significance of cavity roosting in Mountain Chickadees and Juniper Titmice. *Condor* 101: 863-866.
- Dawson, R.D., Lawrie, C.C., O'Brien, E.L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia* 144: 499-507.
- Davies-Colley, R.J., Payne, G.W., van Elswijk, M. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24: 111-121.
- Didham, R.K. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17-30.
- du Plessis, K., Martin, R.O., Hockey, P.A.R., Cunningham, S.J., Ridley, A.R. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology* 18: 3063-3070.
- Endler, J.A., Théry, M. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. *American Naturalist* 148: 421-452.
- Ewers, R.M., Banks-Leite, C. 2013. Fragmentation impairs the microclimate buffering effect in tropical forests. *PLoS ONE* 8: e58093.
- Francis, W.J. 1968. Temperature and humidity conditions in potential pheasant nesting habitat. *Journal of Wildlife Management* 32: 36-46.
- Gehlhausen, S.M. Schwartz, M.W., Augspurger, C.K. 2000. Vegetation and microclimate edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147: 21-35.
- Gloutney, M.L., Clark, R.G. 1997. Nest-site selection by Mallards and Blue-Winged Teal in relation to microclimate. *Auk* 111: 381-395.
- Gómez, C., Tenorio, E.A., Montoya, P. Cadena, C.D. 2016. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B* 283: 20152458.

- González del Pliego, P., Scheffers, B.R., Bashum, E.W., Woodcock, P., Wheeler, C., Gilroy, J.J., Uribe, C.A.M., Haugaasen, T., Freckleton, R.P., Edwards, D.P. 2016. Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. *Biological Conservation* 201: 385-395.
- Grüebler, M.U., Widmer, S., Korner-Nievergelt, F., Naef-Daenzer, B. 2014. Temperature characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic alternatives. *International Journal of Biometeorology* 58: 629-637.
- Haby, N.A., Conran, J.G., Carthew, S.M. 2013. Microhabitat and vegetation structure preference: an example using southern brown bandicoots (*Isoodon obesulus obesulus*). *Journal of Mammalogy* 94: 801-812.
- Hollander, F.A., Van Dyck, H., San Martin, G., Titeux, N. 2011. Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *PLoS ONE* 6: e25703.
- Jones, I.M., Koptur, S., Gallegos, H.R., Tardanico, J.P., Trainer, P.A., Peña, J. 2017. Changing light conditions in pine rockland habitats affect the intensity and outcome of ant-plant interactions. *Biotropica* 49: 83-91.
- Joseph, L., Stockwell, D. 2000. Temperature-based models of the migration of Swainson's Flycatcher (*Myiarchus swainsoni*) across South America: a new use for museum specimens of migratory birds. *Proceedings of the Academy of Natural Sciences of Philadelphia* 150: 293-300.
- Karr, J.R., Freemark, K.E. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64: 1481-1494.
- Karr, J.R., Roth, R.R. 1971. Vegetation structure and avian diversity in several New World areas. *American Naturalist* 105: 423-435.
- Kearney, N., Handasyde, K., Ward, S., Kearney, M. 2007. Fine-scale microhabitat selection for dense vegetation in a heathland rodent, *Rattus lutreolus*: insights from intraspecific and temporal patterns. *Austral Ecology* 32: 315-325.
- Krijgsveld, K.L., Visser, G.H., Daan, S. 2003. Foraging behavior and physiological changes in precocial quail chicks in response to low temperatures. *Physiology and Behavior* 79: 311-319.
- Larsson, L.C., Pruett, C.L., Wolfe, D.H., Patten, M.A. 2013. Fine-scale selection of habitat by the Lesser Prairie-Chicken. *Southwestern Naturalist* 58: 135-149.
- Laube, I., Graham, C.H., Böhning-Gaese, K. 2015. Niche availability in space and time: migration in *Sylvia* warblers. *Journal of Biogeography* 42: 1896-1906.

- Lee-Yaw, J.A., Sechley, T.H., Irwin, D.E. 2015. Conflicting effects of microclimate on Long-toed Salamander (*Ambystoma macrodactylum*) movement: implications for landscape connectivity. *Canadian Journal of Zoology* 93: 1-7.
- Levey, D.J., Stiles, F.G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *American Naturalist* 140: 447-476.
- Lunn, D., Jackson, C., Best, N., Thomas, A., Spiegelhalter, D. 2013. The bugs book: a practical introduction to Bayesian analysis. CRC Press, Boca Raton, FL, pp.166-167.
- Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185-194.
- Meyer, S.T., Leal, I.R., Tabarelli, M., Wirth, R. 2011. Ecosystem engineering by leaf-cutting ants: nests of *Atta cephalotes* drastically alter forest structure and microclimate. *Ecological Entomology* 36: 14-24.
- Monahan, W.B., Tingley, M.W. 2012. Niche tracking and rapid establishment of distributional equilibrium in the House Sparrow show potential responsiveness of species to climate change. *PLoS ONE* 7: e42097.
- Montgomery, R.A., Chazdon, R.L. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82: 2707-2718.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58-62.
- Nakazawa, Y., Peterson, A.T., Martínez-Meyer, E., Navarro-Sigüenza, A.G. 2004. Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. *Auk* 12: 610-618.
- Parrish, J.D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. *Ecology* 76: 1813-1820.
- Patten, M.A., Smith-Patten, B.D. 2012. Testing the microclimate hypothesis: light environment and population trends of Neotropical birds. *Biological Conservation* 155: 85-93.
- Patten, M.A., Wolfe, D.H., Shocat, E., Sherrod, S.K. 2005. Effects of microhabitat and microclimate selection on adult survivorship of the Lesser Prairie-Chicken. *Journal of Wildlife Management* 69: 1270-1278.

- Piper, W.H. 2011. Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology* 65: 1329-1351.
- Pollock, H.S., Cheviron, Z.A., Agin, T.J., Brawn, J.D. 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. *Biological Conservation* 188: 116-125.
- Pringle, R.M., Webb, J.K., Shine, R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84: 2668-2679.
- Rahn, H., Ackerman, R.A., and Paganelli, C.V. 1977. Humidity in the avian nest and egg water loss during incubation. *Physiological Zoology* 50: 269-283.
- Root, T. 1988. Energy constraints on avian distributions and abundance. *Ecology* 69: 330-339.
- Sam, K., Koane, B., Jeppy, S., Novotny, V. 2014. Effect of forest fragmentation on bird species richness in Papua New Guinea. *Journal of Field Ornithology* 85: 152-167.
- Salewski, V., Bruderer, B. 2007. The evolution of bird migration – a synthesis. *Naturwissenschaften* 94: 268-279.
- Schefferes, B.R., Edwards, D.P., Macdonald, S.L., Senior, R.A., Andriamahohatra, L.R., Rosian, N., Rogers, A.M., Haugaasen, T., Wright, P., Williams, S.E. 2017. Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica* 49: 35-44.
- Seavy, N.E., Alexander, J.D. 2011. Interactive effects of vegetation structure and composition describe bird habitat associations in mixed broadleaf-conifer forests. *Journal of Wildlife Management* 72: 344-352.
- Shaw, A.K., Couzin, I.D. 2013. Migration or Residency? The evolution of movement behavior and information usage in seasonal environments. *American Naturalist* 181: 114-124.
- Swaine, M.D., Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.
- Taylor, C.M., Norris, D.R. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters* 3: 280-283.
- Vandermeer, J.H. 1972. Niche theory. *Annual Review of Ecology, Evolution, and Systematics* 3: 107-132.

- Varner, J., Dearing, M.D. 2014. The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS ONE* 9: e104648.
- Whitbeck, K.L., Oetter, D.R., Perry, D.A., Fyles, J.W. 2016. Interactions between macroclimate, microclimate, and anthropogenic disturbance affect the distribution of aspen near its northern edge in Quebec: implications for climate change related range expansions. *Forest Ecology and Management* 368: 194-206.
- Zellweger, F., Baltensweiler, A., Ginzler, C., Roth, T., Braunisch, V., Bugmann, H., Bollmann, K. 2016. Environmental predictors of species richness in forest landscapes: abiotic factors versus vegetation structure. *Journal of Biogeography* 43: 1080-1090.
- Zink, R.M. 2011. The evolution of avian migration. *Biological Journal of the Linnean Society* 104: 237-250.

Appendix A: Tables

Table 1 – Summary of uninformed relationships between microclimate variables and the presence of migrants on the breeding and wintering grounds. ↑ indicates a positive relationship, while ↓ indicates a negative relationship. Percent value represents the percentage of posterior parameter values that were positive or negative (depending on arrow).

Species	Breeding			Wintering		
	Temperature	Light	Relative Humidity	Temperature	Light	Relative Humidity
WEVI	↓ 54.5%	↑ 97.1%	↑ 93.0%	↓ 100%	↓ 66.0%	↓ 91.7%
BAWA	↓ 91.6%	↓ 80.9%	↑ 98.7%	↑ 85.3%	↑ 69.3%	↑ 88.5%
HOWA	↓ 100%	↓ 100%	↓ 100%	↑ 91.9%	↓ 86.2%	↑ 52.9%
KEWA	↑ 93.4%	↓ 97.0%	↑ 97.3%	↑ 64.0%	↓ 53.6%	↓ 74.7%
SUTA	↑ 94.8%	↓ 97.7%	↑ 88.7%	↑ 96.2%	↓ 75.4%	↑ 90.7%

Table 2 – Summary of relationships between vegetation variables and the presence of migrants on the breeding and wintering grounds. ↑ indicates a positive relationship, while ↓ indicates a negative relationship. Percent value represents the percentage of posterior parameter values that were positive or negative (depending on arrow).

Species	Breeding				Wintering			
	Canopy Cover	Canopy Height	Live cover	Density	Canopy Cover	Canopy Height	Live cover	Density
WEVI	↑ 68.6%	↓ 81.2%	↑ 99.8%	↓ 63.9%	↓ 72.0%	↓ 89.3%	↓ 75.0%	↑ 99.6%
BAWA	↓ 71.9%	↑ 97.7%	↓ 97.2%	↑ 96.4%	↑ 77.8%	↑ 84.7%	↓ 70.7%	↓ 95.8%
HOWA	↑ 91.7%	↓ 70.1%	↓ 98.1%	↑ 63.2%	↑ 100%	↓ 80.8%	↓ 90.9%	↑ 61.2
KEWA	↑ 78.3%	↑ 76.1%	↑ 95.0%	↑ 87.0%	↓ 63.8%	↓ 75.6%	↓ 76.4	↑ 97.8%
SUTA	↓ 92.1%	↑ 64.7%	↓ 70.3%	↓ 93.6%	↓ 96.1%	↑ 84.8%	↑ 82.0%	↓ 84.2%

Table 3 – DIC scores for ‘uninformed’ and ‘informed’ breeding ground models. Uninformed and informed DIC scores for the microclimate and vegetation models of each species are compared. Bolded scores represent models that were more predictive.

Species	Microclimate		Vegetation	
	Uninformed Breeding	Informed Breeding	Uninformed Breeding	Informed Breeding
WEVI	73.89	73.42	71.68	71.15
BAWA	58.81	57.59	61.91	61.23
HOWA	33.74	34.7	62.39	61.67
KEWA	55.46	53.91	59.90	59.23
SUTA	53.18	59.19	63.20	62.32

Table 4 – DIC scores for ‘uninformed’ and ‘informed’ wintering ground models. Uninformed and informed DIC scores for the microclimate and vegetation models of each species are compared. Bolded scores represent models that were more predictive.

Species	Microclimate		Vegetation	
	Uninformed Wintering	Informed Wintering	Uninformed Wintering	Informed Wintering
WEVI	72.28	71.77	75.81	75.28
BAWA	75.37	75.72	75.83	75.32
HOWA	77.24	2.0E+10	64.85	63.90
KEWA	46.86	48.65	45.66	44.24
SUTA	66.75	67.02	64.55	64.26

Appendix B: Figure Legend

- Fig. 1** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Hooded Warbler (HOWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 2** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Summer Tanager (SUTA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 3** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Black-and-white Warbler (BAWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 4** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the White-eyed Vireo (WEVI). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 5** Relative influence of microclimate variables (temperature, light, relative humidity) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Kentucky Warbler (KEWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 6** Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Black-and-white Warbler (BAWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.
- Fig. 7** Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Hooded Warbler (HOWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.

Fig. 8 Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the White-eyed Vireo (WEVI). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.

Fig. 9 Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Summer Tanager (SUTA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.

Fig. 10 Relative influence of vegetation structure variables (canopy cover, canopy height, live ground cover, vegetation density) on standardized means (+ 95% BCI) of β parameters in the breeding and wintering grounds of the Kentucky Warbler (KEWA). Empty circles represent breeding ground parameter means, and filled circles represent wintering ground parameter means.

Appendix C: Figures

Figure 1

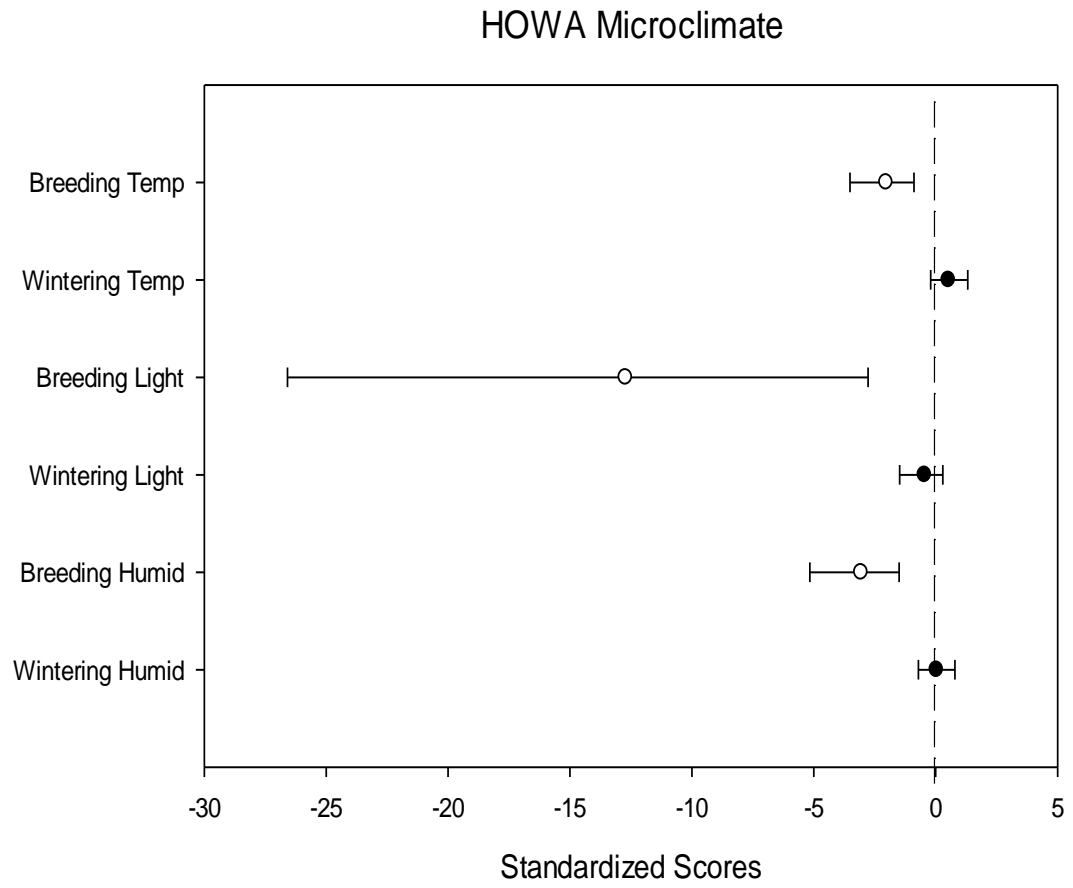


Figure 2

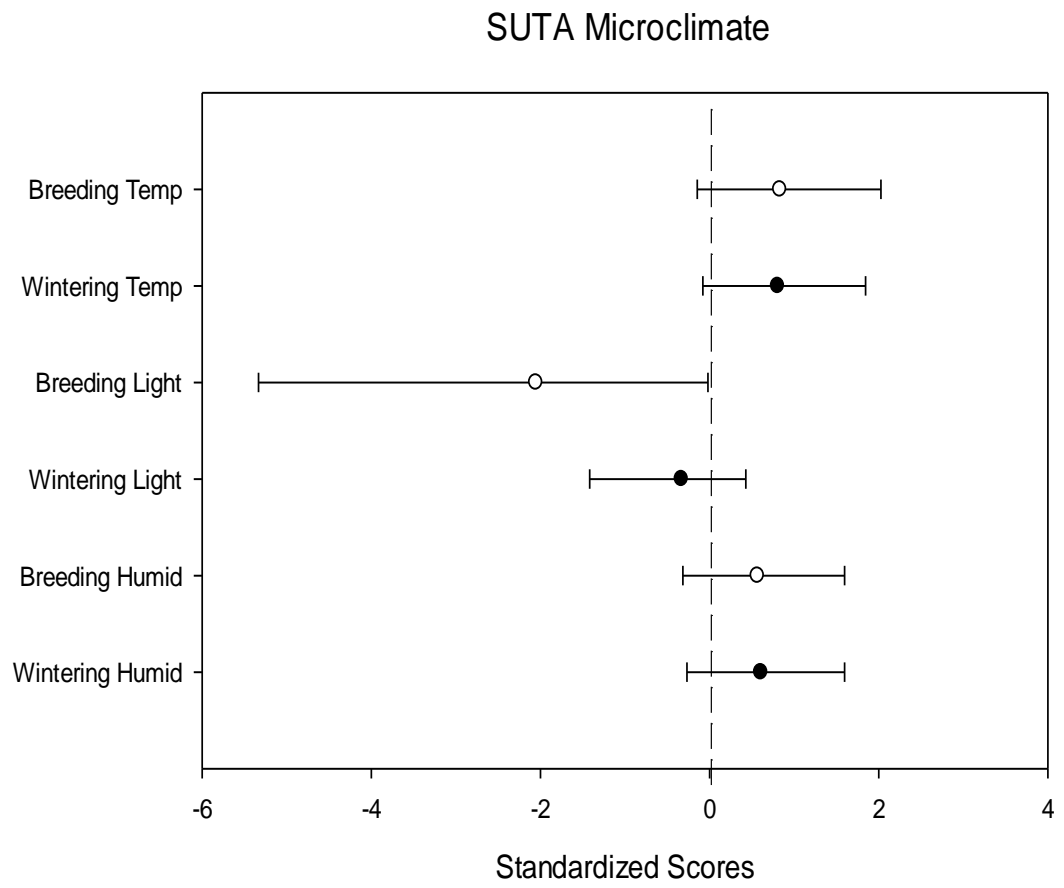


Figure 3

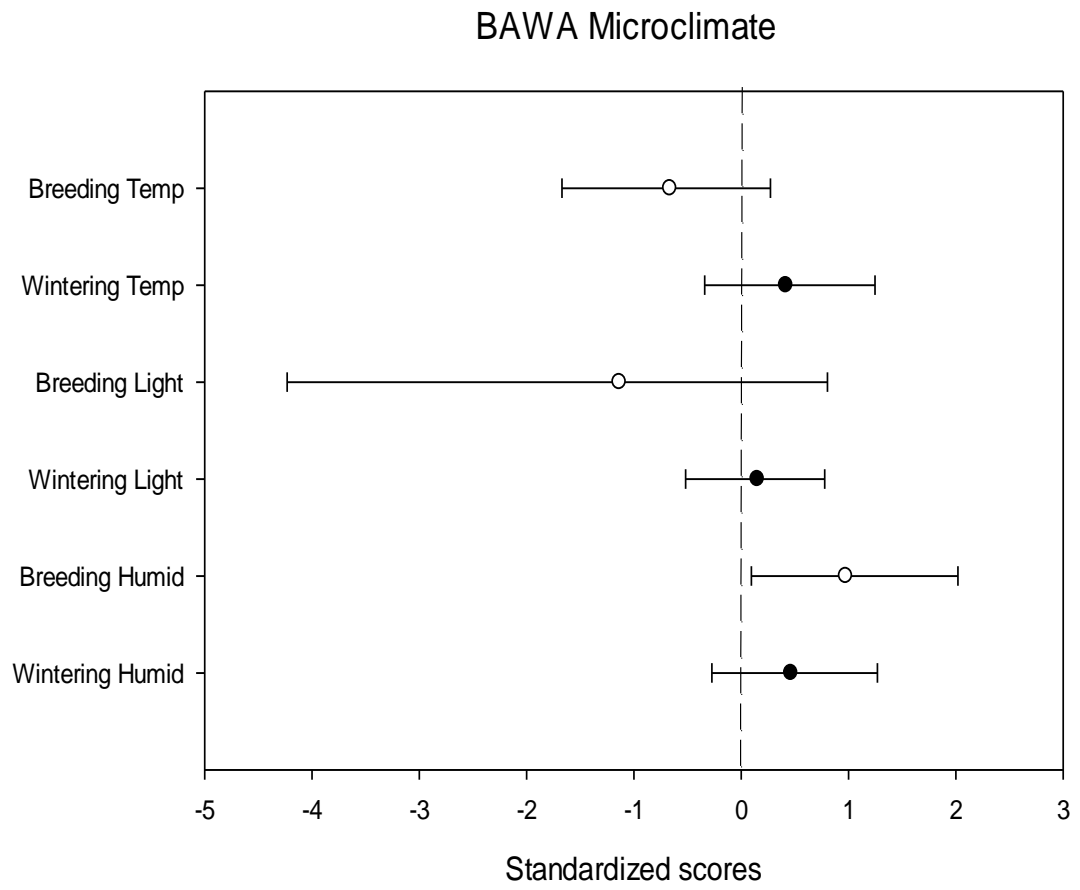


Figure 4

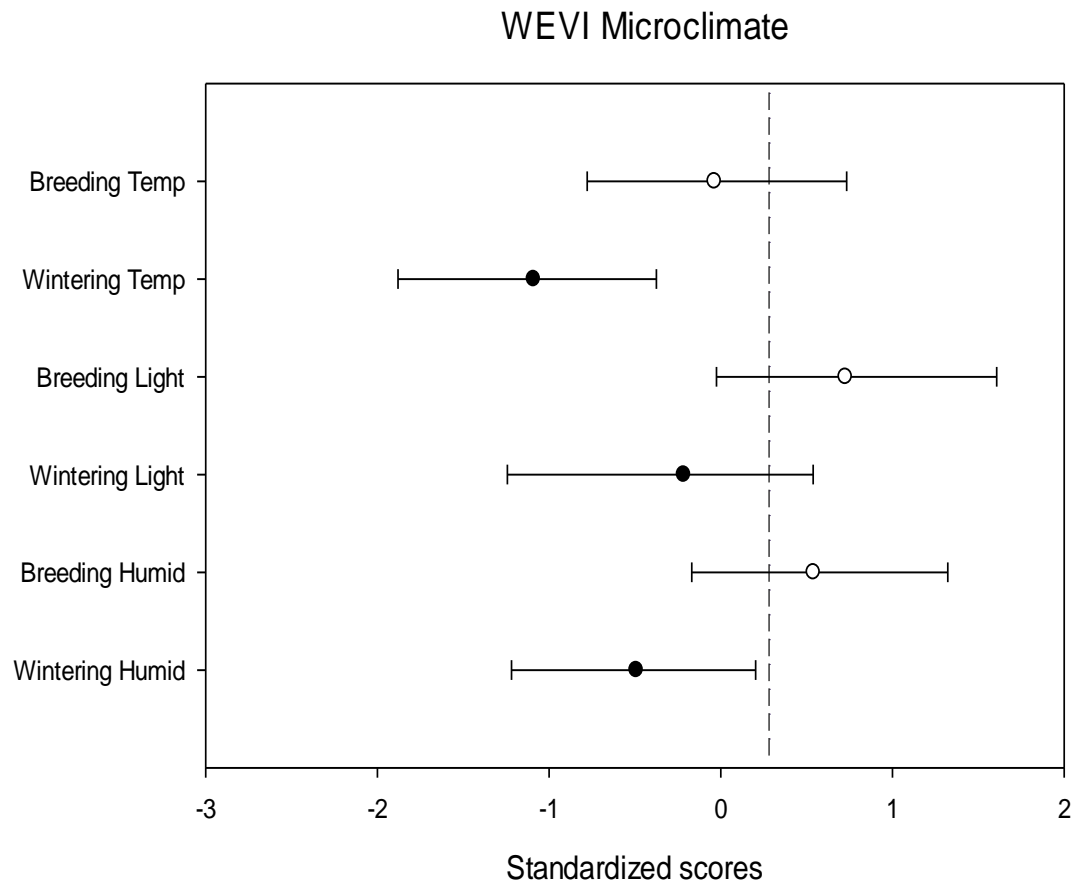


Figure 5

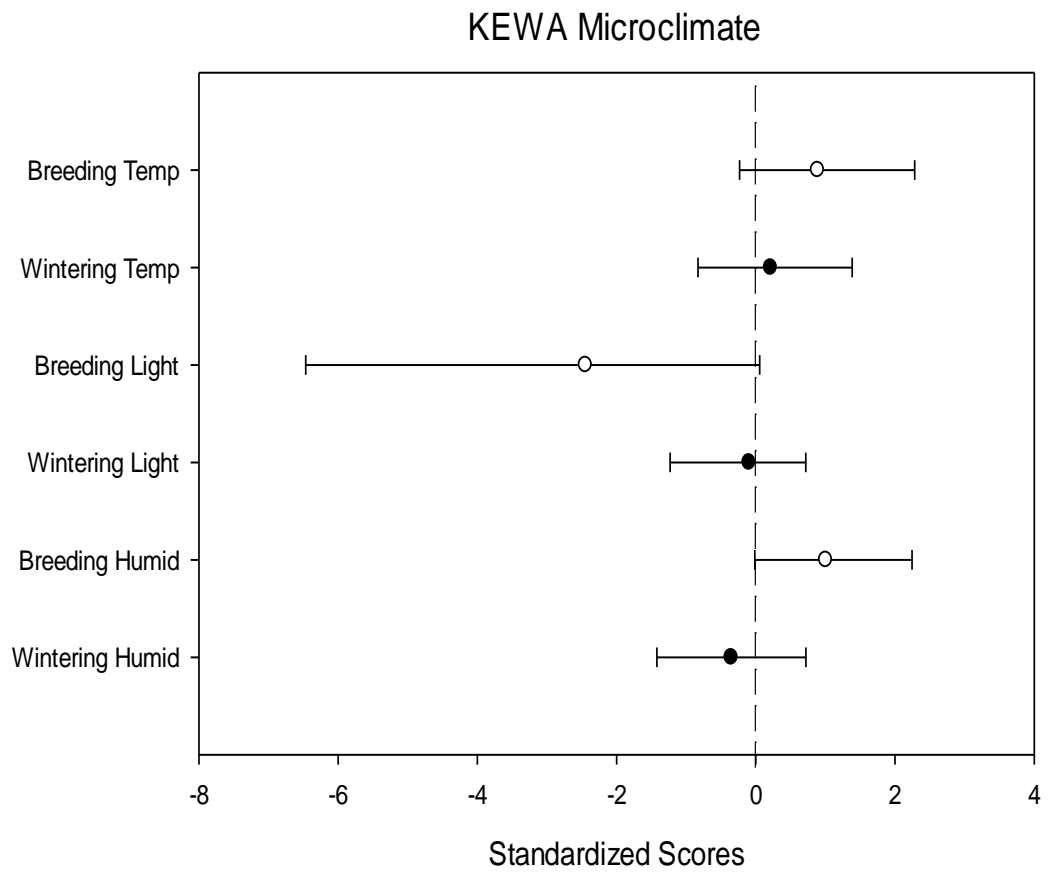


Figure 6

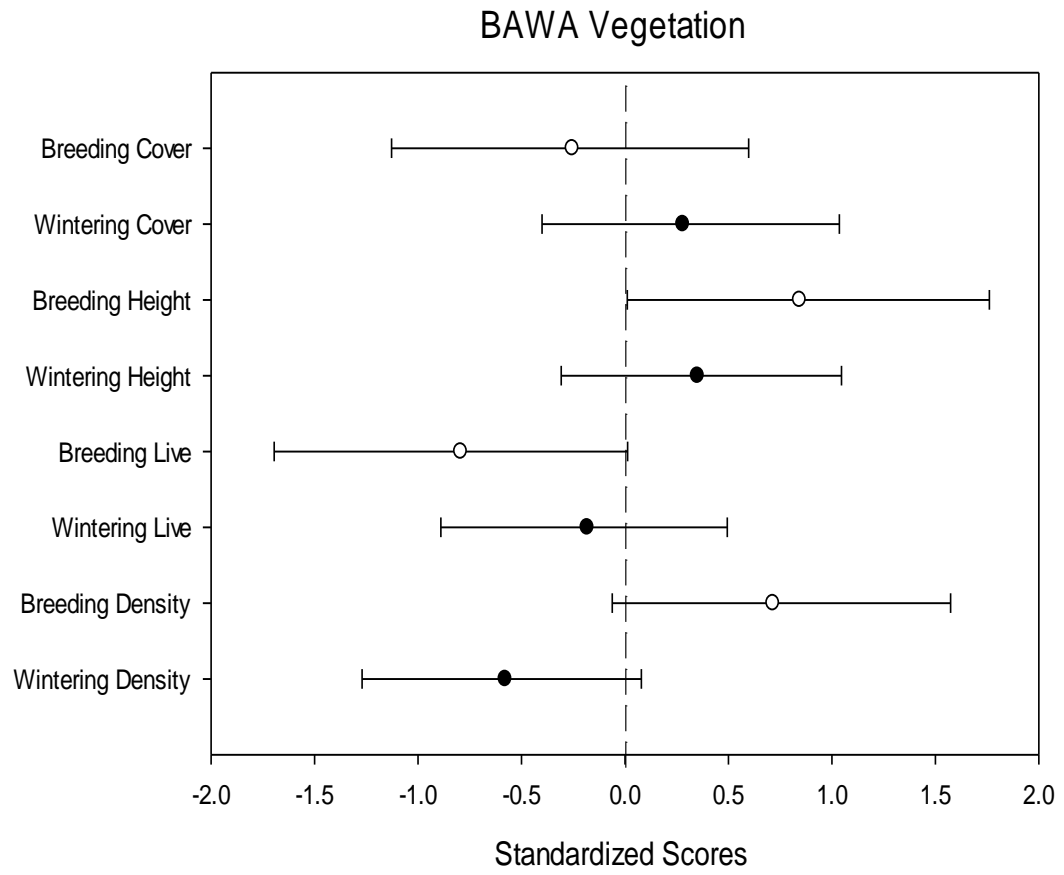


Figure 7

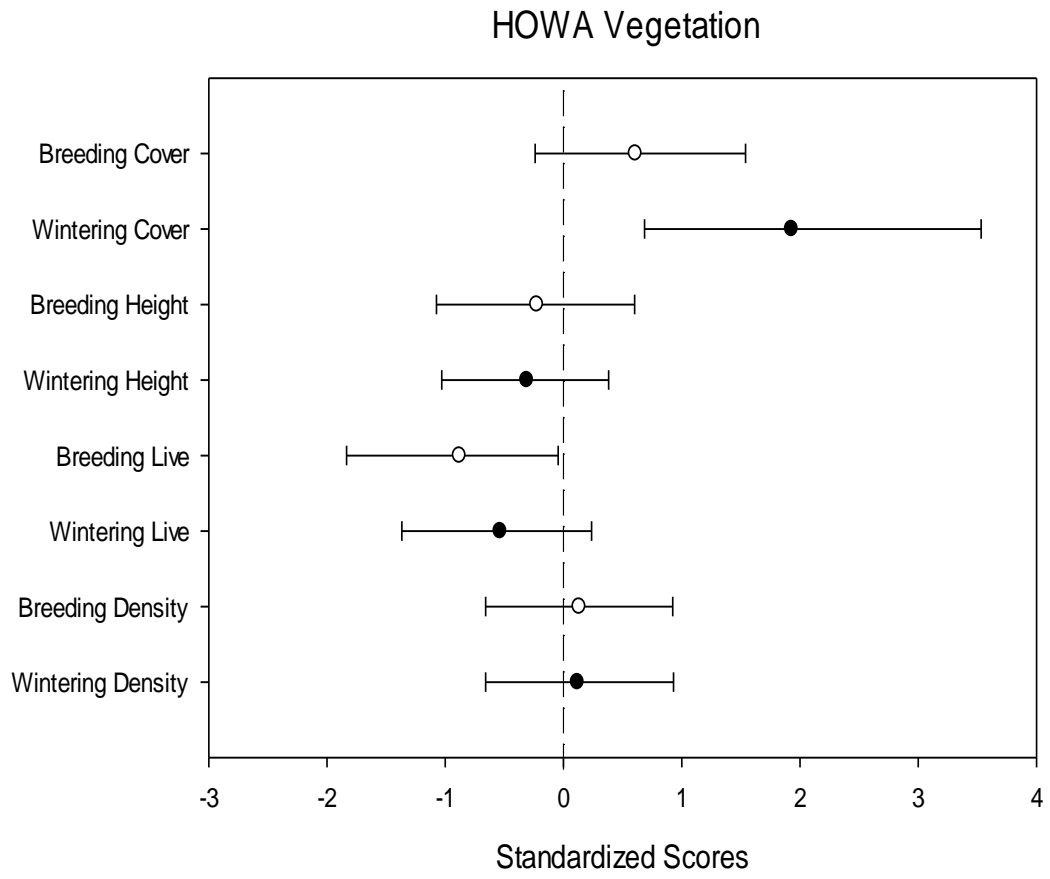


Figure 8

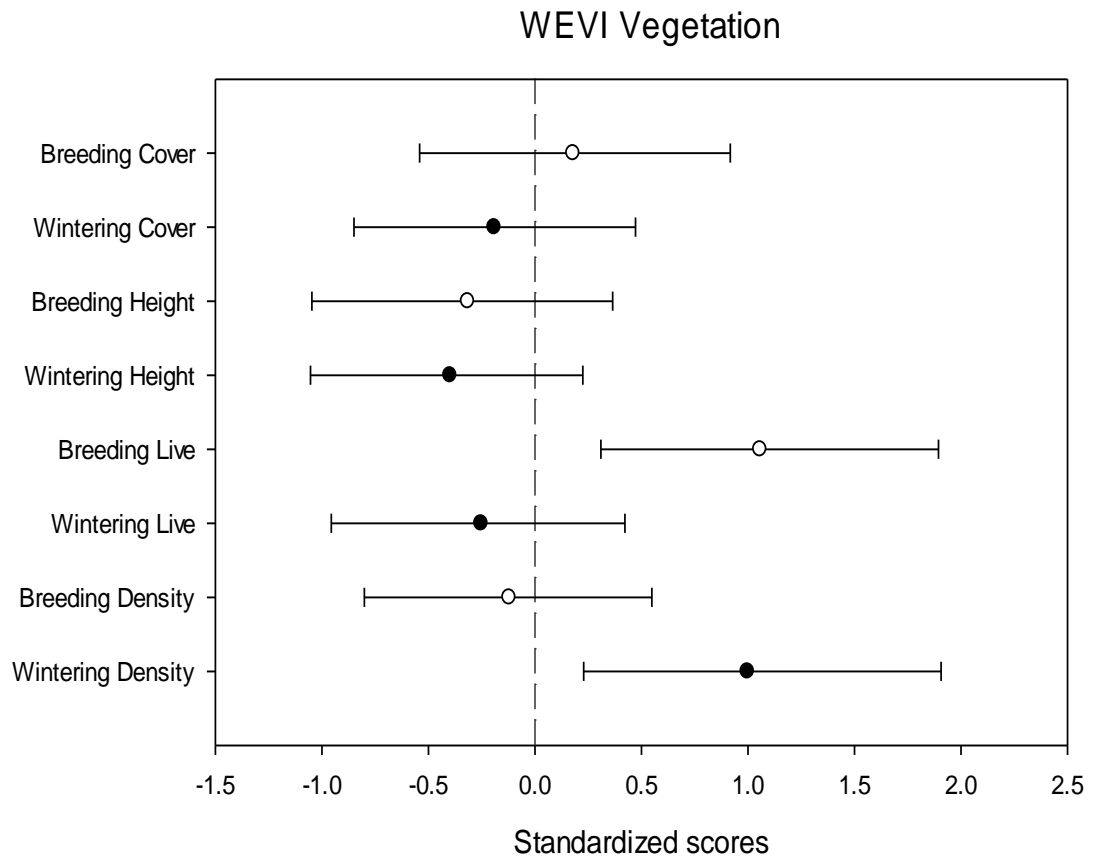


Figure 9

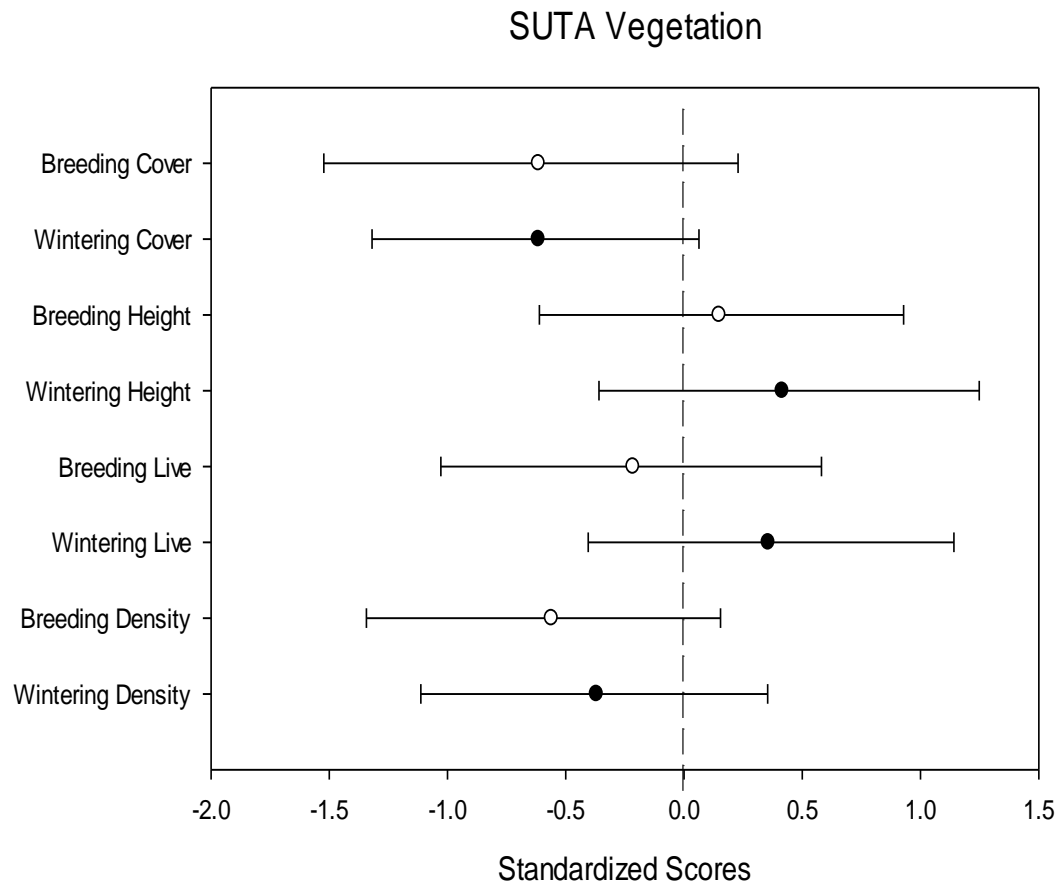


Figure 10

