EXPERIMENTS ON THE EDGE: GLOBAL DISTRIBUTIONS AND LIMITING FACTORS OF TRAILING-EDGE POPULATIONS

by

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(Under the Direction of Richard Chandler)

ABSTRACT

Trailing-edge populations, near the receding edge of a shifting range, are predicted to be at high risk of climate-induced extinction, but lack of information on the factors limiting trailing-edge populations hinders conservation efforts. Additionally, little is known about the global distributions of these populations, which are often genetically unique and important to ecosystem function. I identified global hotspots of trailing-edge population diversity using BirdLife International's database of the ranges of all extant terrestrial bird species. At one hotspot, the southern Appalachian Mountains, I assessed the role of abiotic and biotic factors in limiting the distributions of two songbird species. Results from a playback experiment and four years of observational data demonstrated that Allee effects are not present at the range boundary of the Canada warbler (*Cardellina canadensis*), rather, climate conditions limit population growth rates. I assessed two mechanisms by which climate may limit the distributions of trailing-edge populations: via spatial variation in hemoparasite prevalence and via physiological constraints on egg development. Consistent with the hypothesis that pathogens contribute to climate-induced range shifts in host species, I found that the distribution of a cool-adapted bird species near its trailing-edge limit was negatively associated with pathogen prevalence. Hemoparasite prevalence did not affect occupancy of a warm-adapted species near the core of its range. I also found evidence that physiological constraints can limit the distribution of trailing-edge populations. Results from a reciprocal egg translocation experiment between two ecologically similar species across their local range boundaries revealed that hatch rates of the cool-adapted species declined when moved to warmer, drier conditions. There was little effect of translocation on eggs of the warm-adapted species. Overall my results demonstrate that both abiotic factors and biotic interactions can limit the distributions of trailing-edge populations. However, additional mechanisms remain to be explored, and future work should assess the influence of climate change on biotic interactions between avian predators and arthropod prey on species range limits. The multitude of limiting factors affecting trailing-edge populations poses challenges to conservation efforts, which will need to account for physiological constraints and pathogen prevalence when attempting to mitigate the impacts of climate change.

INDEX WORDS: Allee effects, birds, climate change, egg swaps, hemoparasites, range limits, range shifts, species distributions, southern Appalachian Mountains, trailing-edge populations

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DEDICATION

This is dedicated to my wife, Dr. Nicole E. Krauss. No matter where we were, and even when I had her work during a tropical storm, she was there to support me. I love her very much and it is great to be loved by her.

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INTRODUCTION AND LITERATURE REVIEW

Background on trailing-edge populations

Efforts to understand species distributions predate modern science, largely because information about the distribution of plants and animals was critical to survival for early hunter-gather societies (Duiker and Spielvogel 2018). Fascination with the dynamics of species distributions eventually transformed into what is now known as the science of ecology, and the fundamental question of why species distributions vary in space and time remains a cornerstone of the discipline. Recently, these questions have taken on a new sense of urgency beyond the scope of basic science. Rapid rates of extinction have prompted the creation of applied branches of ecology that seek to harness information about species distributions to manage wildlife populations, control invasive species, and reduce the rate of human-induced extinction (Urban 2015, 2018).

Because abiotic and biotic factors can affect spatio-temporal variation in birth and death rates, which affect range limits and extinction risk, detailed information on the factors limiting species distributions is needed to guide effective conservation aimed at curtailing extinction (Sexton et al. 2009, Cardillo and Meijaard 2012, Conde et al. 2019). Identifying these factors can be difficult because the effects of limiting variables may depend on range position (Sexton et al. 2009, Cahill et al. 2014). For example, temperature may limit a species near its high-latitude range margin while having have little or no effect at the core of the species' range. Likewise, factors limiting species at low-latitude range margins (*e.g.* competitors) may not be present in the core or high-latitude portion of the range (MacArthur 1972). Recently, ecologists have focused on understanding interactions between limiting factors and range position, while accounting for temporal dynamics resulting from range shifts (Sekercioglu et al. 2008, Cahill et al. 2014).

The ranges of many species are shifting towards higher latitudes and elevations in response to global climate change (Parmesan and Yohe 2003, Hickling et al. 2006, Sexton et al. 2009, Chen et al. 2011, Williams and Blois 2018). Until recently, most studies of range shifts focused on the dynamics of populations at the core or leading edge of advancing ranges (Parisod and Joost 2010, Angert et al. 2011, Cahill et al. 2014, Beauregard and de Blois 2016, Angert et al. 2020). This focus on leading-edge populations is warranted as individuals are regularly appearing outside their expected high-latitude range limit and because these pioneering populations are vital if species are to survive by tracking optimal habitat conditions (Sexton et al. 2009, Angert et al. 2020). Despite the importance of leading-edge populations, it has been argued that trailing-edge populations are of greater conservation concern due to their high risk of extinction, high genetic diversity, and contributions to regional biodiversity and ecosystem function (Petit et al. 2003, Parisod and Joost 2010, Cahill et al. 2014, Ferrari et al. 2018).

The theoretical foundations of recent studies of trailing-edge populations come from Biogeography, which has sought to assess the relative roles of abiotic factors and biotic interactions in shaping species distributions (Darwin 1859, MacArthur 1972, Brown et al. 1996). Populations near high latitude range boundaries are generally believed to be limited by climatic extremes like cold temperatures (Brown et al. 1996). Biotic interactions are predicted to exert more influence on species' distributions at lower latitudes because of latitudinal gradients in the diversity of competitors, predators, and diseases (Darwin 1859, MacArthur 1972, Cahill et al. 2014). This suggests that climate change is likely to influence trailing-edge populations by changing interactions among species as range limits shift. However, support for this hypothesis is equivocal and the subject of much debate.

The influence of biotic interactions on low-latitude range boundaries was first emphasized by Charles Darwin (1859):

> "*When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually getting rarer and rarer, and finally disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But this is a very false view: we forget that each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food; and if these enemies or competitors be in the least degree favoured by any slight change of climate, they will increase in numbers, and, as each area is already fully stocked with inhabitants, the other species will decrease. When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favoured, as in this one being hurt. So it is when we travel northward, but in a somewhat lesser degree, for the number of species of all kinds, and therefore of competitors, decreases northwards; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the directly injurious action of climate, than we do in proceeding southwards or in descending a mountain. When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements*" (Chapter 3, p. 66).

Subsequent research found support for the hypothesis that the strength of interspecific interactions is linked to latitudinal trends in biodiversity (Darwin 1859, Gross and Price 2000, Cunningham et al. 2009, Jankowski et al. 2010, Freeman and Montgomery 2016). However, abiotic factors have received more attention than biotic interactions in empirical research because broad scale climate and environmental data are widely available and biotic interactions can be difficult to quantify in the field (Krebs 1972, Wiens 1992). Nonetheless, examples of biotic interactions contributing to climate-induced range shifts include evidence of montane birds experiencing range contractions as competitors shift into higher elevations (Jankowski et al. 2010, Warren et al. 2016). A recent study of *Catharus* thrushes found that the distribution of a high-elevation, cool-adapted species was limited by aggressive interactions with a low-elevation competitor (Freeman et al. 2016). Predation can also limit species distributions and contribute to range shifts. Snowshoe hares (*Lepus americanus*) in Wisconsin experienced increased predation pressure when translocated south of their low-latitude range limit (Sievert and Keith 1985).

In addition to competition and predation, species distributions can be limited by pathogens (Ricklefs 2011). Perhaps the best example is the introduction of malaria (*Haemoproteus & Plasmodium*) and avian pox (*Avipoxvirus*) to the islands of Hawai'i (Vanriper et al. 1986, Woodworth et al. 2005, Freed and Cann 2013). While the initial introduction of avian malaria was the product of human movement, the resulting range shift to higher elevations by endemic Hawaiian birds was primarily a response to the expanding range of introduced mosquito species (Scott et al. 1986, Vanriper et al. 1986, Woodworth et al. 2005). Hawaiian birds have persisted by finding refuge at high elevations where mosquitos could not survive. This example occurred in relative isolation, and most bird species on major continents appear to have been exposed to malaria at some point; however, other diseases may limit species even in the absence of human intervention (Ricklefs 2011, Fuller et al. 2012). Recent research indicates that as global temperatures increase, the prevalence of many pathogens and their associated vector ranges will expand (Harvell et al. 2002, Harvell et al. 2009, Altizer et al. 2013). It is largely unknown how shifting pathogen distributions will affect trailing-edge populations of cool-adapted species.

Despite predictions about the importance of biotic interactions, mounting evidence demonstrates that abiotic factors play a critical role in shaping trailing-edge range limits (Root 1988b, Hampe and Petit 2005, Aitken et al. 2008, Eisen et al. 2008, Cahill et al. 2013, Cahill et al. 2014, Freeman and Freeman 2014, Freeman et al. 2018). Climate conditions may limit species distributions at the trailing-edge via numerous mechanisms. For individuals at low-latitude range boundaries, where a species may be at its physiological limit, climate change may impact physiological processes such as metabolism and reproductive behavior (Root 1988a, Hoffmann and Blows 1994, Sekercioglu et al. 2008). A study of Shiras moose (*Alces alces shirasi*) showed that reproductive rates decreased over three decades in low-latitude herds because of increased thermal stress from rising temperatures and lack of high-quality forage resulting from decreased precipitation (Monteith et al. 2015, Ruprecht et al. 2016). Changes in other abiotic factors, like precipitation and humidity, may also have consequences for trailing-edge populations. House finch (*Haemorhous mexicanus*) eggs translocated outside their natal climate conditions hatched at lower rates than un-manipulated eggs because of structural adaptations to the environment in which they were laid (Stein and Badyaev 2011). Additionally, climate cycles such as the El Niño Southern Oscillation have been shown to negatively impact survival, body condition, and fecundity in migratory songbirds (LaManna et al. 2012, McKellar et al. 2015, Tuttle et al. 2017, Gonzalez et al. 2020), and affect growth of low-latitude tree populations (Rozas et al. 2015). Global environmental change may alter the timing and frequency of climate cycles, which could cause phenological mismatches leading to changes in species distributions driven by altered population dynamics (Sillett et al. 2000, Victor et al. 2001, Parmesan and Yohe 2003, Adeney et al. 2006, Sekercioglu et al. 2008).

Recent trends in research on trailing-edge populations

In this section, I review recent trends in research on trailing-edge populations, beginning with the landmark paper by Hampe and Petit (2005), which presented a review of the literature and made a series of arguments for why conservation of rear edge populations is vital. Hampe and Petit (2005) distinguished between rear edge populations and trailing-edge populations, reserving the latter for instances where a species range shift is the result of extirpation of low-latitude populations leading to a low-latitude change in the species distributions. Although their paper focused on ‘stable’ rear edges, not trailing-edge populations, many of the ecological and conservation justifications for focusing on rear edge population pertain to the trailing-edge.

Hampe and Petit (2005) describe three important areas of research and conservation that would improve the understanding and outlook for rear and trailing-edge populations. The first recommendation was to identify areas of rear-edge diversity, likely resulting from glacial refugia. The second recommendation was to determine how climate change impacts rear and trailing-edge populations using multiple methods including modeling, genetics, and experimentation. The final recommendation was to develop conservation strategies targeting rear and trailing-edge populations while taking into consideration their unique characteristics.

Below, I assess 1) the impact of the seminal paper by Hampe and Petit (2005) on the study of rear and trailing-edge populations, 2) the extent to which the three primary recommendations have been followed, 3) the extent to which research and conservation on rear and trailing-edge populations improved in the last 16 years, and 4) areas in need of improvement where future efforts should be focused.

Publications citing Hampe and Petit (2005)

I used the Web of Science citation index to identify all publications citing Hampe and Petit (2005) up to April 19, 2021. I then searched the resulting list for publications pertaining to rear and trailing-edge populations using the following search terms: “trailing-edge”, “warm”, “warm-edge”, “low-latitude”, “low-elevation”, “southern”, “equator*”, “rear-edge” in the title. Because the original paper does an excellent job of explaining species range shifts, especially in relation to climate change, many studies focusing on leading-edge populations also cite it. I therefore also searched the original search results for publications pertaining to the leading-edge using the following search terms: “leading-edge”, “high-latitude”, “high elevation”, “cool-edge”, “cool”, “northern”, “front-edge”.

In total 1301 publications cited Hampe and Petit (2005) as of April 19, 2021. Of those, 293 (22.5%) focused on rear or trailing-edge populations, 188 (14.5%) focused on leading-edge populations, and the other 820 publications either did not focus on these edges, did not explicitly mention them in the title, or focused on range shifts but did not mention a specific part of a species range in the title (Figure 1). The majority (53.69%) of publications focusing on rear or trailing-edges referred to this range margin as “southern” (Fig 2A). Rear and trailing-edge range margins were also commonly referred to as “rear-edge” (19.39%) and “trailing-edge” (8.1%), other search terms ranged from 1 to <8% (Fig 2A). The majority (63.81%) of publications with a focus on leading-edges referred to this range margin as “northern” (Fig 2B). Leading-edge range margins were also commonly referred to as “leading-edge” (9.51%), “high-latitude” (9.33%), “high-elevation” (9.33%), other search terms ranged from 1.1% to <8% (Fig 2B).

Impact of Hampe and Petit (2005)

Hampe and Petit (2005) reported that 86% of latitudinal range margin studies focused on high-latitude range margins, whereas only 14% of the studies they reviewed focused on low-latitude range margins. Since then, the total number of publications focusing on low-latitude, rear edge, and trailing-edge range margins has increased, leading us to conclude that this seminal paper had its intended effect in increasing research on low-latitude, rear edge, and trailing-edge populations.

Where are rear and trailing-edge populations?

The first of the three recommendations proposed by Hampe and Petit (2005) was to identify areas of rear and trailing-edge diversity, likely resulting from glacial refugia (Hewitt 2000, 2004). As the authors point out, this is a daunting task because these populations are likely small and difficult to detect. Despite this, some progress has been made towards realizing this goal. Efforts in identifying rear and trailing-edge populations range from the identification of a single population or genetic lineage to regional assessments of the distribution of trailing-edge populations. Examples focused on a single population or species include identification of a unique genetic lineage of red seaweed (*Gracilaria vermiculophylla*) along the coast of China resulting from glacial barriers (Hu et al. 2018), discovery of a population of high-elevation oak (*Quercus spp.*) trees in Myanmar (Meng et al. 2019), assessment of the genetic diversity and integrity of brook trout (*Salvelinus fontinalis*) populations in the southern Appalachian Mountains, USA (Pregler et al. 2018), detailed examination of the viability of an endemic plant species *Petrocoptis pseudoviscosa* in Spain (Garcia 2008), and a description of the genetic diversity of Canada lynx (*Lynx canadensis*) at the species southern range margin (Koen et al. 2014). Most examples focus on plants, likely because plants are usually sessile and animals are mobile, often avoid humans, and inhabit inaccessible habitat.

Efforts to identify rear or trailing-edge communities, rather than a single species or genetic lineage, has also increased. Although generally less detailed, these studies provide information at regional scales, which can be of great benefit to conservation organizations with the goal of multi-species or ecosystem-level conservation. A few examples include the documentation of high elevation cryptogam biota on the slopes of Mt. Katahdin, Maine (Dibble et al. 2009), identification of plant diversity patterns, growth form composition, and species turnover in the Riviersonderend Mountains of South Africa (Agenbag et al. 2008), and examination of patterns of species richness in mammals of the Western Palaearctic and the effect that glacial refugia had on speciation in these populations (Morales-Barbero et al. 2018). Finally, I found no studies attempting to identify trailing-edge populations at a global scale (but see Chapter 2).

Performance of rear and trailing-edge populations

The second recommendation by Hampe and Petit (2005) was to assess the performance of rear and trailing-edge populations through interdisciplinary research including genetics, modeling, and long-term experiments. Although Hampe and Petit do not define population performance, the term generally refers to metrics like population growth rate, survival, and reproduction. More progress has been made towards realizing this recommendation than locating trailing-edge populations. A study on a declining population of grey jays (*Perisoreus canadensis*) showed that warmer autumns followed by late cold winters at the species' trailing-edge led to delayed breeding and reduced reproductive success as a result of perishing food caches on which the species relies (Waite and Strickland 2006). Gimenez-Benavides et al. (2011) reported high mortality and declining population growth rates in low-altitude populations of *Siline ciliata* at the species' southern range margin in the Sierra de Guadarra mountains of Spain. Additionally, population trends appeared to be stable in core populations but declining at low altitudes (Gimenez-Benavides et al. 2011). Recently, Oldfather and Ackerly (2019) added to a growing body of literature supporting the complex nature of species range limits by showing that heterogeneity in microclimate conditions can have complicated effects on population dynamics. These results suggest that it is not possible to make reliable predictions about population dynamics and viability over a single gradient, like latitude (Sexton et al. 2009, Abeli et al. 2014, Pironon et al. 2017).

The use of modeling in the field of ecology has grown considerably and powerful tools now exist to assist in meeting this recommendation. Models have been used to identify threats and inform conservation of numerous species, including a threatened felid, *Neofelis diardi* (Macdonald et al. 2018) and two tundra plants at the rear-edge of their distribution (Doak and Morris 2010). Process-based tree growth models have been used to assess forest vulnerability to climate change at the rear edge of tree species in Spain (Sanchez-Salguero et al. 2017).

An additional part of this recommendation was to include long-term experiments aimed at separating climate effects from other potential limiting factors like predation, competition, and habitat loss (Hampe and Petit 2005). Only a few articles reported results from long-term experiments. A 3-year common garden experiment on oak leaf phenology showed that experimentally warming seedlings advanced leaf phenology, leading to longer growing seasons and higher mortality (Morin et al. 2010). Phenological changes to species breeding, migration, and growing seasons may have cascading effects on population dynamics. Another study used northern-edge mixtures, southern-edge mixtures, and monocultures of bog plants in a latitudinal common garden experiment to show the importance of climate-mediated interspecific interactions, adaptation, and resilience at different parts of a species range (Schwarzer et al. 2013). Other experiments and observational studies that span entire species distributions are essential to exposing the effects of climate change on populations in different parts of a species range.

Finally, many recent papers focused on the genetics of marginal populations, including 50 articles published in Conservation Genetics, 92 articles published in Molecular Ecology, and 38 articles published in Tree Genetics & Genomes. In most cases, genetics articles focus on plants, a trend that Hampe & Petit (2005) also observed in their literature search, leading them to suggest that genetic work should be expanded beyond floral communities.

Conservation of rear- and trailing-edge populations

Few published articles describe detailed conservation plans and almost none describe conservation actions focused on rear or trailing-edge populations, making it difficult to assess progress towards the third recommendation of Hampe and Petit (2005). However, one example describes forest management for conservation of trees in Romania, highlights challenges associated with the current approach, and makes suggestions for improvement (Postolache et al. 2019). The focus of the study was not solely on rear or trailing-edges but the authors recognized that tree populations at those range margins are key to successful conservation (Postolache et al. 2019). In general, few conservation initiatives focus on rear or trailing-edge populations.

Research needs

The recommendations of Hampe & Petit (2005) remain relevant 16 years later and progress has been made towards realizing all three. Regardless, several knowledge gaps remain, including:

1) Little is known about the global distribution of trailing-edge populations, which prevents the identification of hotspots in need of conservation.
2) Few long-term demographic studies have been conducted to identify the factors limiting trailing-edge populations via effects on population dynamics.
3) Few studies have combined observational and manipulative research methods to understand the mechanisms influencing climate-induced range shifts.

The aim of this dissertation is to address these knowledge gaps.

Objectives

The first objective of this dissertation, addressed in Chapter 2, is to identify the global distribution of trailing-edge populations of birds. In Chapters 3-5, I test several hypotheses regarding the importance of abiotic and biotic factors in limiting songbird distributions in a global hotspot of trailing-edge population diversity, the southern Appalachian Mountains. In Chapter 3, I describe results from experimental and observational methods used to test if socially-mediated Allee effects are present at the range margin of a cool-adapted songbird. Chapter 4 examines the prevalence of hemoparasites in cool- and warm-adapted songbirds, and tests whether climate or infection drives songbird occupancy in the southern Appalachian Mountains. Chapter 5 employs a reciprocal translocation experiment to assess whether egg hatch rates of cool-adapted birds will be negatively affected by climate change.

Study Area

The southern Appalachian Mountains are one of the most diverse areas in the western temperate region (SAMAB 1996, Campbell et al. 2010, Milanovich et al. 2010). The region also has a high diversity of trailing-edge populations (see Chapter 2). The southern Appalachian Mountain region covers over 37 million acres, mostly forested, and is home to the headwaters of several major river systems (SAMAB 1996). The region's forests are diverse, ranging from bottomland hardwoods at low elevations to spruce fir forests at the highest elevations in the Black Mountains of North Carolina and the Smoky Mountains. They are distinct from the northern Appalachian Mountains of New York and New England in that they escaped glaciation during the last glacial maximum (Walker et al. 2009).

Although few studies have focused on trailing-edge populations in the southern Appalachian Mountains, recent research has explored the potential impact of climate change on different taxa. For example, many tree species in eastern North America are expected to shift to higher latitudes or to higher elevations in response to current or accelerated climate change (Iverson et al. 2008). These shifts suggest a change in species composition in the southern Appalachian Mountains, with extirpation of some cool-adapted species, and the colonization of some warm-adapted species (Matthews et al. 2004). Several studies indicate species endemic to the region are likely to go extinct if climate change continues at its current rate. For example, many *Plethodontid* salamanders may face high extinction risk due to climate driven habitat loss (Milanovich et al. 2010). Unique genetic makeup, potential for speciation, and high risk of extinction, make conserving southern Appalachian trailing-edge populations of great importance.

My research was conducted in and around the Coweeta Hydrologic Laboratory in the Nantahala National Forest in southwestern North Carolina. This site is appropriate for testing hypotheses regarding the importance of abiotic and biotic factors in limiting trailing-edge populations because it is possible to identify the local range boundary of many cool-adapted species and their warm-adapted counter parts. It is also an area where climate conditions change rapidly over short distances and elevations. The elevation gradient in the study area ranges from 800 m to 1500 m, with higher elevations being cooler and wetter than low elevations.

Why Birds?

This dissertation primarily focuses on birds. This is partially due to my own interest and love for birds and because they make excellent study organisms for several reasons. First, most birds are conspicuous and thus easily observed. Second, birds are conducive to manipulative experiments at the nest, individual, and population levels. Third, birds can be good indicator species because they are often easily counted and it is possible to link changes in their abundance, occurrence, and reproduction to changes in the environment (Carignan and Villard 2002). Finally, and perhaps most importantly, birds are disappearing and approximately 3 billion birds have been lost from North America in the last century, making research aiding their conservation a priority (Rosenberg et al. 2019).

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Figures

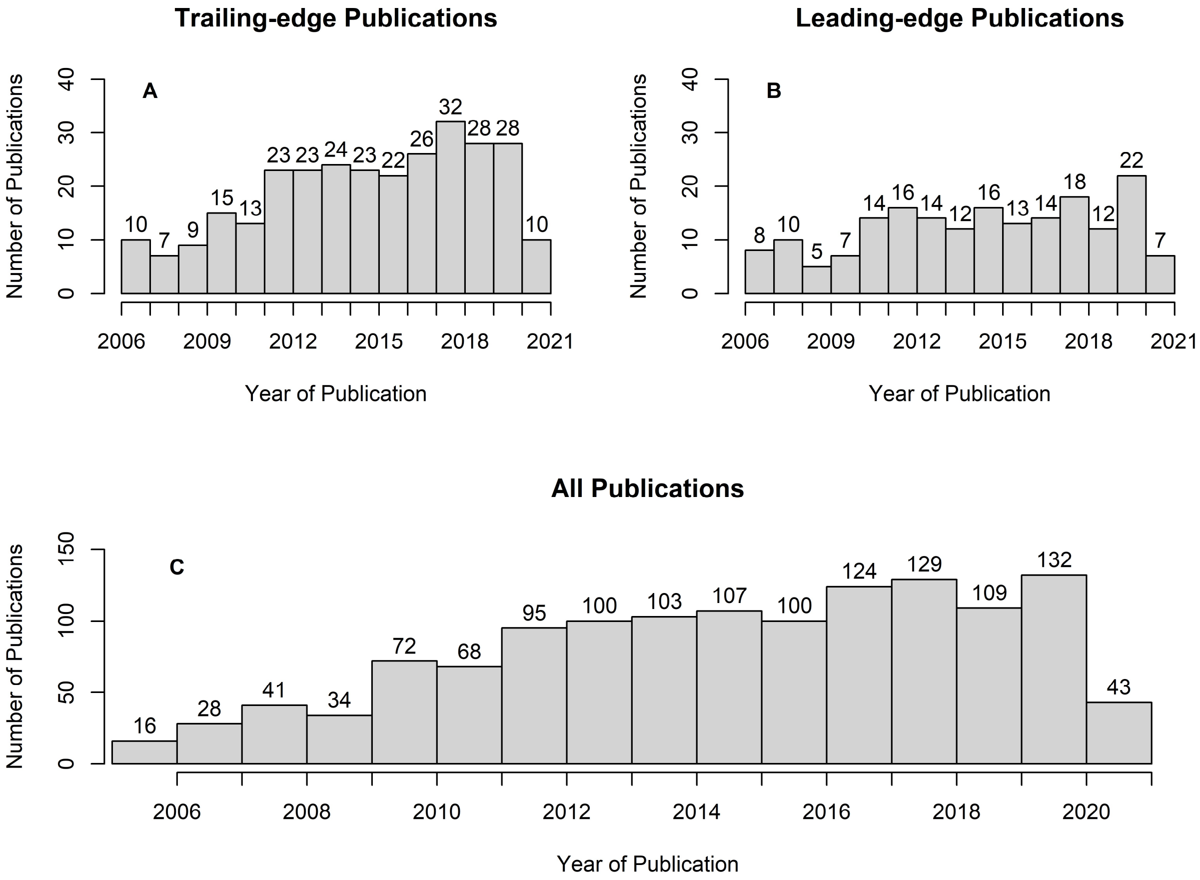
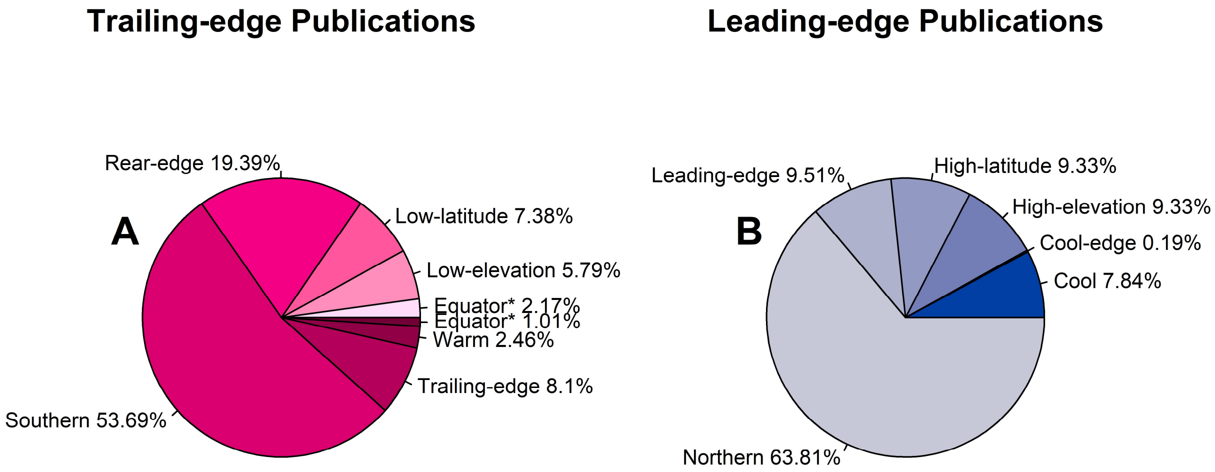


Figure 1.1 Number of publications citing Hampe and Petit (2005) and focused on A) trailing-edges, B) leading-edges, and C) all publications, with duplicates removed, as of April 19, 2021.


Trailing-edge Publications

Leading-edge Publications

Figure 1.2. Percent of search terms linked to publications that cited Hampe and Petit (2005), stratified by A) trailing-edge publications and B) leading-edge publications. All publications were retrieved from Web of Science on April 19, 2021.

CHAPTER 2

IDENTIFYING GLOBAL HOTSPOTS OF AVIAN TRAILING-EDGE POPULATION DIVERSITY[1]

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Abstract

Climate change is causing the ranges of many species to shift poleward and to higher elevations. Trailing-edge populations near the low-latitude edge of a shifting range are predicted to be at high risk of climate-induced extinction, but conservation efforts are hindered by a lack of information about the global distribution of trailing-edge populations. We used a large spatial dataset on the ranges of nearly all extant avian species to identify potential hotspots where trailing-edge populations represent a large proportion of the total avifauna. We identified potential trailing-edge population hotspots by isolating and overlaying low latitude regions of species' ranges, and computing the proportion of total species richness in a location comprised of low-latitude populations. We identified potential hotspots on all continents other than Antarctica. Potential trailing-edge population diversity was highest near the equator, low-latitude margins of mountain ranges, desert edges, and along coastlines. Because a potential trailing-edge population hotspot might not be an actual trailing-edge population hotspot if the low-latitude populations are not declining, information on population trends is necessary for confirmation. As a case study, we focused on one of the identified hotspots, the Southern Appalachian Mountains, where our analysis indicated that 30 bird species have potential trailing-edge populations. Even though more population studies have been conducted in the Appalachian Mountains than in most of the other potential hotspots that we identified, there was insufficient information available from the high elevations where these species occur to make strong inferences about population declines. Our research highlights the need for a concerted effort to gather more information about population trends in the regions we identified as potential hotspots of trailing-edge population diversity.

Keywords: Appalachian Mountains, biodiversity hotspots, breeding bird survey, climate change, low-latitude populations, range shifts

Introduction

Global environmental change is causing the ranges of many species to shift poleward and to higher elevations (Parmesan and Yohe 2003, McDonald et al. 2012, Morelli et al. 2012, Auer and King 2014, Mason et al. 2015). Although range shifts are expected to become more pervasive, their outcomes and consequences are difficult to predict without a thorough understanding of the underlying ecological processes. Several studies have investigated recent range shift dynamics by focusing on high-latitude, leading-edge populations, but little work has been done on trailing-edge populations (Angert et al. 2011, Cahill et al. 2014, Beauregard and de Blois 2016). Trailing-edge populations are populations near the receding margin of a shifting species range (Hampe and Petit 2005), and information about trailing-edge populations is needed because they are predicted to be at high risk of climate change induced extinction (Cahill et al. 2014).

Although it has been argued that conservation efforts should not target low viability populations (Gilbert et al. 2019), loss of trailing-edge populations could negatively affect regional biodiversity because they represent a large portion of species richness in some regions (Cahill et al. 2014). Additionally, loss of trailing-edge populations could have detrimental impacts on species-level genetic diversity because these populations are often older and more genetically diverse than populations at the range center or leading-edge (Hampe and Petit 2005, Ferrari et al. 2018). Conservation of trailing-edge populations requires information about their global distribution, but distributional data is lacking. Although there is a dearth of spatial data available on trailing-edge population distributions, their distributions must be shaped by the same factors that influence species' range limits, which is a subject that has been extensively studied for over a century (Darwin 1859, MacArthur 1972, Gross and Price 2000).

The relative influence of biotic interactions and abiotic conditions on species distributions often varies spatially and among species, making it difficult to predict where the diversity of trailing-edge populations is likely to be highest. At a coarse scale, range limits are often shaped by continental geology. For example, in the Americas, physical features such as the Andes and the Rocky Mountains influence the longitudinal range boundaries of many species (Baselga et al. 2012). Conversely, in the Eurasian landmass, longitudinal limits are often shaped by the east-west orientation of mountain ranges (Baselga et al. 2012). Latitudinal limits often occur in the absence of predominant physical landforms, potentially as the result of competition and other biotic interactions (MacArthur 1972, Cahill et al. 2014). However, for species adapted to cool climates, low-latitude range limits regularly occur near the southern terminus of mountain ranges (Stefanescu et al. 2004, Wilson et al. 2005).

Their unique genetic structure and high extinction risk make trailing-edge populations an important conservation priority, but no studies have attempted to document the global diversity and distribution of trailing-edge populations. One challenge that hinders efforts to identify the global distribution of trailing-edge populations is that spatial datasets on ranges are not available for many species. Birds are an exception, and we used a large dataset on the global distribution of nearly all extant avian species to identify potential trailing-edge population hotspots: regions where trailing-edge populations comprise a large portion of the local avifauna. Birds are also a useful taxonomic group to focus on because they occur on all continents. One difficulty associated with identifying trailing-edge population hotspots is that a population can only be considered a trailing-edge population if the population is declining. We therefore sought to confirm the status of one potential trailing-edge hotspot, the Southern Appalachian Mountains, where we expected to find more information on population trends than in other parts of the world.

Methods

Identifying potential trailing-edge population hotspots

We identified regions of high trailing-edge population diversity using range maps provided by BirdLife International for nearly all extant avian species (Birdlife International and Handbook of the Birds of the World. version 2018.1 2018). The BirdLife International range map dataset was provided as a collection of polygon shapefiles. For migratory species, separate range maps were provided for breeding and non-breeding season ranges. For simplicity, we discarded range maps for migration routes and nonbreeding grounds, although shifting nonbreeding ranges are certainly important from a conservation standpoint. We limited our analysis to terrestrial species because range maps for pelagic species are often more indicative of foraging locations than of breeding sites. We converted polygons to rasters with 1.2 km resolution using the 'raster' package (v 2.7-15) in R (Hijmans and van Etten 2018, R Core Team 2020).

Because temperature niches appear to be shifting to higher latitudes, with species expected to follow, we identified potential trailing-edge population hotspots by isolating low-latitude portions of species' ranges. We used two thresholds, the 5th and 10th percentiles, to crop the low-latitude region of each species' range. Specifically, our algorithm involved: (1) computing the area of the entire range, (2) computing the area of a subset of the range defined by an increment of one degree of latitude from the equator, and (3) computing the percentage of the range within this subset. The algorithm stopped if the percentage of the area of the subset was greater than the threshold at the end of step (3). Otherwise, steps (2) and (3) were repeated by adding an additional increment of one degree of latitude. In some cases, for example when a species' range was restricted to a small island, the entire range of a species occurred within a single degree of latitude. We discarded these species because the designation of a trailing-edge population is arbitrary for such a small range. After running the algorithm for all species, we overlaid each subset and computed the total number of low latitude populations at each cell of 1.2 km resolution global raster layer. We designated potential trailing-edge population hotspots as regions where 15% of the avifauna was comprised of low-latitude populations and where at least 10 low-latitude populations were present.

Trailing-edge populations in the Southern Appalachian Mountains

A population can be classified as a trailing-edge population if it occurs near the receding edge of a shifting range, which by definition, suggests that trailing-edge populations are experiencing local population declines (Hampe and Petit 2005, Koen et al. 2014, Mota et al. 2015). Without knowledge of global population trends, we refer to the regions identified above as *potential* trailing-edge population hotspots. To confirm whether a potential hotspot could be considered an actual trailing-edge population hotspot, we focused on the Southern Appalachian Mountains of the United States, one of the most diverse regions in the temperate zone and a region where long-term trend data is available (SAMAB 1996, Riddell et al. 2018). The region is large, covering over 37 million acres and encompassing the headwaters of several major rivers (SAMAB 1996). Forests in this region are diverse, ranging from bottomland hardwoods at low elevations to spruce-fir forests at high elevations (Yarnell 1998). They are distinct from the northern Appalachian Mountains because they escaped glaciation during the last glacial maximum (Walker et al. 2009).

To verify that the potential trailing-edge populations have been experiencing population declines, we used publicly available Breeding Bird Survey (1966-2015) estimates to assess population trends of birds in the Southern Appalachian Mountains (Sauer et al. 2015). We subsetted trend estimates by bird species and by region. Regions included the Appalachian

Mountains (S28), Alabama (ALA), Georgia (GA), North Carolina (NC), Tennessee (TEN), West Virginia (WV), and Virginia (VA). The Appalachian Mountain region (S28) also includes Kentucky, Ohio, Pennsylvania, New Jersey, and New York which are not considered part of the Southern Appalachian Mountains. We assessed the regional credibility measure codes for each trend estimate. Credibility measures are as follows: G – representing the highest quality data, described as having at least 14 samples over the entire study period; Y – Data with a deficiency, such as low abundance estimates, fewer than 14 routes sampled, or imprecise results; R – Data where regional abundance estimates are very low, fewer than 5 routes sampled, or results are extremely imprecise.

Results

Potential trailing-edge population hotspots

All terrestrial avian populations along the equator are, by definition, potential trailing-edge populations because they occur at the lowest possible latitude at similar elevations (Figs. 2.1a-b). Thus, it is unsurprising that areas near the equator had the highest trailing-edge population diversity. Specifically, equatorial South America, equatorial east Africa, and Indonesia had the highest diversity of potential avian trailing-edge populations. Equatorial South America and Africa had just under 500 species with trailing-edge populations identified using the 10th percentile threshold, and approximately 330 bird species identified using the 5th percentile threshold (Fig. 2.1a, Appendix 2.1a).

Beyond the equatorial zone, regions with high potential avian trailing-edge population diversity occur near low-latitude margins of mountain ranges, deserts, and coastlines (Figs. 2.1a-c). In addition, northern Australia and southern India were highlighted as having high potential avian trailing-edge population diversity with 100-120 species. Other hotspots include southern Iran and Pakistan, the northwest coast of Africa, the southern coast of California, the Central Rocky Mountains, the Southern Appalachian Mountains, the Gulf Coast of North America (including S. Florida), the northern Andes, the Southern Himalayan mountains, the Korean Peninsula, and the Indochina Peninsula (Fig. 2.1d).

Trailing-edge populations in the Southern Appalachian Mountains

Our results indicate that the Southern Appalachian Mountain region is a hotspot of trailing-edge population diversity, with 30 species of birds having their low-latitude breeding range limit occurring in this region (Figure 2). The Southern Appalachian Mountains had many more potential trailing-edge populations than in the surrounding Piedmont, Coastal Plain, and Alleghany Plateau (Figs. 2.2 & 2.3). Approximately 20% of the avifauna in the Southern Appalachian Mountains is comprised of species with potential trailing-edge populations in the region (Figure 2.3).

We found Breeding Bird Survey (BBS) population trend estimates for 29 of the 30 bird species on our list of species with trailing-edge populations in the Southern Appalachian Mountains (Table 2.1). There were no estimates for northern saw-whet owl (*Aegolius acadius*). For some species, like black-throated green warbler (*Setophaga virens*) and blue-headed vireo (V*ireo solitarius*), trend estimates were available for every state in the region (Sauer et al. 2015). For other species, like Canada warbler (*Cardellina canadensis*) and dark-eyed junco (*Junco hyemalis*), trend estimates were available for only a few states, even though these species are known to breed in most states in the region (Nolan Jr. et al. 2002, Reitsma et al. 2009, Sauer et al. 2015). Breeding Bird Survey data indicate that five of the 29 bird species showed negative trends and two showed positive trends (95% CIs excluding zero) in the Appalachian Mountains during the most recent decade (2005-2015, Table 2.1). Three of the five negative trends and both positive trends were reported to have at least one data deficiency, as described in the Methods section. Twenty-two species had population trends with 95% CIs including zero. Four species showed a decline, and 14 increased (95% CIs excluding zero), over the entire 49-year study period (Table 2.1, (Sauer et al. 2015)). Unfortunately, 21 of 29 trend estimates were reported as having one or more data deficiencies over the time period. These estimates are from a region which includes states north of the Southern Appalachian Mountains, but data sparsity and data quality issues became even more problematic when we tried to conduct an analysis of state-level trends. Specifically, many species on our list were not sampled in every state although they are known to breed there. This is likely because most BBS routes do not sufficiently sample high elevations. Additionally, 95% of state level trend estimates had at least one data deficiency or were not available for some species (Appendix D).

Discussion

Conserving global biodiversity requires more than preventing species-level extinctions. The high levels of genetic and phenotypic diversity among populations within species indicates that attention must be given to the most vulnerable population segments within a species' range (Hughes et al. 1997). Trailing-edge populations are predicted to be the most vulnerable population segments to climate-induced extinctions, and our results represent the first effort to describe the global distribution of trailing-edge populations and to identify trailing-edge population diversity hotspots (Hampe and Petit 2005).

Our analysis of the ranges of all extant terrestrial bird species indicated that the highest diversity of potential trailing-edge populations occurred along the equator, where overall vertebrate biodiversity is greatest (Pianka 1966, Myers et al. 2000, Pimm et al. 2014). We also found that trailing-edge population diversity was high near the low-latitude margins of mountains, deserts, and coastlines. Many of these regions are also recognized as important hotspots of species-level biodiversity (Myers et al. 2000). For example, Brazil's Atlantic Coast, Caucasus, Mesoamerica, South-Central China, and Western Ghats/Sri Lanka are all listed by Myers et al. (2000) as being important biodiversity hotspots. However, several regions that we identified as potential trailing-edge population hotspots are not considered to be biodiversity hotspots, including northern Australia, northwestern Africa, eastern Asia, southeastern United States (primarily Florida), and the central Rocky Mountains of the United States. The discordance between trailing-edge population hotspots and overall biodiversity hotspots highlights the need for conservation efforts to focus on both population-level and species-level patterns of diversity.

Our method of identifying potential hotspots of trailing-edge population diversity relied on range maps and an algorithm based on latitude. Consistent with previous efforts to identify hotspots (Marchese 2015), our aim was not to model species distributions, only to identify where potential trailing-edge populations occur. Indeed, range maps can be regarded as outcomes of simple species distribution models, and we therefore did not use climate variables or elevation in our analysis because the effects of these variables are already represented in species range maps. Additionally, we only focused on the lowest-latitude portions of the range and not the entire low-latitude margin of a species' range, which might span thousands of miles, because the most sensitive populations to climate change are predicted to be at the lowest latitudes of the existing range (Cahill et al. 2014). An alternative approach to identify trailing-edge populations could have focused on both low latitudes and low elevations; however, the effect of elevation can be negligible in some parts of a species' range, suggesting that an algorithm based on an interaction between latitude and elevation would be necessary. We did not have sufficient data to parameterize such an algorithm. Finally, non-breeding season distributions are important to the viability of many species (Marra et al. 2015, Taylor and Stutchbury 2016) and investigating their response to environmental change should be a focus of future research.

Our results demonstrate that the Southern Appalachian Mountains harbor a high diversity of potential avian trailing-edge populations. However, trend estimates in this region are based on sparse data that were not sufficient for making strong inferences about population declines. For example, state-level trend estimates are unavailable for many bird species, and over half of the estimates for birds with trailing-edge populations in the Southern Appalachian Mountains had a data deficiency. This was especially apparent at high elevations, indicating that this region would benefit from additional high elevations routes or that different survey methods may be necessary. Even though data quality was poor in this region, it can still be considered data rich compared to other regions around the world where trend estimates are completely unavailable.

Although we have made progress towards identifying the global distribution of trailing-edge hotspots, much of the information needed to guide conservation efforts in the face of rapid environmental change is lacking. Specifically, most of the forecasts of range shifts have not been based on mechanistic models that include ecological processes (Iverson et al. 2008, Matthews et al. 2011, Prasad et al. 2013). Understanding how population processes such as survival, recruitment, and movement are affected by environmental and biological change is key to future conservation efforts and should be a research priority (Chandler et al. 2018). It is also unknown how biotic interactions, like competition and predation, will affect these populations or whether trailing-edge populations are able to adapt fast enough to changing biotic and abiotic pressures (Sekercioglu et al. 2008, Urban 2015, Riddell et al. 2018). In addition, a greater understanding of the physiology of species at their low-latitude range limit is needed because many populations at range boundaries occur near their physiological limits (Riddell et al. 2018).

To advance knowledge of trailing-edge populations and the ecological processes contributing to range shifts, we suggest a global-scale research initiative is needed to evaluate hypotheses by coupling observational studies with manipulative experiments (Cotterill and Foissner 2010). To properly identify causes of range shifts at low latitudes, observational data is needed to quantify long-term trends in population parameters. Furthermore, the addition of occupancy, mark-recapture, and natural history data would allow for inference on spatial and temporal variation in demographic processes contributing to these shifts (Royle et al. 2013). While collecting these data at large spatial scales is difficult, it may be possible to pair this data with count or rapid assessment data (Chandler et al. 2018). Although it would be logistically challenging, combining large scale observational work with manipulative experiments may be the best approach to identifying the causal relationships underlying range shifts.

Our work provides a first glimpse into the global diversity and distribution of trailing-edge populations, but additional research is needed. By following the research agenda outlined above, the understanding of how climate change impacts range shifts can be advanced beyond simple identification and forecasts of species distributions. Moving beyond conventional species distribution modeling to understand the demographic mechanisms involved with range shifts at the trailing-edge, and at other portions of the range, will provide the information necessary to inform conservation efforts aimed at mitigating the impacts of climate change on global biodiversity.

Data availability

The avian range data used in this analysis is available by request from BirdLife International. USGS Breeding Bird Survey data is publicly available at https://www.pwrc.usgs.gov/bbs/

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Author Contributions: S.A.M. wrote and formatted the manuscript, formatted the data, and conducted the analysis. R.B.C. conceived the ideas, planned the analysis, and edited the manuscript.

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Tables and Figures

Table 2.1 Breeding Bird Survey trend estimates, 95% credible intervals, and regional credibility measure codes (G – representing the highest quality data, described as having at least 14 samples over the entire study period; Y – Data with a deficiency, such as low abundance estimates, fewer than 14 routes sampled, or imprecise results; R – Data where regional abundance estimates are very low, fewer than 5 routes sampled, or results are extremely imprecise) for bird trailing-edge populations in the southern Appalachian Mountains. For all species a trend estimate is available for the entire Appalachian Mountain range (Sauer et al. 2015). See Appendix D for state-level trend estimates.

Species	1966-2015 Trend Est. (CI)	2005-2015 Trend Est. (CI)	Regional Credibility Measure
Sharp-shinned hawk (*accipter striatus*)	1.51 (0.40, 2.44)	1.94 (-0.92, 4.66)	R
Ruffed grouse (*Bonasa umbellus*)	-1.55 (-3.09, -0.11)	-0.83 (-4.91, 3.05)	R
Yellow-bellied sapsucker (*Sphyrapicus varius*)	5.81 (4.30, 7.20)	1.02 (-1.92, 3.91)	Y
Alder flycatcher (*Empidonax alnorum*)	2.77 (1.62, 3.99)	-0.31 (-3.46, 2.65)	Y
Least flycatcher (*Empidonax minimus*)	-2.46 (-3.04, -1.93)	-2.49 (-4.15, -0.85)	G
Blue-headed vireo (*Vireo solitarius*)	3.16 (2.15, 4.09)	1.42 (-0.32, 3.20)	Y
Common raven (*Corvus corax*)	4.48 (3.37, 5.45)	5.59 (3.11, 7.97)	Y
Black-capped chickadee (*Poecile atricapillus*)	0.65 (0.19, 1.11)	-0.97 (-2.39, 0.36)	G
Red-breasted nuthatch (*Sitta canadensis*)	4.10 (2.71, 5.47)	3.89 (-0.33, 8.03)	R
Brown creeper (*Certhia Americana*)	0.47 (-0.90, 1.81)	0.93 (-2.72, 4.05)	Y
Winter wren (*Troglodytes hiemalis*)	2.74 (1.16, 4.30)	-3.50 (-7.83, 0.19)	Y
Golden-crowned kinglet	1.13 (-0.83, 3.12)	0.36 (-5.99, 5.42)	R

(*Regulus satrapa*)			
Veery (*Catharus fuscescens*)	-0.32 (-0.68, 0.04)	0.34 (-0.54, 1.36)	G
Hermit thrush (*Catharus guttatus*)	2.31 (1.28, 3.39)	0.19 (-2.44, 2.85)	Y
Swainson's thrush (*Catharus ustulatus*)	2.04 (-0.63, 4.94)	1.27 (-7.15, 6.98)	R
Cedar waxwing (*Bombcilla cedrorum*)	1.64 (1.00, 2.24)	1.31 (-0.49, 3.13)	G
Golden-winged warbler (*Vermivora Chrysoptera*)	-8.56 (-9.77, -7.29)	-7.65 (-10.95, -3.05)	Y
Chestnut-sided warbler (*Setophaga pensylvanica*)	0.00 (-0.68, 0.58)	-0.63 (-1.89, 0.55)	G
Magnolia warbler (*Setophaga magnolia*)	2.39 (1.63, 3.15)	2.65 (0.26, 4.62)	Y
Black-throated blue warbler (*Setophaga caerulescens*)	0.22 (-0.93, 1.22)	-0.25 (-2.09, 1.46)	Y
Blackburnian warbler (*Setophaga fusca*)	-0.16 (-1.31, 0.84)	-3.01 (-5.39, -0.68)	Y
Yellow-rumped warbler (*Setophaga coronate*)	2.13 (0.23, 4.00)	-5.86 (-10.50, -1.19)	Y
Black-throated green warbler (*Setophaga virens*)	1.19 (0.53, 1.82)	0.3 (-1.10, 1.71)	G
Northern waterthrush (*Parkesia noveboracensis*)	-1.52 (-3.27, 0.28)	-0.62 (-4.97, 4.94)	R
Mourning warbler (*Geothlypis philadelphia*)	-0.38 (-2.58, 1.21)	0.13 (-3.76, 3.63)	Y
Canada warbler (*Cardellina canadensis*)	-1.00 (-2.32, 0.16)	-0.19 (-2.20, 1.85)	Y
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	-0.82 (-1.35, -0.28)	-2.64 (-4.37, -1.03)	G
Dark-eyed junco (*Junco hyemalis*)	1.36 (0.62, 2.06)	1.36 (-0.27, 2.93)	G
Purple finch (*Haemorhous purpureus*)	0.02 (-0.73, 0.74)	-1.03 (-3.37, 1.13)	Y

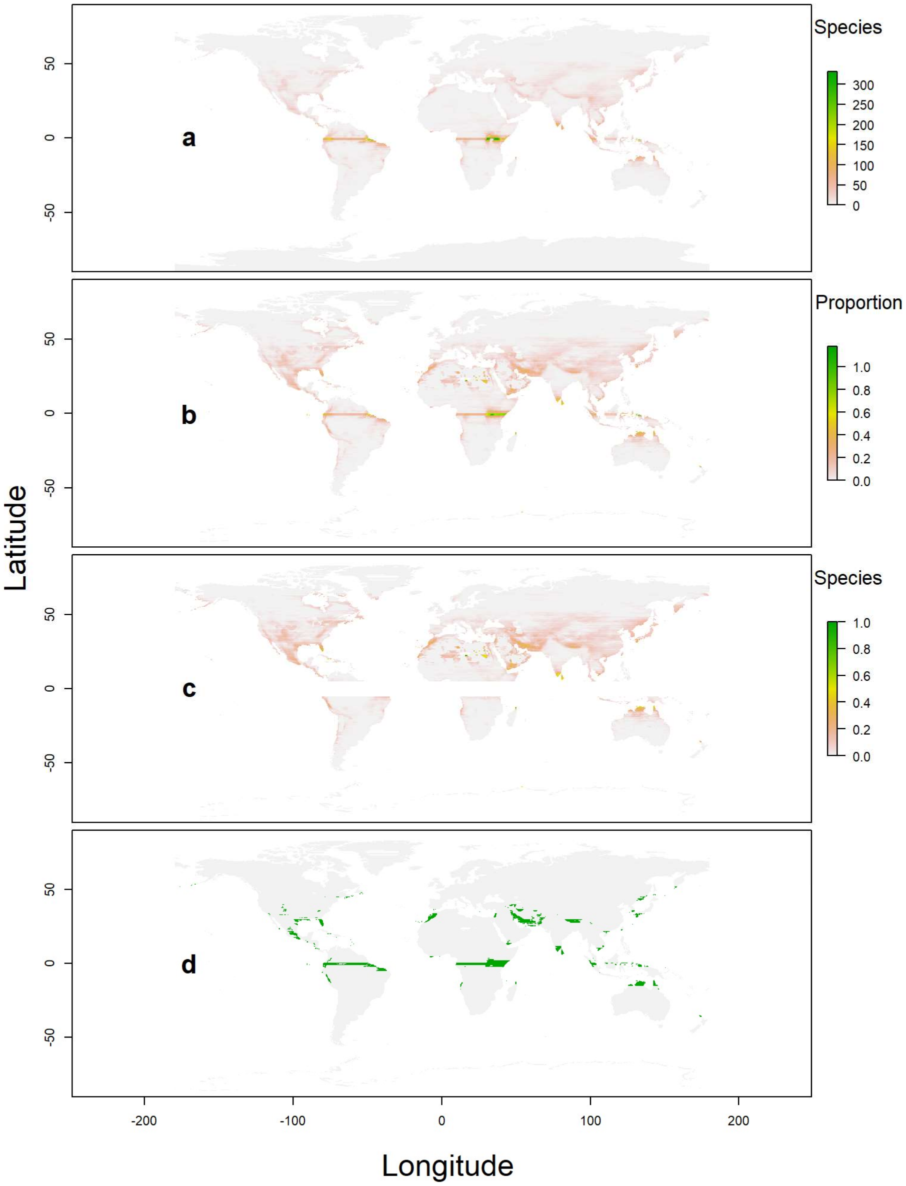

Figure 2.1 Global diversity and distribution of potential trailing-edge populations of bird species represented by (a) species richness and (b) proportional richness of local avifauna. Regions within five degrees of latitude north or south of the equator are removed in panel (c). Panel (d) indicates regions where ≥15% of the local avifauna is comprised of potential trailing-edge populations, excluding areas with fewer than 10 species. Low-latitude range segments were defined as the lower 5th percentile of each species' range. See Appendix A for low-latitude segments using 10th percentiles of each species' range.

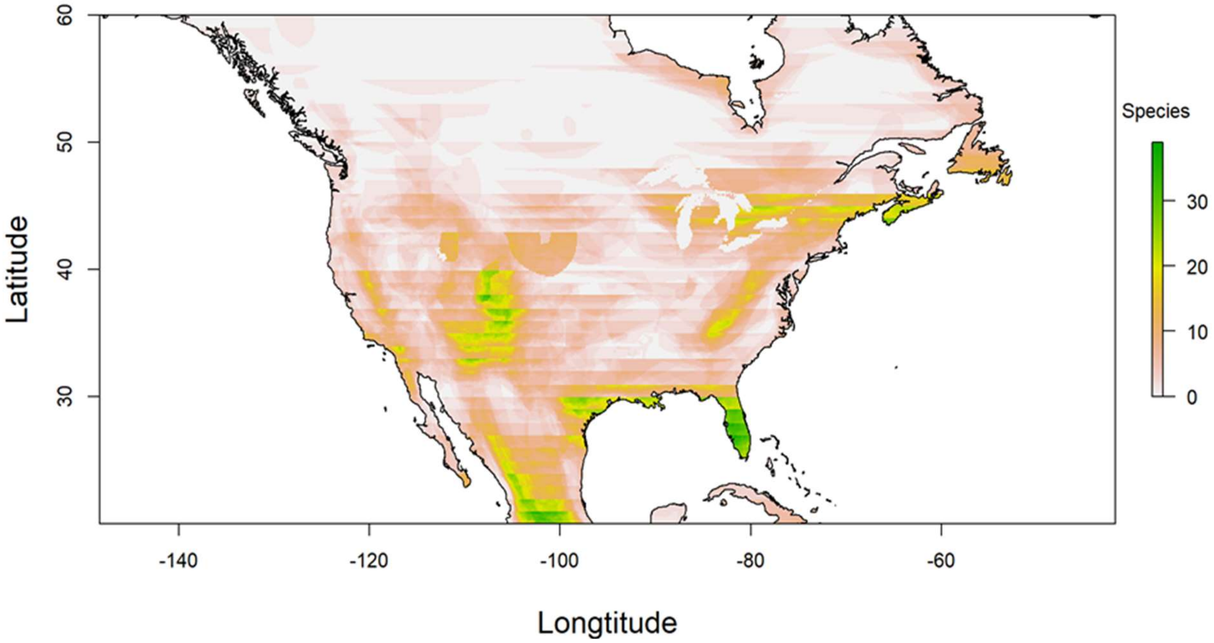

Figure 2.2 Distribution of potential avian trailing-edge populations in North America. Colors indicate the number of species with low-latitude range segments at each terrestrial location. Low-latitude range segments were defined as the lower 5th percentile of each species' range. See Appendix B for low-latitude segments using 10th percentiles of each species' range.

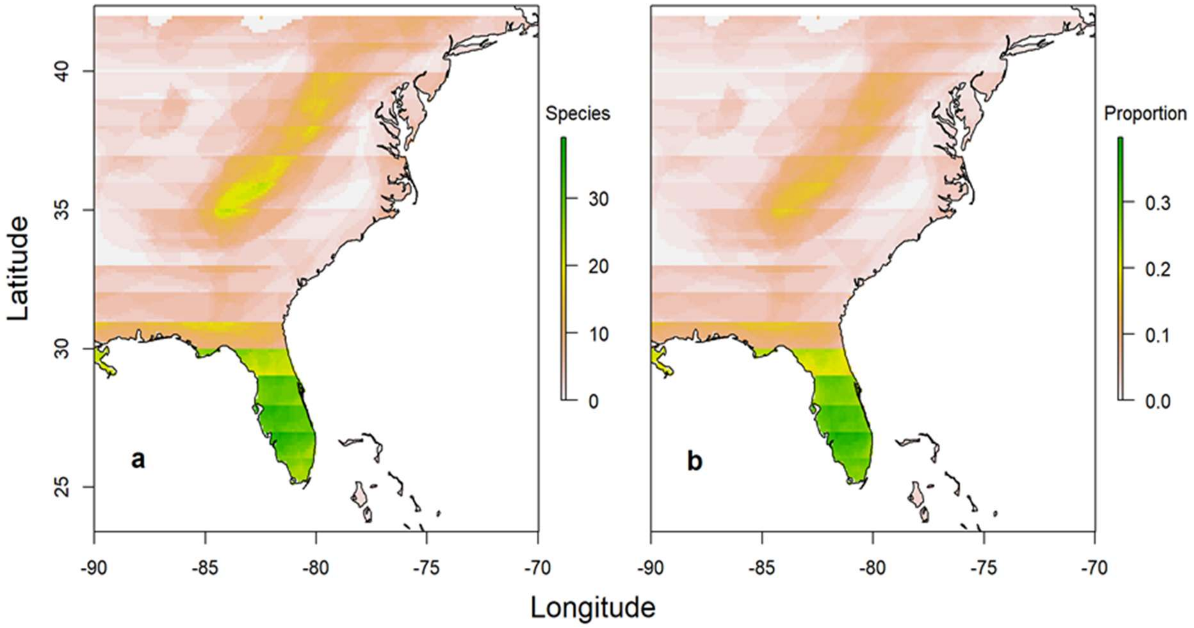

Figure 2.3 Diversity and distribution of trailing-edge populations in the Southeastern United States, represented by (a) species richness and (b) the proportion of the local avifauna comprised of potential trailing-edge populations. Both figures used the lower 5th percentile to designate low-latitude range segments for each species. See Appendix C for low-latitude segments using 10th percentiles of each species' range.

CHAPTER 3

AN EXPERIMENTAL TEST OF THE ALLEE EFFECTS RANGE LIMITATION HYPOTHESIS [1]

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Abstract

Understanding how climate change impacts trailing-edge populations requires information about how abiotic and biotic factors limit their distributions. Theory indicates that socially-mediated Allee effects can limit species distributions by suppressing growth rates of peripheral populations when social information is scarce. The goal of our research was to determine if socially-mediated Allee effects limit the distribution of Canada warbler (*Cardellina canadensis*) at the trailing-edge of the geographic range. Using four years of observational data from 71 sites and experimental data at 10 sites, we tested two predictions of the socially-mediated range limitation hypothesis: (1) local growth rates should be positively correlated with local density, and (2) the addition of social cues immediately outside the trailing-edge range boundary would result in colonization of formerly unoccupied habitat and increased growth rates. During the third breeding season, social cues were experimentally added at 10 formerly unoccupied sites within and beyond the species' local range margin to determine if the addition of social information could increase density and effectively expand the species' range. No experimental sites were colonized after adding social cues and no evidence of Allee effects was found. Rather, temperature, precipitation, and negative density dependence strongly influenced population growth rates. Although theoretical models indicate that the presence of socially-mediated Allee effects at species range boundaries could increase the rate of climate-induced range shifts and local extinctions, empirical results from the first test of this hypothesis suggest that Allee effects play a minimal role in limiting species' distributions.

Keywords: Canada warbler, climate change, density dependence, population dynamics, range limits, social cues

Introduction

The distributions of many species are shifting toward higher elevations and latitudes in response to climate change (Parmesan & Yohe 2003; Parmesan 2006; Zuckerberg *et al.* 2009; Mason *et al.* 2015; Orihuela-Torres *et al.* 2020). Trailing-edge populations near low-elevation and low-latitude range boundaries are predicted to experience strong negative impacts of climate change because these populations are often near their physiological limits and in contact with competitors and predators that are better adapted to encroaching climate conditions (Aitken *et al.* 2008; Cahill *et al.* 2014, Merker & Chandler 2020). Extinction of these populations could result in the loss of unique genetic diversity possibly leading to a decay of ecosystem function (Hampe & Petit 2005). Understanding the mechanisms by which climate change will impact trailing-edge populations requires information about the roles that abiotic and biotic factors play in limiting species distributions at low-latitude, low-elevation range boundaries (Cahill *et al.* 2014). One way in which biotic interactions can limit species distributions is through Allee effects, but the role of Allee effects in climate-induced range shifts has received little attention outside theoretical contexts (Keitt *et al.* 2001; Holt *et al.* 2004; Holt *et al.* 2005; Schmidt *et al.* 2015).

Allee effects can result from biotic interactions that cause population growth rate to be positively correlated with population density (Allee *et al.* 1949; Stephens *et al.* 1999; Kramer *et al.* 2009). Examples include impaired mating opportunities and reduced pollination rates at low densities (Lande 1987; Groom 1998; Legendre *et al.* 1999; Berec *et al.* 2018). Prey species can also be impacted by Allee effects when confronted with subsidized predators capable of maintaining or increasing predation rates when the prey population is declining (de Roos *et al.* 1998; Keitt *et al.* 2001). Allee effects can increase extinction risk because population declines result in decreased growth rates, contrary to the stabilizing force that negative density dependence plays in regulated populations (Bessa-Gomes *et al.* 2004; Angulo *et al.* 2018).

Theoretical work has demonstrated that Allee effects at the periphery of a species' range can result in stable range boundaries, even in the absence of other limiting factors, as long as Allee effects are not present in the interior of the range (Keitt *et al.* 2001; Holt *et al.* 2004; Holt *et al.* 2005). The models predict that low density populations near range margins can exhibit positive density dependence, which would prevent range expansion, whereas interior populations should be regulated via negative density dependence. These predictions have not been evaluated empirically.

Socially-mediated Allee effects represent a mechanism by which positive density dependence near range margins could limit species' distributions and contribute to climate-induced range shifts (Stamps 1988; Courchamp *et al.* 2008; Schmidt *et al.* 2015; Angulo *et al.* 2018). Socially-mediated Allee effects occur when a population's growth rate depends on the availability of social cues. Many species utilize social cues when selecting breeding habitat because social cues can be a fast and often reliable way for individuals to determine if habitat is suitable (Schlossberg & Ward 2004; Ward & Schlossberg 2004; Ahlering *et al. 2010;* Betts *et al.* 2010). Several studies of passerines have shown that experimental introduction of conspecific song can cause individuals to colonize previously unoccupied habitat, regardless of habitat quality (Ward & Schlossberg 2004; Betts *et al.* 2008; Rushing *et al.* 2015). For example, playing *Vireo atricapilla* (black-capped vireo) song recordings during the post-migration arrival and settlement periods in unoccupied habitat even in sites where reproductive performance ultimately proved to be poor (Ward & Schlossberg 2004). These results suggest that the absence of social cues near range boundaries, where density is typically low and stochasticity is often high (Brown 1984; Brown *et* *al.* 1996; Hampe & Petit 2005), could prevent range expansion, and result in stable range boundaries as predicted by theoretical models (Fig. 3.1).

Our objective was to determine if socially-mediated Allee effects can limit species distributions at the trailing-edge of a geographic range. Specifically, we assessed the hypothesis that trailing-edge population range boundaries can be maintained by socially-mediated Allee effects in which population growth rate decreases with local density as a result of decreasing amount of social cues available to inform habitat selection decisions (Fig. 3.1). To evaluate this hypothesis, we tested the predictions that (1) local growth rate should be positively correlated with local density near the periphery of a range boundary and (2) that the addition of social cues immediately outside the trailing-edge range boundary would result in colonization of formerly unoccupied habitat and increased population growth rates. We also evaluated the alternative hypothesis that range boundaries are shaped by the impacts of abiotic climate variables on population growth rates.

Materials and methods

Study System

We conducted our research on *Cardellina canadensis* (Canada warbler), a neotropical migrant passerine that breeds in the eastern United States and across Canada and winters in northern South America. As a result of long-term population declines, it has been designated as threatened by the Committee on the Status of Endangered Wildlife in Canada (Hallworth *et al.* 2008; Hunt *et al.* 2017, Westwood *et al.* 2020). Canada warblers have a restricted breeding range in the southeastern United States, occurring only at high elevations in the Appalachian Mountains (Reitsma *et al.* 2020; Becker *et al.* 2012). The Canada warbler was selected as a focal species to test the socially-mediated Allee effects hypothesis because its range boundary is clearly defined within the climate gradient that occurs in the southern Appalachian Mountains, and numerous studies have demonstrated that passerines use song as a breeding habitat selection cue (Schlossberg & Ward 2004; Ward & Schlossberg 2004; Betts *et al.* 2008, Rushing *et al. 2015*). Canada warblers are also known to respond to conspecific song during the breeding season. Additionally, because adult Canada warblers, individuals entering ≥ second breeding season, show strong site fidelity we anticipated that only young birds, individuals entering their first breeding season, would colonize our experimental sites (Reitsma et al. 2020).

We conducted field work near the trailing-edge breeding boundary of *C. canadensis* in the United States Forest Service (USFS) Nantahala National Forest within and adjacent to the Coweeta Hydrologic Laboratory in southwestern North Carolina, USA. The area is characterized by steep topography ranging from 660–1590 m elevation. Precipitation increases with elevation; ranging from 1870 mm year^{-1} at low elevations to 2500 mm year^{-1} at high elevations (Hwang *et al.* 2014). Daytime temperature tracks closely with elevation, becoming cooler at higher elevations. The study site is heavily forested with mixed hardwoods at low elevations transitioning to northern hardwood forests at higher elevations (Webster *et al.* 2012; Hwang *et al.* 2014). The understory is primarily *Kalmia latifolia* (mountain laurel), *Rhododendron maximum* (big rhododendron), and *Vaccinium spp.* (Webster et al. 2012). Some areas have few shrubs and are relatively open from the forest floor to the canopy.

Data Collection

We collected data on spatio-temporal variation in Canada warbler abundance and growth rate using point-count surveys at 71 locations from 2014-2017. Survey locations were positioned in a regular 500 m grid spanning the species local range boundary of from approximately 800 m to 1400 m elevation (Fig. 3.2). Canada warbler territory sizes are small, ranging from 0.2 – 1.5 ha making it unlikely that we double-counted individuals between survey points (Reitsma et al. 2020). Each survey lasted 10 minutes, and consisted of four, 2.5-min periods, during which every individual seen or heard within 100 m of the point was recorded. Surveys were conducted by expert observers able to identify Canada warblers by sight and vocalizations. Variables that could influence detection probability, including noise, time, and wind were recorded during each survey on a 0-5 scale. Point-count surveys were conducted on days with little or no precipitation, low wind, and were limited to 0600-1100 hours, when birds are most active and likely to vocalize.

Conspecific Attraction

We used methods similar to those of Ward and Schlossberg (2004) to experimentally add social information (i.e., broadcast song recordings) to previously unoccupied sites both within and outside the local range boundary of *C. canadensis* in southwestern North Carolina. The local range boundary and locations of unoccupied sites were identified using data from the first two years of point-count surveys. Five experimental sites out of the 71 survey sites were selected within the range and five experimental sites were selected outside the range, below 1000 m elevation (Fig. 3.2) (Chandler & Hepinstall-Cymerman 2016; Chandler *et al.* 2018). The remaining 61 sites served as controls that allowed us to account for extraneous sources of spatial and temporal variation in abundance and growth rate. All experimental sites included some combination of thick *Rhododendron maximum,* steep topography, and small first-order streams all of which are key elements of Canada warbler habitat in this region (Reitsma et al. 2020).

We played recordings of *C. canadensis* song at 10 sites between 19 April and 7 May 2016 and at eight sites between 20 April and 11 May 2017, respectively. Recordings represented local Canada warbler dialect and were broadcast intermittently from 0400 to 1000 hours each day.

Periods of silence and songs from other passerines from different families were included in playback to avoid habituation by Canada warblers and potential competitive interactions that may exist between this species and other warblers. Sample size decreased from 10 experimental sites to eight sites in 2017 due to destruction of playback units by *Ursus americanus* (American black bear). These dates are within the period when *C. canadensis* arrive on the breeding grounds in North Carolina, establish territories, and begin nesting. Each playback unit consisted of a Raspberry Pi® computer (Sony, Pencoed, Wales), a small amplifier, and a Yamaha® outdoor speaker. Each unit was powered by two, 12 v sealed lead batteries. Playback was set to between 80-90 dB. Playback units could be heard from over 100 m (pers. obs) and if neighboring points also had playback it could not be heard between points. Playback units were designed, constructed, and programmed by the University of Georgia's Instrument Fabrication and Design shop.

Climate data

We used publicly available precipitation and temperature data in the form of 30-year normals from 1981-2010 (PRISM Climate Group 2016). This data describes general climate patterns in the area. PRISM data were in raster format with a resolution of 800 m. Temperature and precipitation were highly correlated (r = -0.90), so we developed a single principle component to reflect the dominant climate gradient in the region. This principle component explained 95.3% of the variation (Fig. 3.3).

Statistical analysis

We represented our hypotheses about the influence of Allee effects on spatial and temporal variation in abundance and growth rate using dynamic N-mixture models that we fit to the point-count data (Royle 2004; Dail & Madsen 2011). These models allow for inference on spatial and temporal variation in abundance while accounting for heterogeneity in detection probability, which can cause bias if ignored. Initial abundance ($N_{i,1}$) at each site ($i = 1,\ldots,71$) was modeled as log-linear function of climate:

$$\log(\psi_i) = \beta_0^{(\psi)} + \beta_1^{(\psi)} CLIMATE_i$$

$N_{i,1} \sim Poisson(\psi_i)$

We modeled abundance in subsequent years ($t = 2,3,4$) as a function of the local growth rate ($\lambda_{i,t}$), which was influenced by climate, treatment (playback or no playback), and conspecific-density in the preceding year:

$$\log(\lambda_{i,t-1}) = \beta_0^{(\lambda)} + \beta_1^{(\lambda)} CLIMATE_i + \beta_2^{(\lambda)} TREATMENT_{i,t} + \beta_3^{(\lambda)} DENSITY_{i,t-1}$$

$$N_{i,t} \sim Poisson(N_{i,t-1}\lambda_{i,t-1})$$

A negative value of β_3 would be indicative of negative density dependence, whereas a positive value would suggest an Allee effect. Allee effects might not involve monotonic increases in the growth rate over a range of densities, and population densities may affect population growth rates differently under different climate conditions. Therefore, we considered eight additional growth rate models, some including quadratic effects of density and climate, and interactions between the density and climate (Table 3.2).

We modeled detection probability in each year as a logit-linear function of covariates that affect an observer's ability to detect an individual, including Julian date, time of day, noise, and wind:

$$\text{logit}(p_{i,j,t}) = \beta_0^{(p)} + \beta_1^{(p)} WIND_{i,j,t} + \beta_2^{(p)} NOISE_{i,j,t} + \beta_3^{(p)} DATE_{i,j,t} + \beta_4^{(p)} TIME_{i,j,t}$$

We used diffuse normal distributions with a mean of 0 as priors for all regression coefficients (Appendix 1). Prior to model fitting all covariates were scaled and centered to facilitate comparisons. Models were fit using Markov chain Monte Carlo in a Bayesian framework. All analyses were conducted in R statistical software version 3.3.2 (R Core Team, 2019) and version

4.0.0 of Just Another Gibbs Sampler (JAGS) (Plummer 2017). Each JAGS model was run with three chains of 500,000 iterations each, a thinning rate of 20, and a burn-in of 1,000. We used Watanabe-Akaike Information Criterion (WAIC) for model selection. We used Moran's I to test for spatial auto correlation in our model residuals (Appendix F). Additionally, we inspected model residuals for spatial autocorrelation by plotting them for each year (Appendix F).

Results

We conducted 284 point-count surveys between 2014 and 2017 (n = 71 per breeding season). We detected 28, 28, 28, and 19 individuals in years 2014—2017, respectively. No more than five individuals were detected at a site and most sites initially occupied by *C. canadensis* in 2014 remained so in the following years (Fig. 3.4). Sites at elevations lower than 1000 m were rarely occupied by *C. canadensis*.

The model with the best WAIC score included a climate effect on initial abundance, and effects of climate, treatment, and density on population growth rate (Table 3.2). The top model received 43.7% of the weight of all models considered. The second-best model, similar to the top model, but including a weak quadratic effect of density, received 25.1% of the weight. All other models received <15% of the model weight. Only results from the top model are reported below.

Contrary to the socially-mediated Allee effect range limitation hypothesis, population growth rate decreased as population density increased (Table 3.2 & Fig. 3.5). There was no evidence of a quadratic relationship between growth rate and density, indicating that density dependence was negative across the range of observed densities. Additionally, there was no evidence of a quadratic effect of climate on growth rates or density, and there was no evidence of an interaction between climate and density, suggesting that negative density dependence was maintained over the entire gradient of climate conditions.

In the warmer and drier conditions population growth rates were never greater than one (Table 3.2). Density and population growth rates of *C. canadensis* were highest at cooler and wetter sites, which generally occur at higher elevations (Fig. 3.5). Population growth rates declined as average temperatures increased and average precipitation decreased. Growth rate was <1 across the range of observed densities in the warmer, drier conditions at lower elevations. In cooler wetter conditions, growth rate was >1 when density was low.

Detection probability during a single 2.5-min period was 0.59 (0.51-0.72) at the average values of the covariates. The probability of detecting an individual over the 10-min survey period was 0.972 (0.94-0.99). Detection of *C. canadensis* was negatively affected by ambient noise and positively affected by Julian date but it was not affected by wind or time of day (Table 3.1).

Consistent with the results from the observation data, experimentation indicated that Allee effects did not limit the distribution of *C. canadensis*. The experimental addition of playback did not result in the colonization of previously unoccupied habitat. No *C. canadensis* were detected at treatment sites where playback was added, regardless of elevation or climate suitability. Finally, we found no evidence of spatial auto correlation in model residuals during any year of the study (Appendices F).

Discussion

Understanding the factors limiting species' distributions is one of the oldest pursuits in ecology, and it has become one of the most important subjects in efforts to conserve global biodiversity impacted by rapid environmental change (Darwin, 1859; MacArthur 1972; Parmesan *et al.* 2005;

Gaston, 2009; Cahill *et al.* 2014). Although most work has focused on abiotic limiting factors, theoretical and empirical work has demonstrated that biotic interactions can limit species' distributions in the absence of abiotic constraints (Jankowski *et al.* 2010 Jankowski *et al.* 2013; Freeman *et al.* 2016; Freeman & Montgomery 2016). However, the role of Allee effects in limiting species' distributions is virtually unknown outside of theoretical contexts, and to our knowledge, this study represents the first empirical test of the socially-mediated Allee effect range limitation hypothesis. Counter to predictions, we found no evidence that socially-mediated Allee effects limit the distribution of *C. canadensis* at their warm-edge range limit. Moreover, there was no evidence of positive density dependence near the range boundary or in the interior sites, indicating that no other process contributed to Allee effects.

Several hypotheses could explain the absence of Allee effects in our study system. The most likely explanation supported by our data is that the southern range limit of *C. canadensis* is shaped by climate conditions rather than Allee effects. Growth rates were closely correlated with local climate conditions, and these results support mounting evidence that climate and other abiotic factors can play a larger role than biotic interactions in limiting species distributions (Hickling *et al.* 2006; Thomas 2010; Cahill *et al.* 2014, Román-Palacios & Wiens 2020). However, the mechanism by which temperature and precipitation affect this population is unclear. For example, it is unlikely that precipitation acts directly on individuals to limit fitness, but it may act indirectly by driving food availability for secondary and tertiary consumers like songbirds (Jones *et al.* 2003; Bolger *et al.* 2005; Holmes 2011). Temperature is more likely to directly limit species distributions because some trailing-edge populations may be at their thermo-physiological limit (Root 1988a, b). As temperature increases, individual fitness may be reduced (Lof *et al.* 2012; Buckley & Huey 2016), leading to a decrease in population growth rates. Increased understanding of how climate acts upon species distributions at the trailing-edge of the range is needed to forecast climate change impacts, and future work should assess the impacts of annual variation in weather conditions on demographic parameters.

Because the southern Appalachian Mountain region is characterized by steep topography, the deep valleys and north facing slopes that make up much of the area may provide refuge by providing climatically suitable pockets to maintain these trailing-edge populations. These climatically suitable pockets may not persist as climate change accelerates, especially if the frequency and duration of extreme weather events increases (IPCC 2014). Furthermore, yearly variation in temperature and precipitation are often driven by major climate cycles such as El Niño and La Niña Southern Oscillations. These cycles can directly influence food resources for migratory birds and greatly affect local abundance and density in subsequent years (Sillett *et al.* 2000; Rodenhouse *et al.* 2003; Rodenhouse *et al.* 2008). Global environmental change may alter the timing and frequency of these climate cycles, with unknown consequences for trailing-edge populations.

From a conservation standpoint, the absence of Allee effects is encouraging because Allee effects can increase extinction risk, making conservation intervention difficult relative to populations regulated by negative density dependence (Courchamp *et al. 2008;* Kramer *et al. 2018*). Allee effects near range boundaries could lead to stability as has been demonstrated theoretically, but they could also lead to rapid range contraction if environmental change and stochastic processes force small peripheral populations below the density threshold where positive density dependence occurs. Although we found no such phenomenon, additional research is needed to determine if this mechanism could explain range contractions of other species.

It is possible that the presence of conspecifics alone may not be a sufficient cue to elicit a habitat selection response. For example, an individual may identify possible breeding habitat through detection of conspecifics but may deem the habitat unsuitable once that habitat has been investigated further (Schmidt *et al.* 2015; Schmidt & Massol 2019). This would run counter to previous studies that demonstrated that social cues can be used to attract individuals to low quality habitat. Another possible explanation for the absence of Allee effects is that *C. canadensis* may use social cues during a different season when selecting habitat. Our research was conducted during the arrival and settlement periods as with *Vireo atricapilla* (black-capped vireo) (Schlossberg & Ward 2004; Ward & Schlossberg 2004). However, recent studies have shown that some warbler species use social cues during the post-breeding season, prior to migration, to select breeding habitat for the following season (Betts *et al.* 2008; Ahlering *et al.* 2010; Betts *et al.* 2010; Rushing *et al.* 2015). Future studies should attempt to assess the role that social information plays at multiple time periods throughout the breeding season, especially over different levels of habitat quality.

Although our results indicate that abiotic climate variables, not Allee effects, are the primary factor limiting trailing-edge distributions, additional research is needed to determine the generality of our inferences. In systems where Allee effects do contribute to range limitation, the mechanism involved – socially-mediated or otherwise – should be identified to guide conservation efforts.

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Authors' contributions

SM and RC designed the study. SM collected the data and performed the analysis. SM wrote the first draft of the manuscript. Both authors contributed to revisions and gave final approval for publication.

Data availability

Data available through Zenodo: https://doi.org/10.5281/zenodo.4238700 (Merker & Chandler, 2020).

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Tables and figures

Table 3.1. Results of model selection using Watanabe-Akaike Information Criterion. The top model included climate effects on initial abundance (N_I), and climate, treatment, and density effects on population growth rate (λ). All models included wind, noise, date, and time of day, as covariates of detection.

Model	WAIC	ΔWAIC	Weight
N_I (climate) λ (climate+treament+density)	1708.00	0.00	0.44
N_I (climate) λ (climate+treatment+density^2)	1709.11	1.11	0.25
N_I (climate) λ (climate*density)	1710.28	2.27	0.14
N_I (climate) λ (climate+density)	1710.42	2.41	0.13
Global	1712.75	4.74	0.04
N_I (climate) λ (.)	1730.33	22.32	0.00
N_I (climate) λ (climate+treatment)	1730.78	22.78	0.00
N_I (climate) λ (climate)	1734.08	25.10	0.00
N_I (.) λ (.)	2682.17	974.16	0.00

Table 3.2. Posterior summary statistics for parameters of the top model of Canada warbler abundance and growth rates in the southern Appalachian Mountains. Local growth rate was modeled as a function of climate variables, density dependence, and the experimental addition of conspecific playback (Treatment). Initial abundance was model as a function of climate variables. Detection was modeled as a function of wind, noise, Julian date, and time of day.

Process	Parameter	Mean	SD	Lower CI	Upper CI
Initial Abundance	Intercept	-2.63	0.39	-3.44	-1.89
	Climate	-1.56	0.21	-1.99	-1.14
Growth Rate	Intercept	-1.08	0.42	-1.96	-0.28
	Climate	-.075	0.30	-1.37	-0.18
	Treatment	-1.46	0.99	-3.81	-0.04
	Density	-0.24	0.13	-0.54	-0.03
Detection	Intercept	0.37	0.15	0.05	0.68
	Wind	0.23	0.14	-0.05	0.53
	Noise	-0.57	0.19	-0.95	-0.17
	Date	0.51	0.24	0.04	0.99
	Time	-0.13	0.16	-0.45	0.17

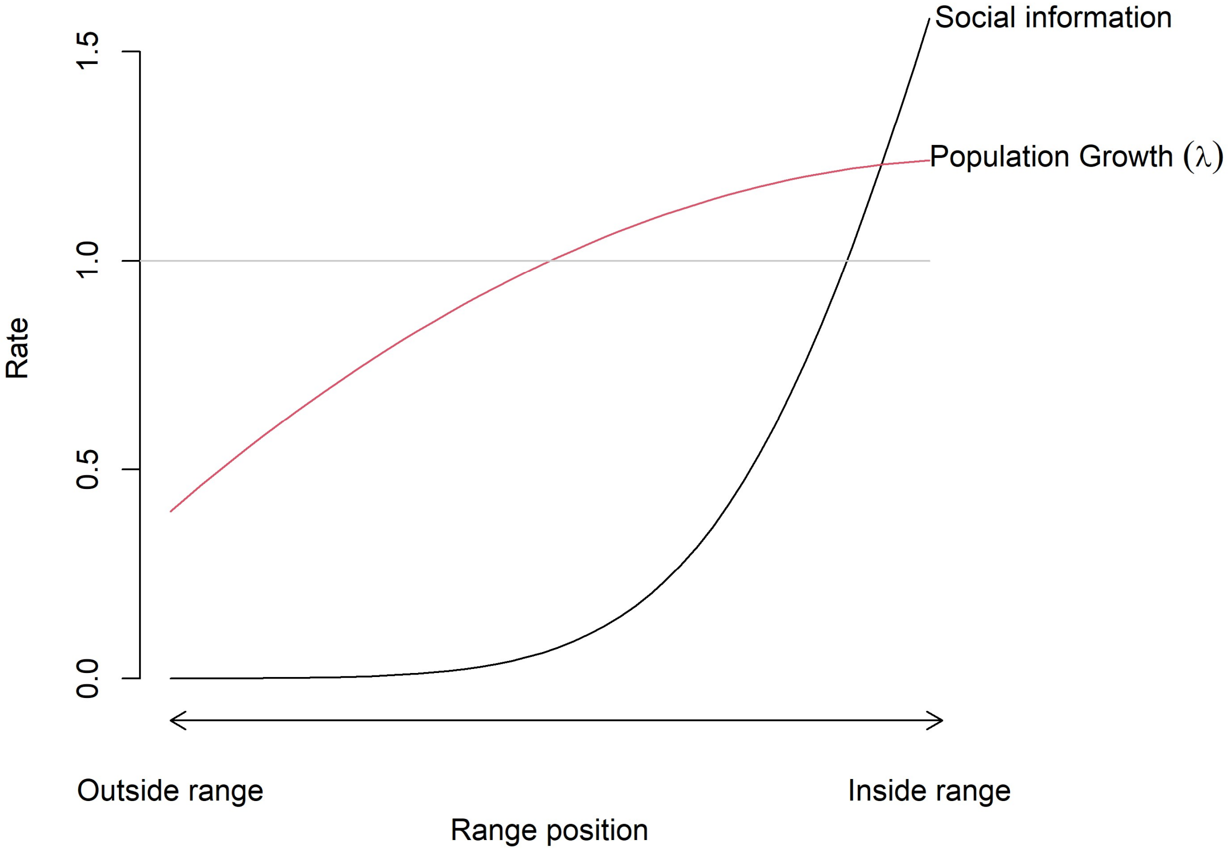

Figure 3.1. Conceptual figure demonstrating the socially-mediated Allee effect range limitation hypothesis. As social information, like bird song, decreases at the edge of the species range so does population growth rate (λ). At the core of a species range social information is abundant and population growth rates are greater than one.

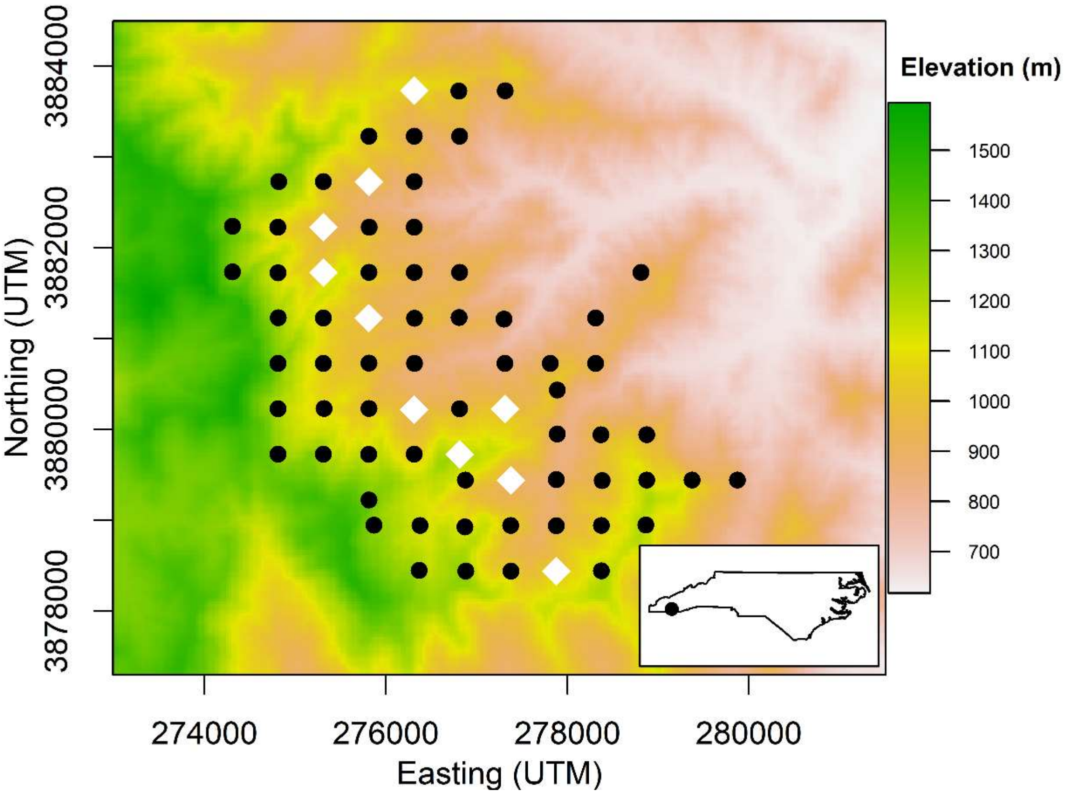

Figure 3.2. Point-count survey locations in the Nantahala National Forest, North Carolina. Survey locations spanned the local range boundary of Canada warbler, which is restricted above 1000 m elevation. Experimental sites are indicated by the white diamonds.

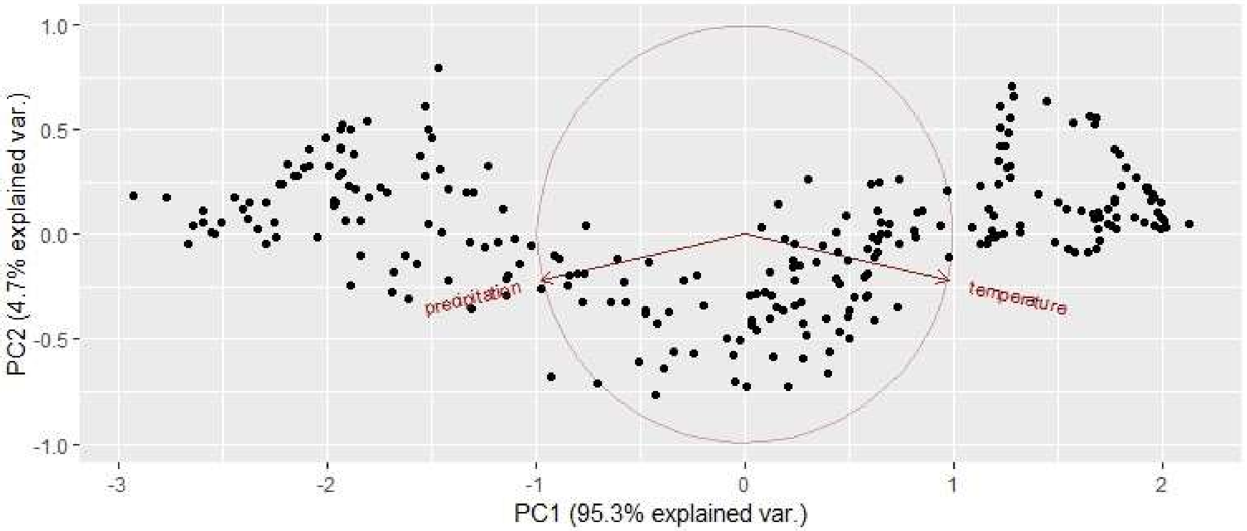

Figure 3.3. Principle components of PRISM temperature and precipitation 30 yr normals. Principle component 1 was used to describe the climate gradient in the study area, and was included as a covariate in models of Canada warbler abundance. Negative values of PC1 represent cooler and wetter conditions. Positive values represent warmer and dryer conditions.

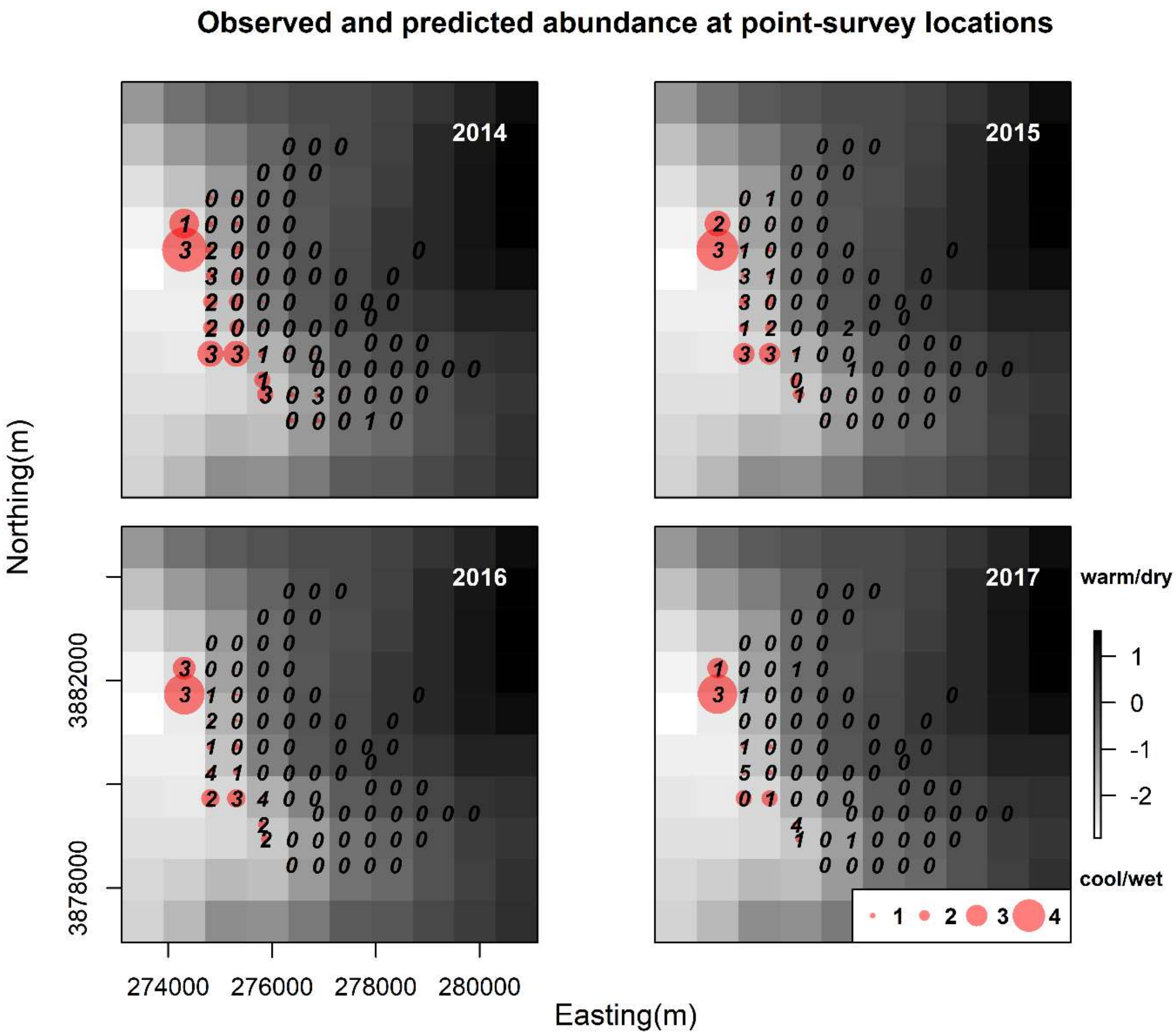

Figure 3.4. Maps of raw observed counts (integers) and model estimates (red circles) of Canada warbler abundance at survey locations in the Nantahala National Forest from 2014-2017. The background raster (800 m^2) shows the climate gradient as a principle component of temperature and precipitation (PRISM Climate Group 2016). Lighter pixels represent cooler and wetter conditions at high elevations.

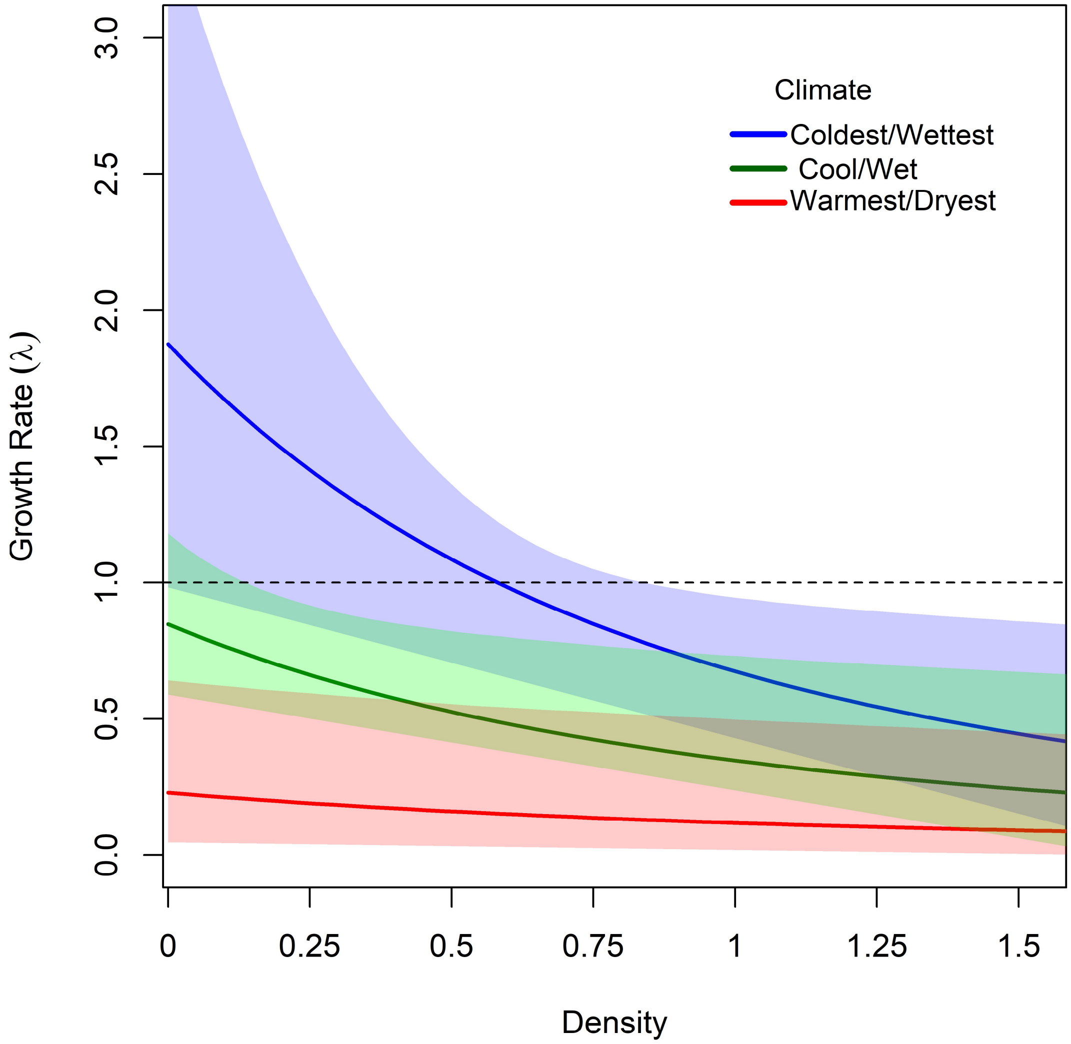

Figure 3.5. Model estimated density-dependent population growth rates for Canada warblers (*C. canadensis*) in three different climate conditions in the Nantahala National Forest, North Carolina. Climate conditions are derived from the principle component analysis and represent combinations of temperature and precipitation.

CHAPTER 4

HEMOPARASITE PREVALENCE AND THE DISTRIBUTION OF BIRD SPECIES OVER A CLIMATE GRADIENT[1]

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[1] Merker, S.A., Kurimo-Beechuck, E., Hernandez, S.M. and Chandler, R.B, to be submitted Nature: Ecology and Evolution

Abstract

Climate change is predicted to alter the distribution of vector-borne pathogens which may contribute to range shifts in host species. We collected 280 blood samples from 17 bird species across 17 sites spanning a climate gradient in the southern Appalachian Mountains, USA. We identified 3 hemoparasite genera: *Haemoproteus spp, Leucocytozoon spp,* and *Trypanosoma spp,* and 1 microfilarial nematode. Hemoparasite prevalence was highest at warmer sites, but substantial variation existed among host species. Host-pathogen occupancy models for a cool-adapted bird species near its warm-edge range margin revealed that host occupancy was negatively associated with pathogen prevalence. Pathogen prevalence did not affect occupancy of the warm-adapted species near the core of its range. Long distance migrants had lower prevalence than species with shorter migration strategies. Our results support the hypothesis that pathogens can contribute to climate-induced range shifts in host species.

Keywords: black-throated blue warbler, climate change, hemoparasites, *Haemoproteus, Leucocytozoon*, occupancy, range limits, wood thrush

Introduction

Climate change is predicted to alter the distribution and transmission of vector-borne pathogens (Patz and Reisen 2001, Gilbert 2010, Zamora-Vilchis et al. 2012, Altizer et al. 2013). Shifts in the distribution of pathogens, their associated vectors, and resulting disease, are linked to changes in temperature and precipitation patterns at multiple scales, but the effects of these changes on host species distributions is not clear (Harvell et al. 2002, Harvell et al. 2009, Van Hemert et al. 2014, Bozick and Real 2015). However, there is evidence supporting the hypothesis that disease can limit species distributions and drive host species range shifts (Ricklefs 2011, Pulgarin et al. 2018).

Climate change is expected to shift the geographic ranges of many pathogens and vectors toward higher latitudes and elevations (Fuller et al. 2012). Examples include climate driven shifts of biting midges (*Culicoides spp.*) to higher latitudes and higher elevations (Elbers et al. 2015), temperature driven shifts in occurrence of ticks (*Ixodidae spp.*)(Gilbert 2010), a northward shift of Dermo disease in eastern oysters (*Crassostrea virginica*) caused by the protozoan *Perkinsus marinus* (Ford 1996, Soniat et al. 2009), and the expansion of mosquito ranges with climate change (Altizer et al. 2013, Elbers et al. 2015). Changes in vector-borne pathogen distribution may affect the distribution of their definitive hosts by limiting populations near range margins (Danielova et al. 2010, Ricklefs 2011, Pulgarin et al. 2018). For example, the introduction of avian malaria to the Hawaiian Islands resulted in upward altitudinal shifts in endemic bird populations (Vanriper et al. 1986, Woodworth et al. 2005, Altizer et al. 2013). For populations at the trailing-edge of a definitive host species distribution, increased infection risk may result in increased extinction risk, especially if host species are unable to track optimal climate conditions via dispersal (Gerber et al. 2005, Pedersen et al. 2007).

Migration strategies of host species may influence the risk of infection from vector-borne pathogens (Altizer et al. 2011, Fuller et al. 2012). There is increasing evidence that long-distance migrants have lower prevalence of hemoparasites than short-distance migrants, and long-distance migrants are unlikely to increase parasite transmission (Rappole et al. 2000, Altizer et al. 2011, Gonzalez et al. 2014, Hall et al. 2014, Hall et al. 2016, Pulgarin-R et al. 2019). Theoretical studies have shown that long-distance migrants may 'escape' infection by migrating between areas of low infection risk (Loehle 1995, Hall et al. 2014, Hall et al. 2016). Additionally, 'migratory culling' may reduce infection rates in long distance migrant populations because the increased stress during migration may cause infected individuals to die (Bradley and Altizer 2005, Hall et al. 2014, Hall et al. 2016).

Our goal was to understand how hemoparasite infections influence the distributions of bird species over a climate gradient spanning the warm-edge range boundary of several cool-adapted host species. We tested the pathogen range limitation hypothesis that the distribution of cool-adapted species occurring near their range edge would be more strongly influenced by infection than warm-adapted species near the core of their range. We predicted that climate would directly influence occupancy of host species, but also indirectly influence occupancy of host species by influencing the prevalence of hemoparasites. We also considered alternative hypotheses in which host species occupancy was influenced by direct climate effects or direct effects of infection, but not by both (Figure 4.1). In addition, we evaluated the effects of migration strategy on the prevalence of common hemoparasites. Specifically, we predicted that migratory species, particularly long-distance migrants, would have lower infection rates than non-migratory or short-distance migrants.

Methods

Study sites spanned a climate gradient in the Nantahala National Forest in southwestern North Carolina, USA. This site is characterized by a relatively abrupt change in climate conditions owing to steep topography in a relatively small geographic area (Hwang et al. 2014). High elevations are cooler and wetter than low elevations with precipitation ranging from 1,870 mm/year at low elevations to 2,500 mm/year at high elevations. Daytime temperature are cooler at higher elevations (Hwang et al. 2014). The region has a high diversity of cool-adapted, trailing-edge bird species that occur near the edge of their low-latitude breeding ranges (Merker and Chandler 2020). We conducted point count surveys for birds from May to June during the 2019 breeding season. Blood samples were collected during the 2019 and 2020 breeding seasons (Federal Bird Banding Permit: 23897, North Carolina Wildlife Collection License: 20-SC01315, IACUC Animal Use Protocol: A2019 11-011-Y2-A1).

Point count surveys

Bird surveys were located on a regular 500 m grid positioned to cover the dominant climate gradient in the study site (Figure 4.2). Each survey lasted 10 min and was separated into four, 2.5-min intervals. During each interval, expert observers identified all individuals seen or heard within 100 m of the point. Factors influencing detection, including noise and wind were recorded during each survey on a 0-5 scale. Surveys were conducted on days with no precipitation and low wind, between 0600 and 1100 hours when birds are most likely to vocalize. Wind was measured on a scale of 0-5, with 0 being still and 5 being strong winds resulting in reduced ability to detect birds visually and by sound.

Blood sample collection & microscopy

Birds were captured using 12 m long, 32 mm mesh mist nets at 17 sites selected to cover precipitation and temperature gradients (Figure 4.4). We divided the temperature and precipitation gradients into terciles, and attempted to sample 3 locations within each of the nine levels of the factorial design. However, two of the nine levels (cold and dry, and warm and wet) were rare and we only sampled 3 sites in these conditions.

At each site, 20 mist nets were positioned in 4 rows, with the outer rows spaced by 50 m and the inner rows spaced by 100 m. Mist nets were operated each day from 0600-1100 hours for 4 days and nets were checked every 30 minutes. Sampling days were usually consecutive unless interrupted by rain or strong winds. Netting operations began during the second week of May and continued no later than the first week of July during the 2019 and 2020 breeding seasons.

We used 25-gauge needles to obtain approximately 25 μL of blood from the brachial vein. Blood was collected in heparinized micro hematorcrit tubes (North Carolina Wildlife Collection License # 20-SC01315). Immediately after collection we made 2-3 blood smears per bird. Smears were then air dried and fixed as soon as possible using a methanol fixative (DipQuick, Jorgenson Laboratories, Inc, Loveland, CO, USA) and stored until further processing. Birds were released immediately after sample collection.

Hemoparasites

We selected the highest quality blood smear from each individual to examine for hemoparasites (Corrons et al. 2004), based on the presence of a of an adequate monocellular layer. Selected smears were stained with a modified Giemsa stain (DipQuick, Jorgensen Laboratories, Inc., Loveland, CO, USA). Slides were then rinsed with deionized water and left to air dry. Because we only wanted to confirm the infection status for each individual, the entire monocellular layer portion of each blood smear was examined for hemoparasites at 1000× under oil immersion. All slides were examined by two trained observers to confirm the presence of hemoparasites. Hemoparasites were identified by morphological characteristics.

Migration strategy

We categorized bird species into four migration strategies: long-distance, medium-distance, short-distance, and resident. Long-distance migrants included species that migrate to South America. Medium-distance migrants included species that migrate to Central America or the Caribbean Islands. Short-distance migrants included species that migrate to northern Mexico or southern North America, often wintering along the coast of the Gulf of Mexico, or make small seasonal movements. Residents were classified as species that do not migrate (Birds of the World, 2020; Appendix J).

Range position analyses

We used logistic regression, a binomial generalized linear model (GLM), to quantify the prevalence of hemoparasites and to model the probability of infection as a function of range position and migratory strategy. The response variable was the presence or absence of hemoparasites. Binomial GLMs are more appropriate than traditional ANOVA methods for binary data because they acknowledge that the expected value is a probability and the variance is not constant (Warton and Hui 2011). All analyses were done using R statistical software version 4.0.3(Team 2020) All interval estimates are 95% CIs.

Climate data

Temperature and precipitation are highly correlated at our study site, and we therefore described the climate gradient by creating a single principle component, which explained 95.3% of the variation in the two climate variables. Temperature and precipitation data were obtained from PRISM, available in 800 m resolution raster format describing 30-year normals from 1981 to 2010 (PRISM Group 2015).

Occupancy analysis

To assess the hypothesis that the distribution of avian species was influenced by hemoparasite prevalence (measured as the probability of infection at a site), we constructed single season occupancy models for species with three or more positive blood smears (MacKenzie et al. 2002). The response variable in these models was the binary detection data from the 109 point count surveys. We included two predictor variables in the occupancy portion of the model: prevalence and climate. Because prevalence was not measured at the point count survey locations, we predicted it using a binomial GLM fitted to the blood smear data from the mist-netting sites, using climate as a predictor. Because each 10-min survey was divided into four, 2.5-min intervals, we were able to estimate the probability of occurrence while accounting for the possibility that a species was present but not detected. Detection probability was modeled as a function of covariates thought to inhibit an observer's ability to detect birds including Julian date, noise, and wind. The global model consisted of the following three components:

Infection (at mist-net sites)

$$\text{logit}(\gamma_s) = \gamma_0 + \gamma_1 \times climate_s$$

$$x_s \sim \text{Bernoulli}(\gamma_s)$$

Occupancy (at point count locations)

$$\text{logit}(\gamma_i) = \gamma_0 + \gamma_1 \times climate_i$$

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 \times \gamma_i + \beta_2 \times climate_i$$

$$z_i \sim \text{Bernoulli}(\psi_i)$$

Detection

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 \times wind_i + \alpha_2 \times noise_i + \alpha_3 \times date_i$$

$$y_{ij} | z_i \sim \text{Bernoulli}(z_i \times p_i)$$

The model describes the hypothesized generative process in which the observed infection data (x) are determined by the probability of infection (γ_s) modeled as a function of climate at each mist-netting site (s=1,…,17). Occupancy at each point count location (z_i) was modeled as a Bernoulli random variable with probability of occurrence (ψ_i) determined by climate and probability of infection (γ_i). The detection data (y_{ij}) were modeled as a function of occupancy and detection probability during each 2.5-min period (j=1,…4).

Because climate could affect occupancy directly and indirectly (through its effect on infection), but our primary hypothesis pertained to the effect of infection probability on occupancy, we computed the marginal effect of infection on occupancy by averaging over the climate conditions at each possible value of infection. Specifically, we computed:

$$\Pr(\text{occupancy} \mid \text{infection}) = \sum_{climate} \Pr(\text{occupancy}|\text{infection}, \text{climate}) \Pr(\text{infection}|\text{climate})$$

In the causal inference literature, this is known as the "back-door adjustment formula" (Pearl 2009), with a "conditionally ignorable" effect of climate (Rosenbaum and Rubin 1983). The prediction can be interpreted as the effect of infection on occupancy, regardless of climate.

We used Bayesian inference implemented in the R statistical software version 4.0.3 (Team 2020) and version 4.3.0 of JAGS (Plummer 2017). Posterior samples were obtained using three Markov chains of 250,000 iterations, following a burn-in of 1,000 iterations and a thinning rate of 10. We used a normal distribution with a mean of 0 and a variance of 2 for the priors on the intercepts of the logit-linear functions, as this implies an approximately flat prior on the probability at the intercept. We used diffuse normal distributions with a mean of 0 and a variance of 10 as priors for all regression coefficients. Estimates reported below are posterior means and 95% CIs.

Results

We detected 697 individuals from 46 bird species at 109 point-count locations, and we examined blood smears from 280 individuals of 17 bird species at the 17 mist-net sites. Twenty-four individuals from 9 different species were infected with at least one of three detected hemoparasite genera: *Haemoproteus spp*, *Leucocytozoon spp*, and *Trypanosoma spp* (Appendix J). We also detected microfilarial nematodes (Appendix J). We detected 11 individuals infected with *Leucocytozoon,* which was the most common parasite detected. *Leucocytozoon* was detected primarily in wood thrush (*Hylocichla mustelina*), but was also detected in a single blue-headed vireo (*Vireo solitarius*). *Haemoproteus* was detected in 9 individuals from 7 species. *Trypanosoma* was detected in a single wood thrush. Microfilariae were detected in two hooded warblers and one ovenbird (*Seiurus aurocapilla*). A single co-infection was identified in a blue-headed vireo, which was infected with both *Haemoproteus* and *Leucocytozoon* (Appendix J). Only two species had three or more positive blood smears: black-throated blue warbler (*Setophaga caerulescens*), a cool-adapted species, and wood thrush, a warm-adapted species. We detected *Haemoproteus spp* in Three of 52 black-throated blue warblers (5.8%) and found *Leucocytozoon spp* in 10 of 25 wood thrush (40%).

The probability of infection varied by range position. The probability of being infected with any hemoparasite was 0.05 (0.025 – 0.097 95%) for cool-adapted species, lower than the probability of infection for warm-adapted species ((0.18, 0.11 – 0.28; Figure 4.3A). Probability of infection also differed by migration strategy. Short distance migrants had the highest probability (0.25; 0.06 - 0.62 95% CI) of being infected with any parasite, followed by medium distance migrants (0.14; 0.92 – 0.22 95% CI), long-distance migrants (0.02; 0.01 – 0.08 95% CI), yet zero infections were detected in resident species (Figure 3B).

For the black-throated blue warbler, the cool-adapted species near its low-latitude breeding range margin, probability of infection with *Haemoproteus* was higher in warmer, drier conditions than in cooler, wetter conditions (Table 4.1). Black-throated blue warbler occupancy was negatively associated with infection probability, regardless of climate conditions (Table 4.1, Figure 4.4). The estimated effects sizes indicate that, conditional on infection probability, climate had a negligible effect on black-throated blue warbler occupancy. In other words, most of the effect of climate occurred indirectly, via its influence on infection probability.

For the wood thrush, the warm-adapted species in the core of its breeding range, *Leucocytozoon* infection probability was higher in the cooler, wetter sites than in the warmer, drier sites (Table 4.1). However, occupancy was not associated with *Leucocytozoon* infection probability (Figure 4.4) or with climate conditions, suggesting that neither hemoparasites or climate limit the species' distribution at this range position.

Discussion

The case of rapid range contractions in Hawaiian avifauna has demonstrated that vector-borne pathogens introduced by humans can limit the distributions of their definitive hosts (Vanriper et al. 1986, Ricklefs 2011, Freed and Cann 2013). Theoretical work suggests that similar processes may occur even in the absence of human intervention (Ricklefs 2011, Bozick and Real 2015). Moreover, it has been predicted that, if climate impacts vectors, and vectors impact hosts, then disease could be a mechanism underlying climate-induced range shifts (Bozick and Real 2015). We found support for this hypothesis using one of the first empirical studies on the effect of parasite prevalence on host distributions across a strong climate gradient.

We found evidence that the effect of parasites depends on range position. The distribution of the trailing-edge species was negatively associated with hemoparasite prevalence, but the species at its range core was not. These results suggest that high prevalence of parasites in warmer and drier climates may explain why black-throated blue warblers are restricted to the higher elevations in our study area. Consistent with the hypothesis that pathogen effects are strongest near range boundaries, we found no effect of hemoparasite prevalence on the warm-adapted species near the core of its range. These results are consistent with studies on introduced house finch (*Haemorhous mexicanus*) populations in the eastern United States where low-latitude populations experienced epidemics of *Mycoplasma gallisepticum* with greater frequency and amplitude than core or high latitude populations (Altizer et al. 2004).

Factors other than climate, such as migratory strategy, can influence pathogen prevalence. Resident species had no infections, and long-distance migrants had low prevalence. This is supported by theoretical studies showing that long-distance migrants may 'escape' infection by vacating areas of high infection risk (Loehle 1995, Hall et al. 2014, Hall et al. 2016). Additionally, infection rates in long-distant migrant populations may be lower due to 'migratory culling', where infected individuals die due to the stress incurred by migration (Bradley and Altizer 2005, Hall et al. 2014, Hall et al. 2016). Other evidence suggests that long-distance migrants have low hemoparasite prevalence and are unlikely to increase parasite transmission (Gonzalez et al. 2014, Pulgarin-R et al. 2019). However, one study found that resident species in Columbia had higher hemoparasite prevalence, which stands in contrast to our results (Gonzalez et al. 2014). For species at their warm-edge range limit, the potential benefits of having a long distance migration may be outweighed by encroaching climate conditions that may benefit vectors (Elbers et al. 2015).

The effect of pathogens on the distribution of the trailing-edge species may have resulted from spatial variation in the abundance of vectors, specifically mosquitoes and biting midges. Vector abundance may be higher in the warmer, low elevation sites avoided by cool-adapted species such as the black-throated blue warbler but we did not measure vector abundance of diversity at each site and the specific species of vectors for each species of parasite has not been definitely determined. Future research should attempt to quantify spatial variation in the abundance of vectors and determine parasitemia rates in infected hosts. Molecular techniques such as PCR would also be useful for determining the diversity of pathogens at the species level (Pulgarin et al. 2018). Information is also needed about the impact of infection on mortality rates and other demographic parameters of wild birds.

In our analysis of migration strategy and range position we did not distinguish between the different parasites because we wanted to test if trailing-edge populations lowered infection risk by avoiding warmer-drier climates, migrating longer distances, or conversely, are at greater risk of infection by being at the edge of their range (Altizer et al. 2004, Hall et al. 2014, Hall et al. 2016). In addition, because so little is known about prevalence of these pathogens in this region and the mode of transmission for both *Leucocytozoon* and *Haemoproteus* is similar we saw little reason to separate them.

The possibility that pathogens influence range boundaries has important implications for understanding the mechanisms influencing climate-driven range shifts. Additionally, pathogen driven range limitation adds a new complication to wildlife conservation in the face of climate change. Specifically, conservation efforts may need to account for the spread of vectors into cooler climates that currently serve as a refuge for trailing-edge populations, which are often genetically distinct and sensitive to environmental change (Hampe and Petit 2005).

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Author Contributions

S.A.M. and R.B.C. designed the study. S.A.M. collected the data, performed the analysis and wrote the first draft of the manuscript. E.K.B. collected and processed data as well as trained observers. All authors edited the manuscript.

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Tables and Figures

Table 4.1. Host-pathogen occupancy model results for wood thrush and black-throated blue warblers infected with *Leucocytozoon* and *Haemoproteus* respectively. Estimates are posterior means, SDs, and 95% CIs.

Wood thrush

Process	**Parameter**	**Mean**	**SD**	**Lower CI**	**Upper CI**
Detection	Intercept	2.76	0.59	1.73	4.06
	Wind	1.88	0.71	0.67	3.48
	Noise	-0.69	0.37	-1.43	0.02
	Date	-0.99	0.47	-1.97	-0.09
Occupancy	Intercept	-0.14	1.06	-2.25	2.00
	Pathogen Prevalence	-6.47	5.83	-18.41	4.07
	Climate	-1.11	1.33	-4.03	1.00
Infection	Intercept	-1.47	0.62	-2.63	-0.20
	Climate	-0.93	0.44	-1.77	-0.01

Black-throated blue warbler

Process	**Parameter**	**Mean**	**SD**	**Lower CI**	**Upper CI**
Detection	Intercept	1.12	0.18	0.77	1.49
	Wind	0.28	0.19	-0.07	0.66
	Noise	0.67	0.25	0.19	1.18
	Date	-0.03	0.23	-0.48	0.42
Occupancy	Intercept	1.14	1.10	-1.02	3.32
	Pathogen Prevalence	-11.04	4.57	-21.7	-3.87
	Climate	-0.35	0.54	-1.47	0.66
Infection	Intercept	-0.02	0.68	-1.32	1.34
	Climate	1.93	0.57	0.91	3.17

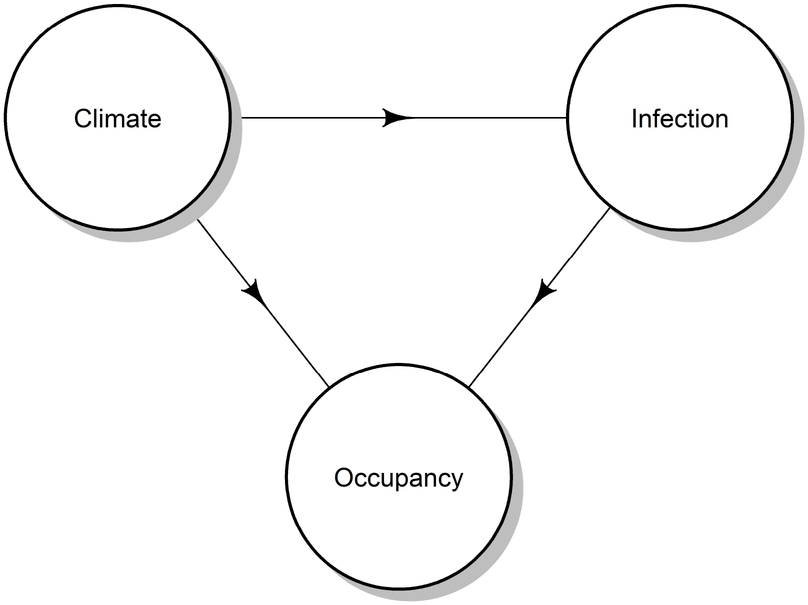

Figure 4.1**.** Directed acyclic graph (DAG) representing hypotheses on the effects of climate and infection on host species occupancy.

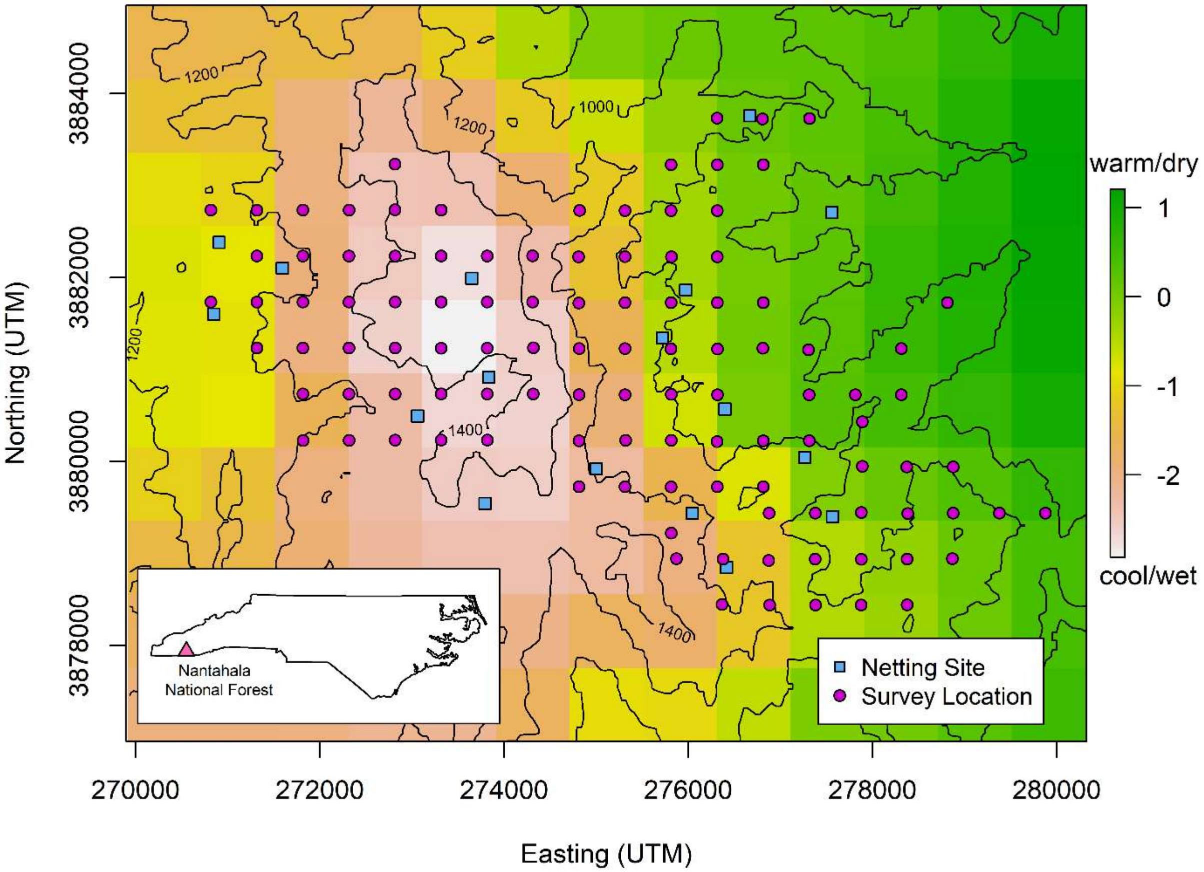

Figure 4.2. Netting sites and point-count survey locations in the Nantahala National Forest, North Carolina, USA**.** Sites were selected to cover the local climate gradient, represented by the color ramp. In general, warmer and drier sites occur at lower elevations whereas higher elevations are cooler and wetter. Elevation is depicted by the contour lines.

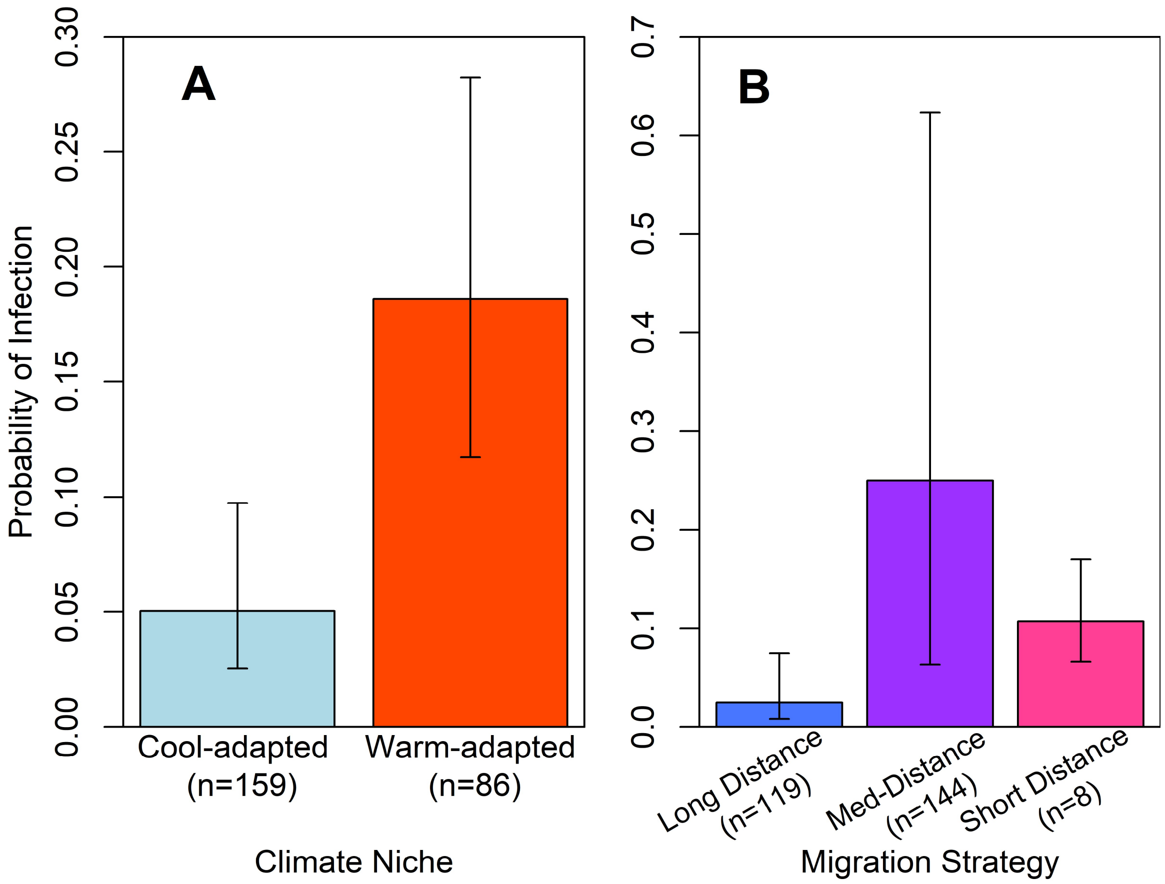

Figure 4.3. Probability of infection with (A) hemoparasites in cool- and warm-adapted songbirds and (B) by migration strategy in the Nantahala National Forest, North Carolina, USA. Results for resident species are not shown because no hemoparasites were detected (n=3). Error bars are 95% CIs.

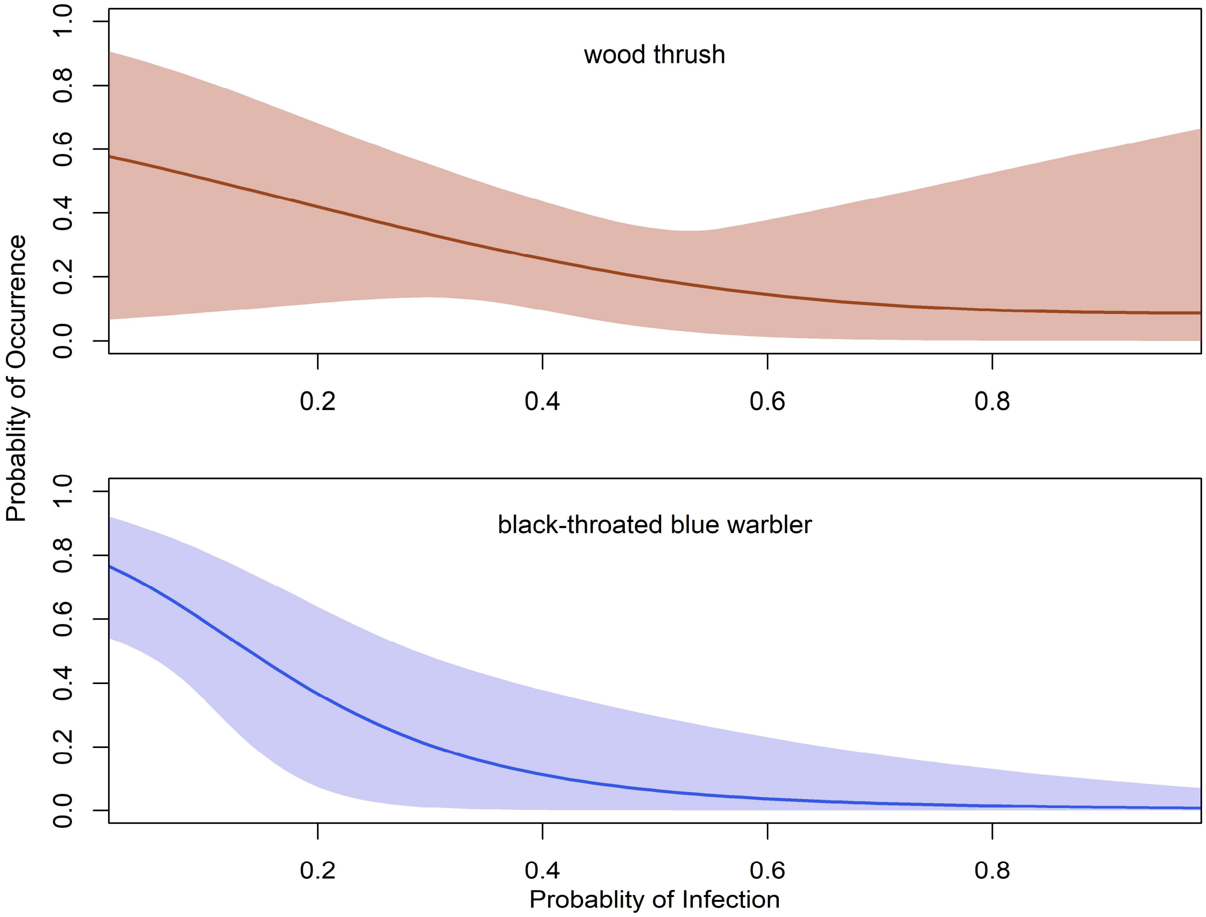

Figure 4.4. Predicted probability of occurrence and 95% CIs from the global model versus probability of infection for black-throated blue warbler (*Setophaga caerulescens*) and wood thrush (*Hylocichla mustelina*), after averaging over the effect of climate.

CHAPTER 5

EFFECTS OF HUMIDITY AND TEMPERATURE ON AVIAN HATCH RATES AT A TRAILING-EDGE RANGE BOUNDARY[1]

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[1] Merker, S.A., Sillet, T.S., Cooper, R.J., and Chandler, R.B, to be submitted to Ecology Letters

Abstract

Trailing-edge populations near low-latitude and low-elevation range boundaries face high risks of climate-induced extinction, but the mechanisms by which climate change influences trailing-edge populations are poorly understood. We used experimental and observational methods to assess a series of predictions stemming from the hypothesis that abiotic conditions limit the trailing-edge distribution of a cool-adapted songbird via temperature and humidity effects on egg hatch rates. A reciprocal transplant experiment involving translocation of eggs across the local range boundaries of two ecological similar species, differing primarily in their climate niche, revealed asymmetric effects of the treatment. Consistent with the abiotic limitation hypothesis, hatch rates of the cool-adapted, trailing-edge species declined from 0.933 (+/- 0.39) to 0.604 (+/- 0.31) when eggs were moved to warmer, drier conditions. As predicted, there was little effect – 0.879 (+/- 0.32) vs 0.807 (+/- 0.49) – of translocation on egg hatch rates of the warm-adapted species occurring near the core of its range. Contrary to expectations, measurements of temperature and humidity within and adjacent to experimental and control nests indicated that high temperatures played a greater role than humidity in contributing to the reduced hatch rates of the cool adapted species. To complement our experiment, we used observational data from 13 years to compare hatch rates at the core- and trailing-edge of the cool-adapted species' breeding range. We found no effect of temperature on hatch rates at either the core or the trailing-edge of the range, suggesting that birds do not occupy sites where high temperatures would negatively impact productivity. However, hatch rates were lower and declined over the observation period in the core of species range. Our results support the hypothesis that the range limit of the trailing-edge population is influenced by the impacts of climate conditions on egg hatch rates. Structurally adaptations of eggs may not exhibit enough phenotypic plasticity to ameliorate the effects of climate change on peripheral populations. Future work should identify the physiological mechanism, be it water loss or oxygen exchange, by which increasing temperatures negatively impact hatch rates of cool-adapted species.

Keywords: Egg-swap, hatch rates, nestling growth, climate change, female behavior, range limits, social cues, nest temperature, relative humidity, black-throated blue warbler, hooded warbler

Introduction

Trailing-edge populations near low-latitude and low-elevation range boundaries face increased extinction risk as a result of climate change (Parmesan and Yohe 2003, Parmesan 2006, Chen et al. 2011, Williams and Blois 2018). Loss of these populations could reduce species-level genetic diversity and impact ecosystem function (Hampe and Petit 2005). Understanding the processes involved in climate change impacts on trailing-edge populations requires information about the factors limiting their distributions. Early hypotheses predicted that biotic interactions should exert more influence on species distributions near low-latitude range margins than abiotic factors (Dobzhansky 1950, MacArthur 1972, Jankowski et al. 2010, Jankowski et al. 2013, Freeman and Montgomery 2016), but there is growing evidence that abiotic factors such as temperature and precipitation limit species distributions at the trailing-edge (Hampe and Petit 2005, Hickling et al. 2006, Cahill et al. 2014, Rubenstein et al. 2020, Merker and Chandler 2021). However, the mechanisms by which climate influences trailing-edge populations are poorly understood.

Although there is evidence supporting the role of temperature in setting species range limits, the ecological processes associated with temperature-mediated range shifts remain unclear (MacArthur 1972, Jankowski et al. 2013). High temperatures can negatively affect reproduction in many taxa, which may influence species distributions (Hansen 2009, DuRant et al. 2013, Mendonca et al. 2018). For example, annual recruitment of moose (*Alces alces*) at southern range boundaries in western North America was reduced when temperature was high in the previous year (Monteith et al. 2015). Rising temperatures at low elevations can also push trailing-edge populations to higher elevations as they track physiologically optimal conditions necessary for reproduction (La Sorte and Jetz 2010a). High elevation birds in the Peruvian Andes shifted their distributions and, in some cases, became extirpated from high elevations as a result of warming temperatures (Freeman et al. 2018). While there is strong support for temperature as a limiting factor, other abiotic factors may also impact species distributions at the trailing-edge.

Humidity can limit species distributions, but it has received far less attention than temperature, especially among vertebrates (Baldauf et al. , Shirazi et al. 1996, Bohning-Gaese and Lemoine 2004, Sales et al. 2016). However, humidity can directly influence animal populations, for example through its impacts on avian egg development (Walsberg 1980, 1983, Gillespie et al. 2000, Hedhly et al. 2009, Jaworski and Hilszczanski 2013). Habitat-specific variation in eggshell pore density is vital for proper gas exchange between the environment and the embryo (Rahn et al. 1979). For example, House**Error! Bookmark not defined.** Finches (*Haemorhous mexicanus*) in their human-introduced range laid eggs with thicker shells and fewer pores than in their natural range where humidity is generally lower (Stein and Badyaev 2011). When *H. mexicanus* eggs were swapped between native (Montana, USA) and introduced ranges (Alabama, USA), embryo survival decreased despite inner nest temperatures remaining in the range necessary for embryo development each location (Stein and Badyaev 2011). These results suggest that humidity is important in determining avian range limits because it is more difficult for birds to manipulate humidity in the nest than it is for them to manipulate temperature (Rahn et al. 1977, Stein and Badyaev 2011, Smith et al. 2018).

Bird eggs are considered ectothermic (Hiebert and Noveral 2007) and need to remain within a relatively narrow temperature range during incubation to fully develop and hatch (White and Kinney 1974, Conway and Martin 2000a, Lundblad and Conway 2021). To ensure eggs remain within this optimal temperature range, incubating birds moderate their behavior to maintain temperatures in the nest as ambient temperature around the nest fluctuates, especially in species where only females incubate (Sturkie 2012, Walters et al. 2016). The trade-off between incubation and foraging is managed by adjusting the amount of time off the nest and the frequency of off-nest excursions (Smith et al. 2018). Time off the nest generally increases as ambient temperature increases (Davis et al. 1984, Walters et al. 2016). However, it is not known if behavioral responses to changing ambient conditions will facilitate species' ability to track their climate optima. Failure to track shifting climate conditions through behavior could result in reduced productivity and ultimately range contraction or extirpation at the trailing-edge.

Our first objective was to determine if the trailing-edge range boundary of a cool-adapted migratory passerine, the black-throated blue warbler (*Setophaga caerulescens*), was limited by temperature and humidity effects on egg hatch rates and nestling growth rates. To evaluate the abiotic range limitation hypothesis, we tested the prediction that eggs experimentally moved to nests outside the species' range would have lower hatch rates than control eggs. Black-throated blue warbler eggs were swapped with eggs of an ecologically-similar but warm-adapted species, the hooded warbler (*Setophaga citrina*). Although all species of birds maintain eggs within narrow temperature and humidity ranges, we predicted negative effects of translocation of cool-adapted eggs because they may not be adapted to ambient climate conditions at low elevation sites. In the event that swapped eggs hatched, we predicted that nestlings in swapped nests would grow at different rates than nestlings hatched in their natal nests (Boyle et al. 2016). We also evaluated the alternative hypothesis that neither ambient temperature or humidity would affect egg hatch rates or nestling growth because female incubation and nestling provisioning behaviors would be adapted to local climate conditions. Our second objective was to assess the abiotic range limitation hypothesis over broader spatial and temporal scales. Using 13 years of data on black-throated blue warbler hatch rates at both the trailing-edge and core of the range, we evaluated the prediction that the negative effect of temperature on hatch rates should be stronger at the trailing-edge than at the range core.

Methods

Study site

Field work was conducted in the Nantahala National Forest in southwestern North Carolina, USA (Figure 1). We selected this region of the southern Appalachian Mountains because it has a high diversity of species with trailing-edge populations, including >20 species of birds (Merker and Chandler 2020). Many of these cool-adapted species have closely related warm-adapted congeners that occur at lower elevations. The site is characterized by steep topography ranging from 800-1590 m over short (<5 km) distances. At high elevations, the climate is cooler and wetter than at lower elevations, providing suitable conditions for many cool-adapted species that do not occur elsewhere in the southeastern United States (Lewis and Cooper 2019, Merker and Chandler 2020, 2021).

Study Species

The black-throated blue warbler *(Setophaga caerulescens*) is a cool-adapted neotropical migrant songbird with a breeding range centered in the northeastern United States and southeastern Canada. A narrow band of the range extends south through the Appalachian Mountains (Figure 5.1). The hooded warbler (*Setophaga citrina*) is a warm-adapted neotropical migrant songbird with a breeding range centered in the southeastern United States (Figure 5.1). Both species build open cup nests in the shrub layer making their nests relatively easy for observers to access. Additionally, both species have similar clutch sizes, diets, and incubation behavior, which is carried out solely by females (Chiver et al. 2020, Holmes et al. 2020). Hooded warblers are slightly heavier (mean=11.1 g) than black-throated blue warblers (mean=9.8 g) (Chiver et al. 2020, Holmes et al. 2020).

Objective 1 – reciprocal egg swap experiment

Nests of focal species were located and monitored throughout the 2018-2020 breeding seasons from late April through early-July. Temperature and relative humidity were measured by placing an iButton hygrochron (DS1923-F5#; Maxim Integrated Products, San Jose, California, USA) sensor in each nest. These small (diameter = 1.5 cm, depth = 0.6 cm) sensors are capable of measuring temperature to +/- 0.5 °C accuracy and relative humidity from 0-100%. As a measure of nest site microclimate, we collected temperature and relative humidity data by hanging a hygrochron within 3 m and at approximately the same height as the nest. Temperature and relative humidity were recorded every 4 minutes during incubation and nestling stages (Smith et al. 2018). Observers visited nests every 8 days to replace hygrochrons. The long interval between nest visits was used to minimize observer presence at the nest and thereby lower the risk of predation during incubation (Conway and Martin 2000b, Ibanez-Alamo et al. 2012, Matysiokova and Remes 2018).

Complete clutches of black-throated blue warbler and hooded warbler eggs were swapped across the local black-throated blue warbler range boundary into nests of the other species. Clutches were swapped from 3 sites selected to represent warm and dry conditions at low elevations and 2 sites selected to represent cool and wet conditions at high elevation. Eggs were swapped on days 1-4 of incubation to ensure that eggs were incubated in their native climate conditions for a minimal amount of time while controlling for egg age at the time of translocation. Clutches were considered eligible to be swapped if a nest of each species was found during the building or laying stage so that the clutch completion date (last egg laid) was known, each nest was within 1-2 days of clutch completion, and nests were at substantially different elevations (mean difference= 350 m, range=247-586 m).

When two eligible nests were found, observers collected complete clutches (USFWS Scientific Collection Permit # MB51229D-0) and placed each clutch in a plastic container lined with foam such that each egg was surrounded completely by foam and allowed minimal movement (Figure 5.2A). Observers placed a hygrochron in the nest, partially within the lining to avoid damaging eggs, so that the humidity sensor pointed inward towards the center of the nest (Figure 5.2B). Observers then placed an equal number of fake plastic eggs in the nest, recorded the time, and departed (Figure 5.2C). Observers used a combination of walking and driving to bring the eggs to the receiving nest of the opposite species. Upon arrival at the receiving nest, observers removed the fake eggs, deposited the real eggs of the opposite species one at a time, and recorded the time. Observers remained within binocular viewing distance (15-20 m) of the nest to confirm that female birds returned to the nest to incubate the eggs of the other species. Nests were checked every other day after swaps and were only approached to switch out hygrochrons or measure nestlings.

We used two types of controls. First, eligible nests without an eligible swap nest of the opposite species were used as positive controls. Positive control clutches were collected and moved the same way as translocated clutches except that they were returned to the same nest. In some cases, due to the remote nature of some nests, eggs were only walked rather than walked and driven. For negative controls, we used nests that were found during incubation or nestling stages but were not manipulated, except for normal monitoring and the addition of hygrochrons.

We investigated the effects of the translocation experiment on nestling development by repeatedly measuring tarsal length, wing chord, bill width, bill depth, and mass of nestlings in experimental and control nests every 2 days. To account for individual variation and asynchronous hatching we marked individual nestlings by coloring their toe-claws and toes with a permanent marker (Slagsvold 1985). When nestlings were large enough (days 5-7) they were marked with a USGS aluminum leg band.

We used binomial generalized linear models (GLMs) to test the prediction that translocated eggs of the cool-adapted species would have lower hatch rates than eggs in control groups. Binomial GLMs are more appropriate than traditional ANOVA methods for proportion data because they acknowledge that the response variable (number of hatched eggs) is integer-valued with an upper bound (number of eggs in the clutch). Binomial GLMs also do not assume a constant variance (Warton and Hui 2011). The sample unit in the analysis was the clutch, not the egg. Hatch rate was modeled as a function of species and treatment, and we evaluated main effects and the interaction of the two variables. We also tested whether ambient conditions or conditions inside the nest affected hatch rates of black-throated blue warbler eggs.

We used a linear model to evaluate whether temperature and relative humidity varied with elevation outside nests. For inner nest temperature and relative humidity, we also included species as a predictor variable. Mean relative humidity is a proportion, and because some values equaled 1, we subtracted 0.001 from every value before applying a logit transformation. We focused exclusively on temperature and humidity data during periods of darkness (2100-0500 hours) when female birds rarely leave the nest (Weathers and Sullivan 1989, Slay et al. 2012). We used mean values of temperature and relative humidity at night because incubation periods varied due to predation and the day of incubation the nest was discovered. In addition to main effects we estimated interactions of species and elevation on temperature and humidity inside and outside the nest.

We modeled species-specific incubation behavior as a function of ambient conditions using linear mixed effects models. We subset the hygrochron temperature data to crepuscular and daylight periods (0530-2100 hours) when females intersperse bouts of foraging and incubation. Using methods similar to those of Smith et al. (2018) we quantified duration of female foraging bouts by first taking the difference between temperature measurements inside and outside nests. Periods of continuously decreasing temperature differences followed by either no change or a sudden increase indicated that the female had returned to the nest and reinitiated incubation. Incubation duration was modeled as functions of mean temperature and mean humidity inside and outside the nest during each bout. We included both nest identity and day of incubation as random effects.

We used linear models to assess the effects of species, treatment, and brood size on hatchling growth rates. We used the change in growth from the first measurement (day 2) to the last measurement (day 6) for each biometric as a response variable. We included brood size as a predictor of nestling growth because nestling development can be affected by the number of nestlings in a brood (Martin 1987).

Objective 2 -- egg hatch rates and temperature across the range

To compare hatch rates at the trailing-edge and core of the black-throated blue warbler breeding range, we used 13 years (2003-2015) of data on nesting black-throated blue warblers from Hubbard Brook Experimental Forest in New Hampshire and the Nantahala National Forest in North Carolina, USA. We included only nests where at least one egg was known to have hatched in order to ensure that we were not using nests that were predated before hatching could occur. Additionally, we removed any nests used in prior experiments at Hubbard Brook (Holmes 2011).

We used binomial GLMs to model hatch rates as a function of temperature at the trailing-edge and core of the black-throated blue warbler breeding range. We used the number of hatched eggs in each nest as a response variable and included mean monthly temperature during the month that females completed their clutch, range position (trailing-edge vs core), and year as predictor variables. For the range-wide, nestling growth rate, and microclimate models we used the Akaike information criterion (AIC) to select which model best predicted each response variable(Akaike 1998) . All analyses were conducted in R Statistical Software version 4.0.2 (R Core Team, 2020). Intervals reported below are 95% CIs.

Results

We found 97 black-throated blue warbler nests and 61 hooded warbler nests over the 2018-2020 breeding seasons. Thirteen reciprocal clutch swaps were performed, 17 clutches were moved as controls, and 50 nests were only monitored and considered as un-manipulated nests. Consistent with the abiotic range limitation hypothesis, hatch rate for black-throated blue warbler eggs translocated from cooler wetter conditions to warmer drier conditions was 0.604 (0.569 - 0.639), lower than all other groups (Figure 5.3). Black-throated blue warbler eggs in control nests hatched at a rate of 0.795 compared to 0.933 in un-manipulated nests (Figure 5.3). Hatch rate for hooded warbler eggs translocated from low to high elevations was 0.807 (0.783 – 0.830, Figure 5.3), which was similar to the hatch rate (0.800, 0.757 – 0.836) of hooded warbler eggs in control nests. Un-manipulated hooded warbler eggs hatched at a rate of 0.876 (0.868 – 0.883), slightly higher than control or translocated eggs. We found that temperature conditions inside nests had the strongest effect on the hatch rate of black-throated blue warbler eggs. Specifically, as inner nest temperatures increased, during both incubation and foraging bouts, hatch rates declined (Figure 5.4). Warmer ambient temperatures had a slightly negative effect on black-throated blue warbler hatch rates (Figure 5.5). Humidity inside and outside nests had no effect on hatch rates.

Mean nighttime temperature inside hooded warbler nests was 30.07 °C (10.59-39.13 °C), higher than 27.05 °C (12.66-38.05 °C) inside black-throated blue warbler nests (Figure 5.6). Both mean night time and mean day time temperatures outside nests decreased with elevation (Figure 5.7 & 5.8). Mean nighttime relative humidity inside hooded warbler nests decreased with elevation but increased inside black-throated blue warbler nests with elevation (Figure 5.6). Mean nighttime relative humidity outside nests varied little with elevation and stayed between 80-100% (Figure 5.7). Mean daytime relative humidity showed a slight, but insubstantial decline with elevation (Figure 5.8).

Female incubation behavior differed between species. Black-throated blue warbler females had shorter incubation and foraging bouts than hooded warbler females regardless of climate conditions (Figure 5.9). Duration of hooded warbler incubation bouts increased with ambient temperature and decreased with ambient humidity (Figure 5.9). Duration of female foraging bouts for either species showed little relationship to temperature or humidity (Figure 5.9).

Hooded warbler nestling mass and growth rate were greater than black-throated blue warbler nestlings regardless of brood size or treatment (Figure 5.10). Nestling tarsal growth from day 2 to day 6 varied by species, treatment, and brood size. Hooded warbler nestlings raised in their native nest showed the greatest tarsal growth in small brood sizes but tarsal growth decreased significantly at higher brood sizes, but showed the opposite trend when raised in a black-throated blue warbler nest (Figure 5.10). Black-throated blue warbler nestlings showed little or no change regardless of which species reared them (Figure 5. 10).

Nestling wing chord growth from day 2 to day 6 varied by species, treatment, and brood size. Hooded warbler nestlings in their natal nest showed the greatest wing chord growth in small brood sizes but wing chord growth decreased significantly at higher brood sizes, showed the opposite trend when raised in a black-throated blue warbler nest (Figure 5.10). Black-throated blue warbler nestling wing chord growth remained constant across all brood sizes and treatments (Figure 5.10).

Growth of nestling bill length (nares to tip) and depth varied by species and brood size but not by treatment. Hooded warbler nestlings had longer and deeper bills than black-throated blue warbler nestlings and growth of both decreased with brood size (Figure 5.10). Growth of nestling bill width did not vary by species or treatment but did decrease significantly at larger brood sizes (Figure 10).

There were no differences between transportation times for clutches in the treatment and positive control groups. Black-throated blue warbler eggs were out of nests for approximately 38 minutes for both swap and control movements (*t*=-0.036, df=20, *p*=0.971; Appendix J). Hooded warbler eggs were out of nests for slightly longer with a mean of 47.33 minutes for control movements and a mean of 44.75 minutes for swaps (*t*=0.262, df=9, *p*=0.799; Appendix J). Although eggs of each species were out of the nest for different amounts of time this difference was not significant (*t*=-1.86, df=31, *p*=0.072; Appendix J).

The top model of hatch rates across the breeding range of black-throated blue warblers included a 3-way interaction between range position, year, and mean temperature (Table 5.3). Hatch rates for black-throated blue warbler eggs differed by range position when averaged across all years. Eggs laid in the core of the species range hatched a lower rate than eggs laid at the trailing-edge regardless of year or mean monthly temperature (Figure 5.11).

Discussion

Contrary to early hypotheses about the importance of biotic interactions at low-latitude range margins, a growing body of literature demonstrates that abiotic climate conditions play a major role in limiting the distributions of trailing-edge populations (Hansen 2009, La Sorte and Jetz 2010b, Stein and Badyaev 2011, DuRant et al. 2013, Cahill et al. 2014, Koo et al. 2014). However, the mechanisms by which climate influences populations at range boundaries are poorly understood. Results from our reciprocal transplant experiment indicate that trailing-edge populations of birds are limited, in part, by physiological constraints that reduce egg hatch rates in unsuitable conditions immediately outside the range. Eggs of the cool-adapted, trailing-edge species hatched at lower rates than control eggs when moved across their local range boundary to warmer conditions. However, for the warm-adapted species near the core of its range, hatch rates were similar between eggs in treatment and control groups. These results suggest that reported declines of trailing-edge songbird populations may be linked to a climate driven reduction in hatch rates at low elevations (White and Kinney 1974, Stoleson and Beissinger 1999, Conway and Martin 2000a, b, Stodola et al. 2013, Sauer et al. 2015, Lundblad and Conway 2021).

Few field studies have evaluated the effects of climate on egg development at a local range boundary. House finch hatch rates were reduced when eggs were translocated between their native range and their recently colonized range – an effect attributed to structural differences in egg shells (Stein and Badyaev 2011). Eggshell thickness and pore-density are critical to embryo development because they control water loss and oxygen exchange (Rahn et al. 1977, Rahn et al. 1979). Although we did not measure egg shell structure, it is likely that eggs of warm- and cool-adapted species at our study site are adapted to their local climate conditions and either water loss or gas exchange rates were negatively affected by conditions outside the range of the cool-adapted species.

We found differences in nighttime temperatures inside nests of the cool-adapted and warm-adapted species. This stands in contrast to studies reporting a consistent, and narrow, range of temperatures necessary for embryo development across multiple bird species (White and Kinney 1974, Conway and Martin 2000a, Lundblad and Conway 2021). This also suggests that different species lay eggs adapted to a specific range of climate conditions, as with house finches in different parts of their range (Rahn et al. 1976, Stein and Badyaev 2011). Females of each species also displayed different incubation behavior, with hooded warbler females spending more time incubating eggs than black-throated blue warblers. Additionally, only hooded warbler females increased their incubation time with warmer ambient temperatures. This result supports previous studies showing that experimentally heating nests leads female birds to spend more time incubating their eggs because they are less constrained by the energetic cost of keeping eggs warm (Bryan and Bryant 1999, Ardia et al. 2009).

Although warmer nest temperatures during incubation and foraging had a negative effect on black-throated blue warbler hatch rates, temperatures inside nests were never high enough to result in embryo death (Conway and Martin 2000a, McKechnie and Wolf 2010, Lundblad and Conway 2021). However, water-loss and gas exchange through eggshell pores can affect hatch rates, and may explain why eggs of the cool-adapted species failed to hatch in warmer conditions (Rahn et al. 1976, Rahn et al. 1977, Morgan et al. 1978, Ar and Rahn 2015). An essential component of incubation is balancing temperature and humidity conditions in the nest to optimize water-loss by altering the duration of incubation and foraging bouts relative to ambient conditions. (Rahn et al. 1976, Rahn et al. 1977, Morgan et al. 1978, Rahn et al. 1979, Ar and Rahn 2015).

Only hooded warblers altered the duration of these behaviors, spending more time on the nest in warmer conditions and less time in humid conditions. This suggests that there is an effect of both ambient conditions and female behavior on hatch rates. Additionally, because of the warmer ambient conditions at low elevations, the cooling effect expected when female hooded warblers leave the nest may result in excess water loss from black-throated blue warbler eggs. Thus ambient conditions have both a direct and indirect negative effect on the hatch rates of black-throated blue warbler eggs.

Although nighttime and daytime relative humidity did not vary with elevation, substantial variation in humidity existed among nests, perhaps as a result of local topography. Despite this, we did not detect an effect of humidity on hatch rates of either species. Hooded warblers always incubated eggs for longer than black-throated blue warblers and decreased incubation time with relative humidity. This suggests that female birds optimize incubation to achieve necessary water loss from their eggs (Rahn et al. 1979, van der Pol et al. 2013). However black-throated blue warblers did not change their incubation behavior in response to humidity suggesting that cool-adapted species at their warm-edge range margin may be unable to adapt their behavior to changing climate conditions at the trailing-edge (Ruiz-Aravena et al. 2014).

Of the nestling growth measurements, only tarsus and wing lengths of hooded warbler nestlings responded to the translocation treatment. Hooded warbler nestlings had shorter tarsi at larger brood sizes in their native nests and longer tarsi at larger brood sizes in translocated nests. Positive association between tarsus length and brood size has been found in other species, likely because larger broods lose less heat from the nest, making longer tarsi beneficial for thermoregulation (Ross 1980, Murphy 1985, Rodríguez and Barba 2016). This explains the longer tarsi of hooded warblers in translocated nests, but it does not explain why tarsi were shorter in their native nests. Nestling wing lengths rarely change with temperature (Ross 1980, Murphy 1985, Rodríguez and Barba 2016), but in our study hooded warbler nestlings had longer wings in manipulated nests at larger brood sizes. It is possible that hooded warbler nestlings moved to cooler environments grow larger wings in order to maintain thermal conditions inside the nest.

We complimented our experimental work with an analysis of observational data spanning a broader spatial and temporal extent. Contrary to the experimental results, we found little evidence that egg hatch rates of the cool-adapted species were associated with the climate gradient at either the trailing-edge or core of the range. Rather, egg hatch rates differed primarily by range position, being slightly higher near the warm-edge of the range than in the core. However, the absence of a temperature effect in the range-wide data may have been the result of black-throated blue warblers not occupying areas where temperatures are high enough to negatively affect embryo development. This supports predictions from hypotheses such as the center-periphery hypothesis because if warm temperatures limit this species at the trailing-edge, then individuals should rarely occur in unsuitable conditions (Hampe and Petit 2005).

We found a slight decline in hatch rates over the 13-year study period that was not related to temperature. Trends in other abiotic factors, like precipitation, could explain this finding, but we did not have precipitation data at the appropriate scale. Future research should investigate the effects of extreme weather events on hatch rates (Sheridan and Lee 2018). Cold springs can result in nest failure in the range core, and an increase in the frequency of extreme cold weather events is predicted (Kug et al. 2015, Sheridan and Lee 2018).

Future research should attempt to identify the physiological mechanism by which high temperatures affect hatch rates of cool-adapted species. Manipulating temperature and humidity inside the nest while monitoring water loss, gas exchange, and embryo development would allow for inferences about the effects of abiotic factors and climate change on reproductive physiology (Bryan and Bryant 1999, Ardia et al. 2009, van der Pol et al. 2013, Higgott et al. 2020). Coupling physiological studies with data on spatial and temporal variation in demographic parameters would enable population-level assessments and forecasts of the mechanism governing climate-induced range shifts.

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Tables and Figures

Table 5.1. Model selection results for linear models of night time temperature (°C) and relative humidity (%) inside black-throated blue and hooded warbler nests in the Nantahala National Forest, North Carolina, USA.

Conditions Inside Nests					
Response	Model	K	AIC	ΔAIC	Weight
Temp	Species	3	271.60	0.00	0.50
	Elevation	3	273.08	1.47	0.24
	Elevation + Species	4	273.52	1.91	0.19
	Elevation*Species	5	275.50	3.89	0.07
Humidity	Elevation*Species	5	87.61	0.00	0.69
	Elevation	3	90.76	3.15	0.14
	Species	3	91.12	4.51	0.12
	Elevation + Species	4	92.75	5.13	0.05

Table 5.2. Model selection results for linear models of black-throated blue and hooded warbler nestling growth from ages 2 to 6 days in the Nantahala National Forest, North Carolina, USA.

Response	Model	K	AIC	ΔAIC	Weight
Mass gain (g)	species	3	92.23	0.00	0.34
	species + treatment	4	93.66	1.43	0.17
	species * brood size * treatment	9	93.89	1.67	0.15
	species + brood size	4	94.20	1.98	0.13
	species * treatment	5	95.41	3.18	0.07
	species + brood size + treatment	5	95.52	3.29	0.07
	species * brood size	5	96.17	3.94	0.05
	species * brood size + treatment	6	97.41	5.18	0.03
	brood size	3	110.74	18.52	0.00
	treatment	3	110.63	18.41	0.00
Tarsus gain (mm)	species * brood size * treatment	9	197.47	0.00	0.98
	species	3	208.86	11.39	0.00
	brood size	3	209.08	11.61	0.00
	treatment	3	208.26	10.78	0.00
	species + treatment	4	209.84	12.37	0.00
	species * treatment	5	211.84	14.37	0.00

	species + brood size	4	210.81	13.34	0.00
	species * brood size	5	212.71	15.24	0.00
	species + brood size + treatment	5	211.63	14.16	0.00
	species * brood size + treatment	6	213.37	15.90	0.00
Wing gain (mm)	species * brood size * treatment	9	258.62	0.00	1.00
	species	3	284.96	26.35	0.00
	brood size	3	289.20	30.59	0.00
	treatment	3	287.68	29.06	0.00
	species + treatment	4	284.65	26.03	0.00
	species * treatment	5	286.64	28.02	0.00
	species + brood size	4	284.54	25.92	0.00
	species * brood size	5	286.02	27.40	0.00
	species + brood size + treatment	5	285.99	27.37	0.00
	species * brood size + treatment	6	287.26	28.65	0.00
Bill length gain (mm)	species + brood size	4	30.16	0.00	0.32
	species * brood size	5	31.31	1.14	0.18
	species + brood size + treatment	5	32.14	1.98	0.12
	species	3	32.46	2.30	0.10
	species + treatment	4	32.51	2.35	0.10
	species * brood size + treatment	6	33.20	3.04	0.07
	species * treatment	5	33.53	3.37	0.06
	species * brood size * treatment	9	34.10	3.94	0.05
	brood size	3	38.60	8.44	0.01
	treatment	3	43.57	13.41	0.00
Bill width gain (mm)	species + brood size + treatment	5	-50.57	0.00	0.35
	species + brood size	4	-49.48	1.09	0.20
	species * brood size + treatment	6	-49.36	1.21	0.19
	species * brood size	5	-47.81	2.76	0.09
	species * brood size * treatment	9	-47.44	3.13	0.07
	species	3	-47.07	3.50	0.06
	species + treatment	4	-45.08	5.49	0.02
	species * treatment	5	-43.12	7.45	0.01
	brood size	3	-37.65	12.93	0.00

	treatment	3	-30.44	20.13	0.00
Bill depth gain (mm)	species + brood size + treatment	5	10.02	0.00	0.26
	brood size	3	10.27	0.25	0.23
	species * brood size * treatment	9	10.76	0.74	0.18
	species + brood size	4	10.89	0.87	0.17
	species * brood size + treatment	6	11.92	1.90	0.10
	species * brood size	5	12.56	2.54	0.07
	species	3	21.58	11.56	0.00
	treatment	3	24.45	14.43	0.00
	species + treatment	4	22.89	12.87	0.00
	species * treatment	5	24.63	14.61	0.00

Table 5.3. Model selection results for generalized linear models of black-throated blue warbler hatch rates at the core and trailing-edge of the range from 2003 – 2015. Nests were monitored over a temperature gradient at each range position.

Response	Model	K	AIC	ΔAIC	Weight
Hatch Rate	Range * year * meanT	8	2074.45	0.00	0.84
	Range * meant	4	2077.73	3.279	0.16
	Year * meant	4	2105.79	31.347	0.00
	meanT	2	2111.23	36.780	0.00

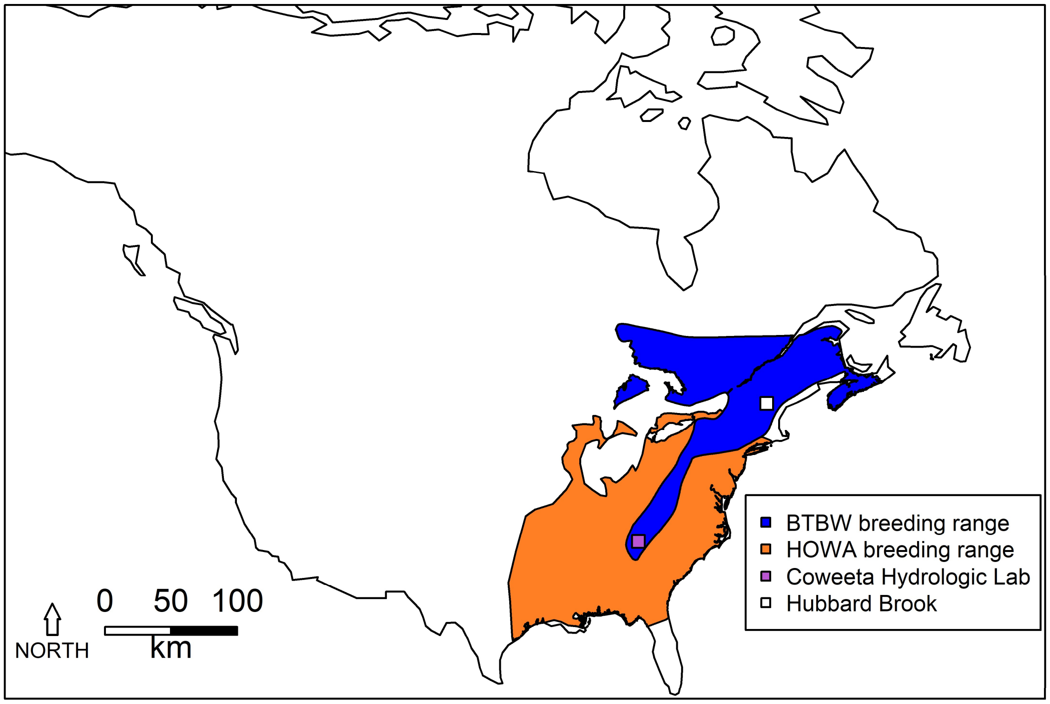

Figure 5.1. Breeding ranges of black-throated blue warbler and hooded warbler. Black-throated blue warblers breed at higher elevations than hooded warblers in the southern Appalachian Mountains of the eastern United States. The Coweeta Hydrologic Lab is located at the trailing-edge and Hubbard Brook Experimental Forest is located at the core of the black-throated blue warbler breeding range.

Figure 5.2. Black-throated blue warbler eggs (A) just after removal from a nest ready to be relocated to lower elevations in the Nantahala National Forest. Example of a hygrochron (B) in a nest. Plastic eggs (C) used as place holders for real eggs in swap and control treatment groups.

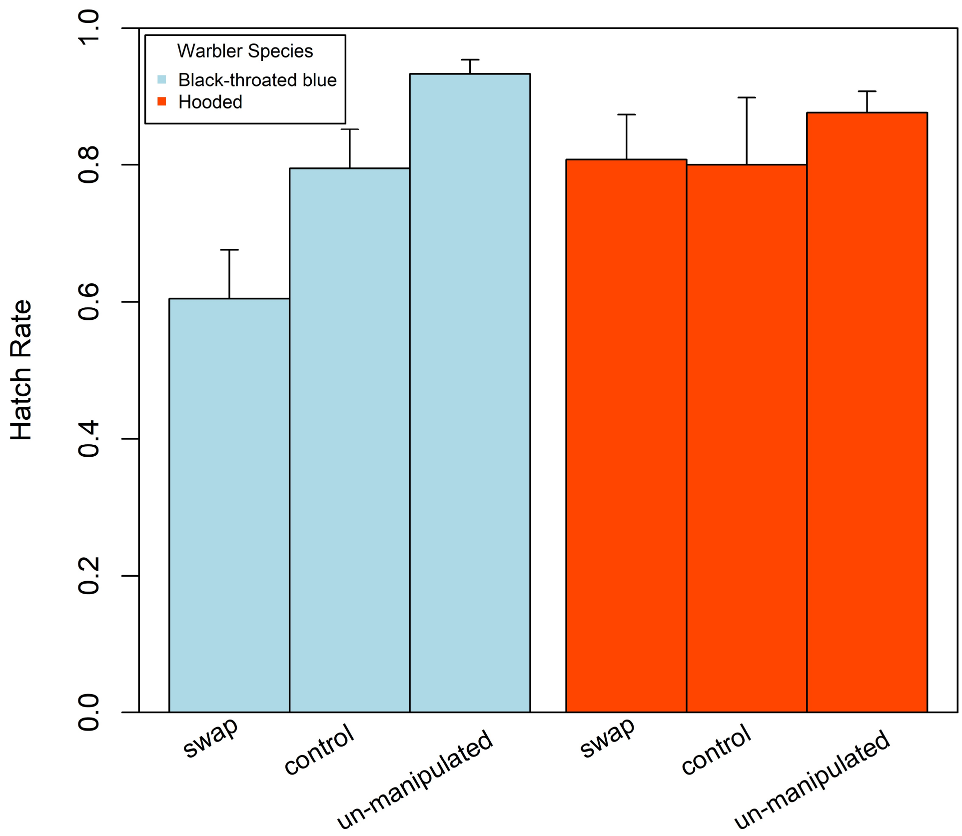

Figure 5.3. Hatch rates of black-throated blue warbler and hooded warbler eggs in swapped, control, and un-manipulated nests. Nests spanned a local climate gradient in the Nantahala National Forest, North Carolina, United States. Error bars are 1 standard error.

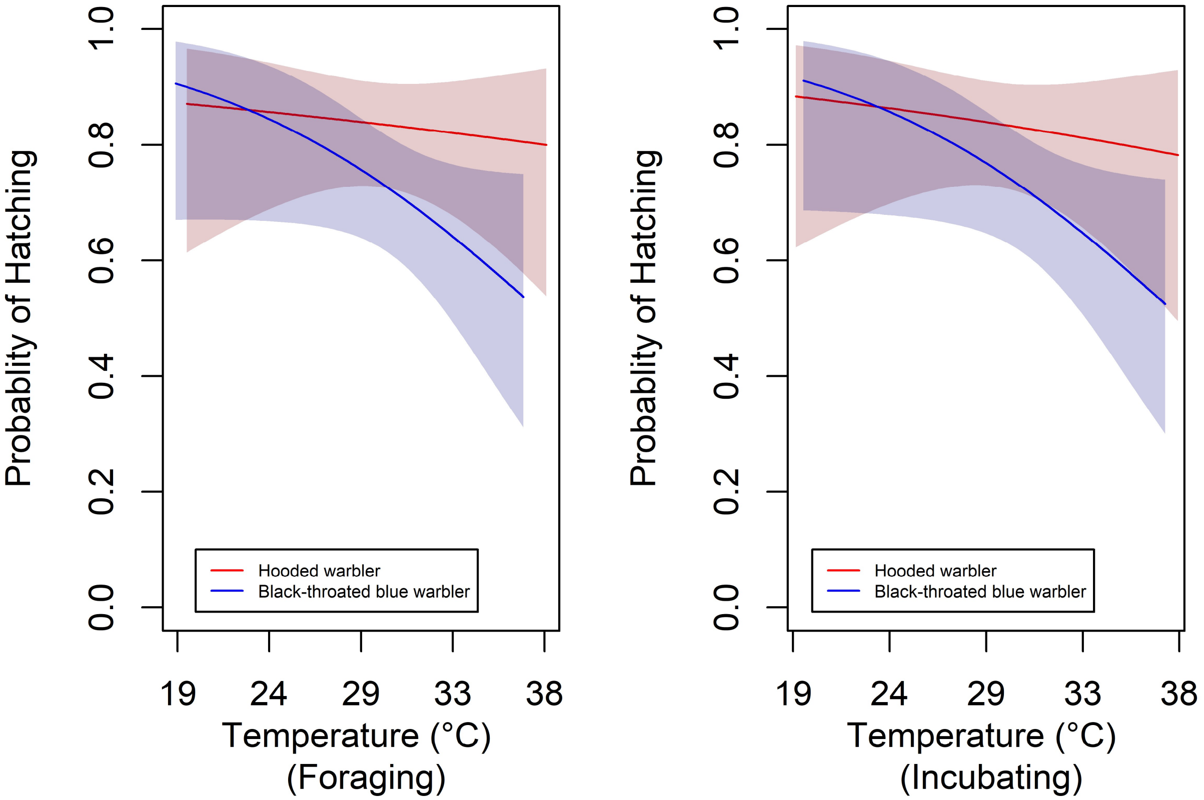

Figure 5.4 Effect of inner nest temperature during foraging and incubation bouts on black-throated blue warbler and hooded warbler eggs.

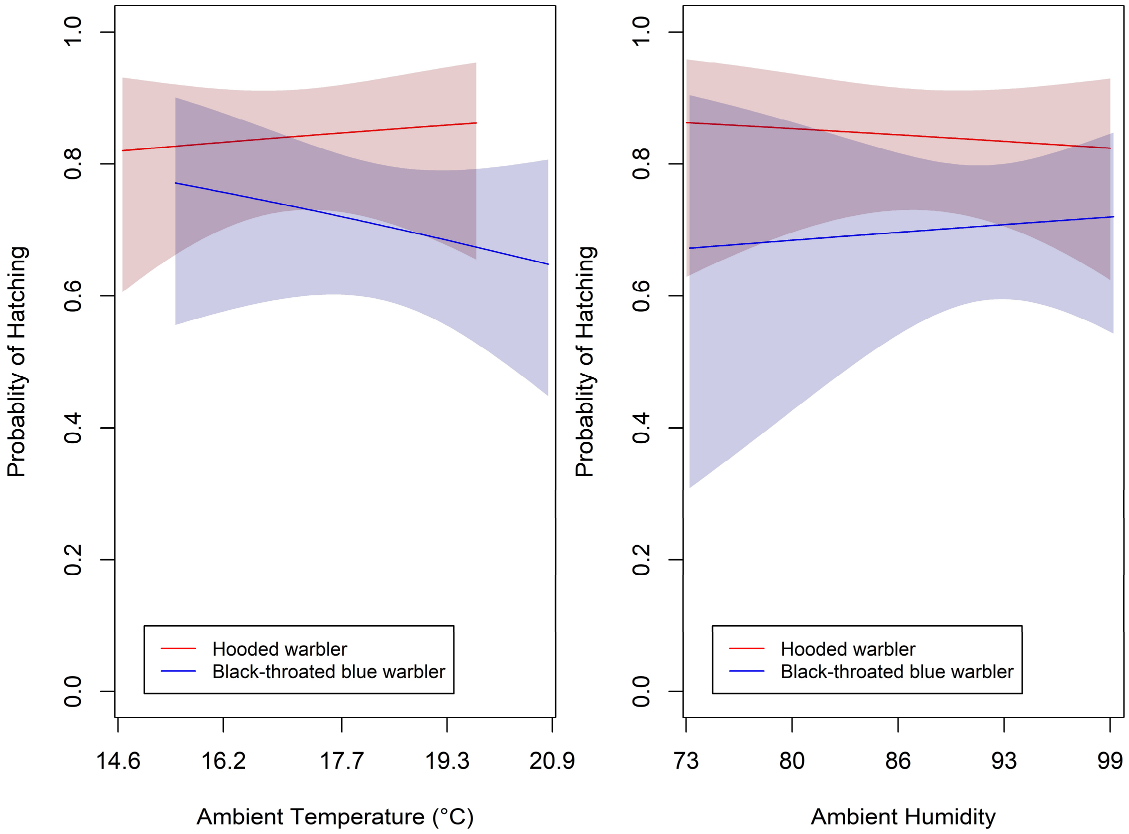

Figure 5.5 Effect of ambient temperature and humidity on black-throated blue warbler and hooded warbler eggs.

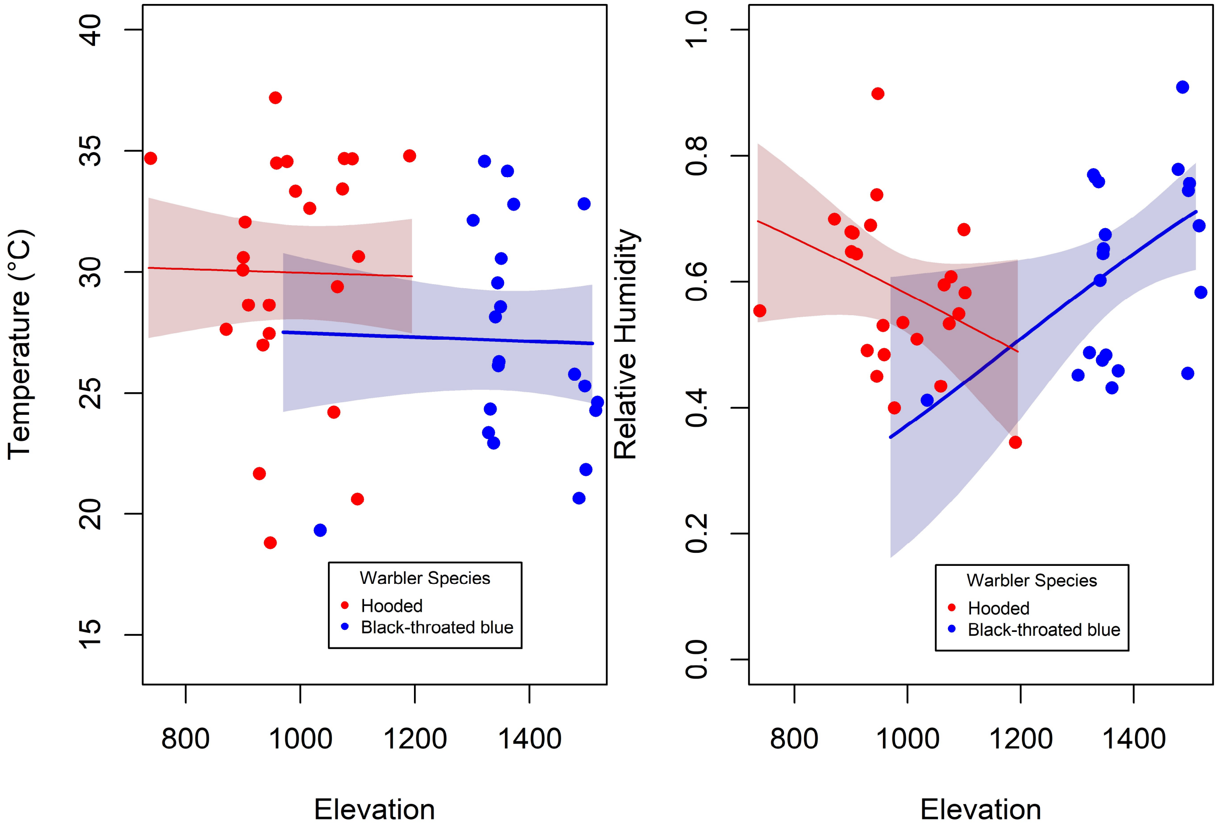

Figure 5.6. Mean nighttime temperature (A) and relative humidity (B) inside black-throated blue and hooded warbler nests over an elevation gradient in the Nantahala National Forest, North Carolina, USA.

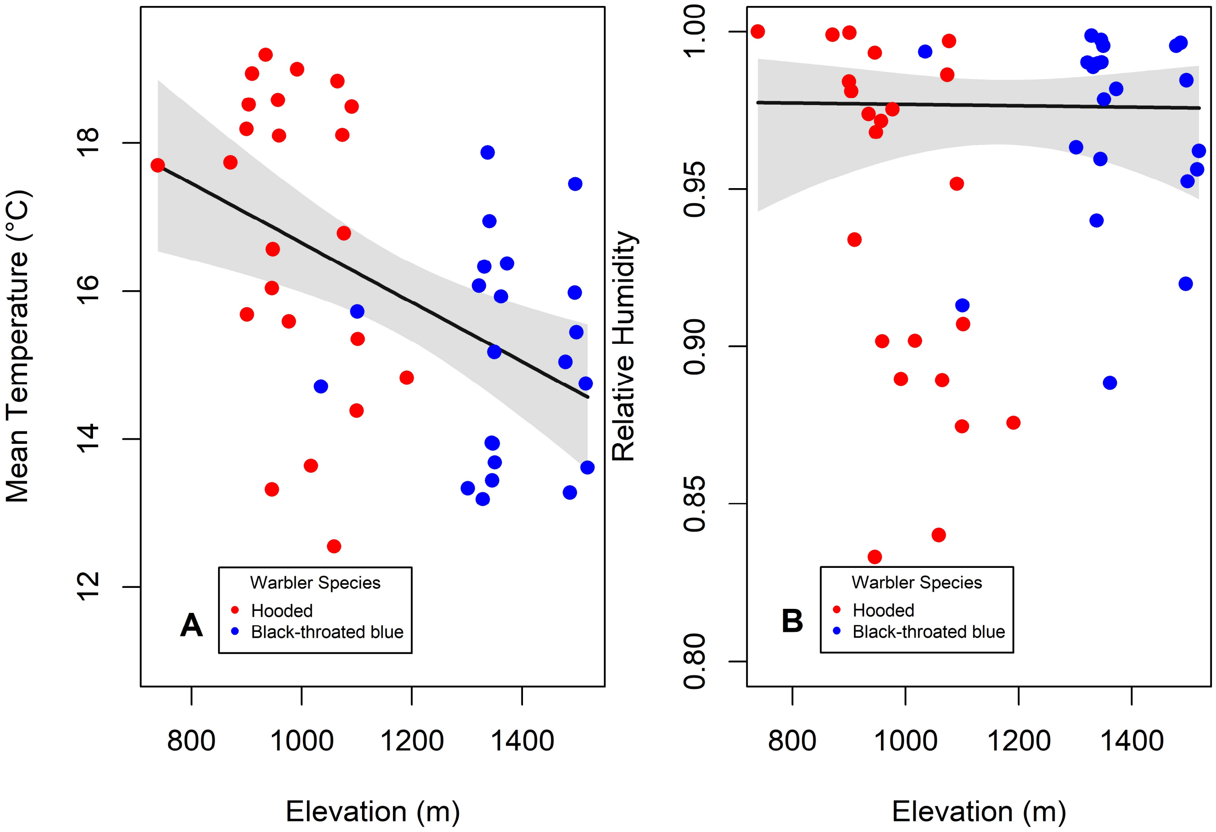

Figure 5.7. Mean nighttime temperature (A) and relative humidity B) at hygrochrons adjacent to black-throated blue warbler and hooded warbler nests over an elevation gradient in the Nantahala National Forest, North Carolina, USA.

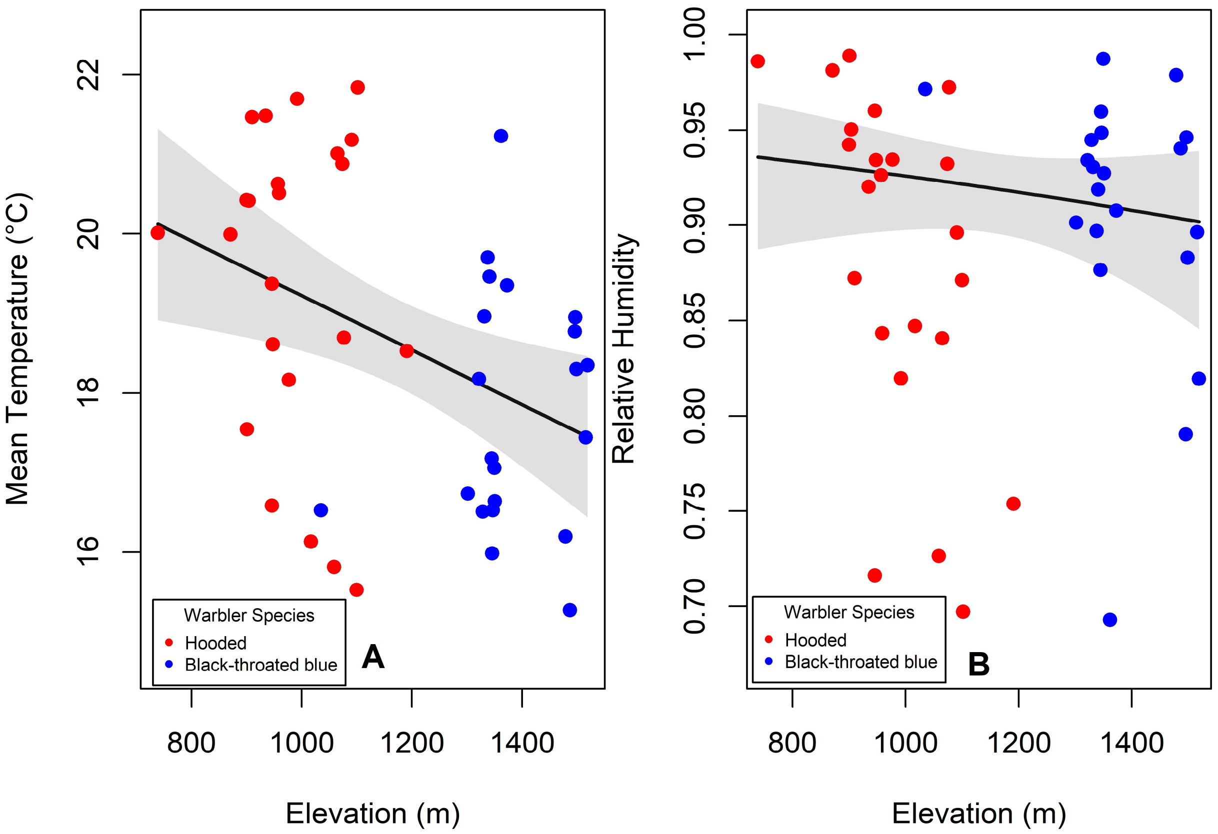

Figure 5.8. Mean daytime temperature (A) and relative humidity (B) at hygrochrons adjacent to black-throated blue warbler and hooded warbler nests over an elevation gradient in the Nantahala National Forest, North Carolina, USA.

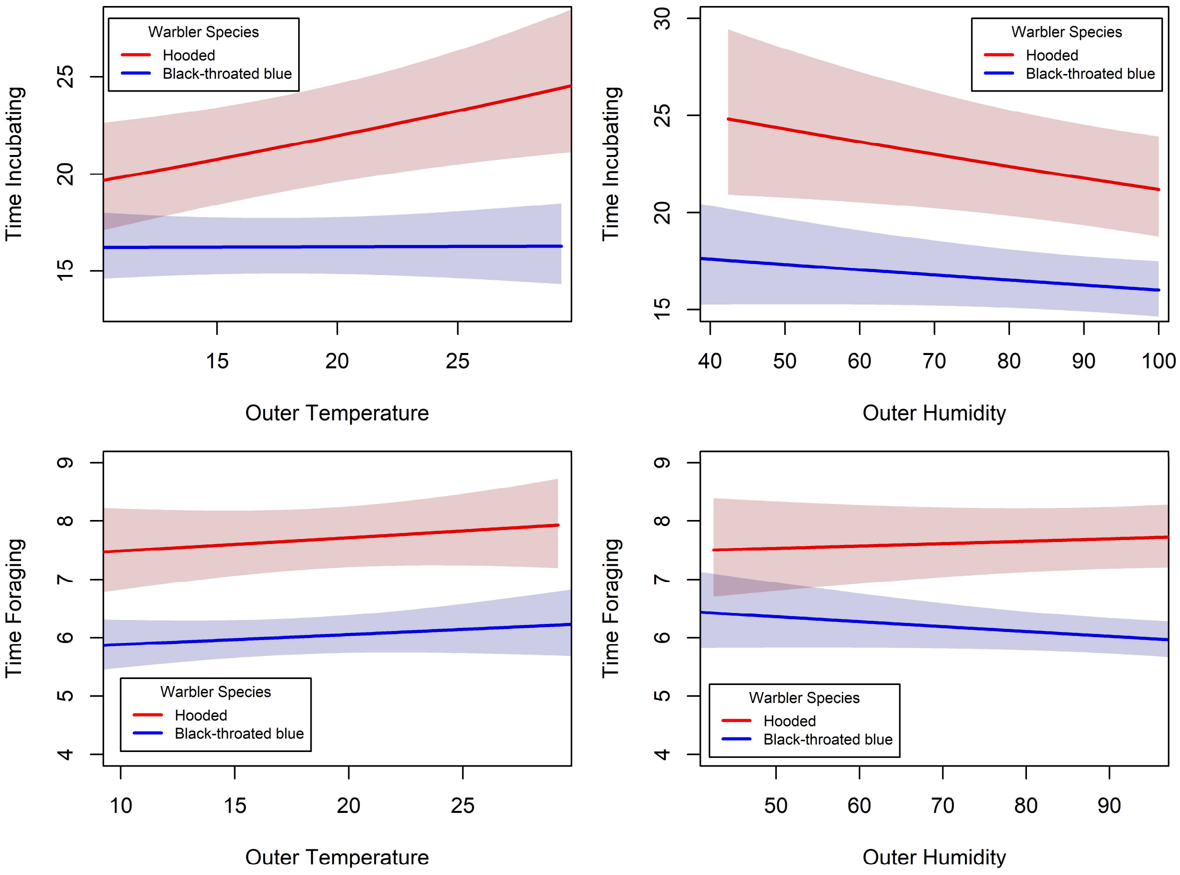

Figure 5.9. Duration of incubation and foraging bouts by female black-throated blue warblers and hooded warblers in the Nantahala National Forest, North Carolina, USA.

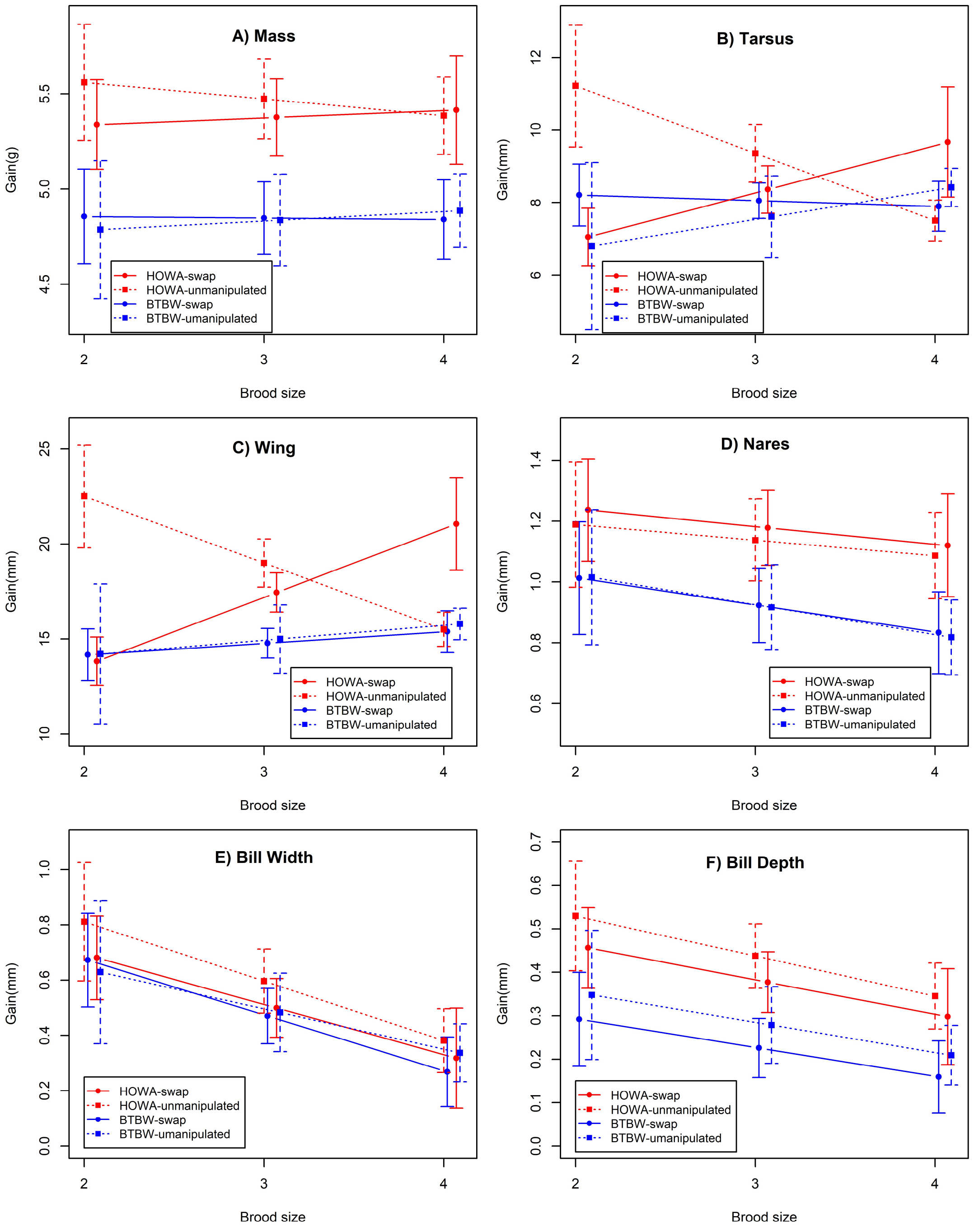

Figure 5.10. Gain in nestling mass (A), tarsus length (B), wing length (C), nares (D), bill length (E), and bill depth (F), from age 2 to 6 days for black-throated blue warbler and hooded warbler nestlings of different brood sizes in North Carolina.

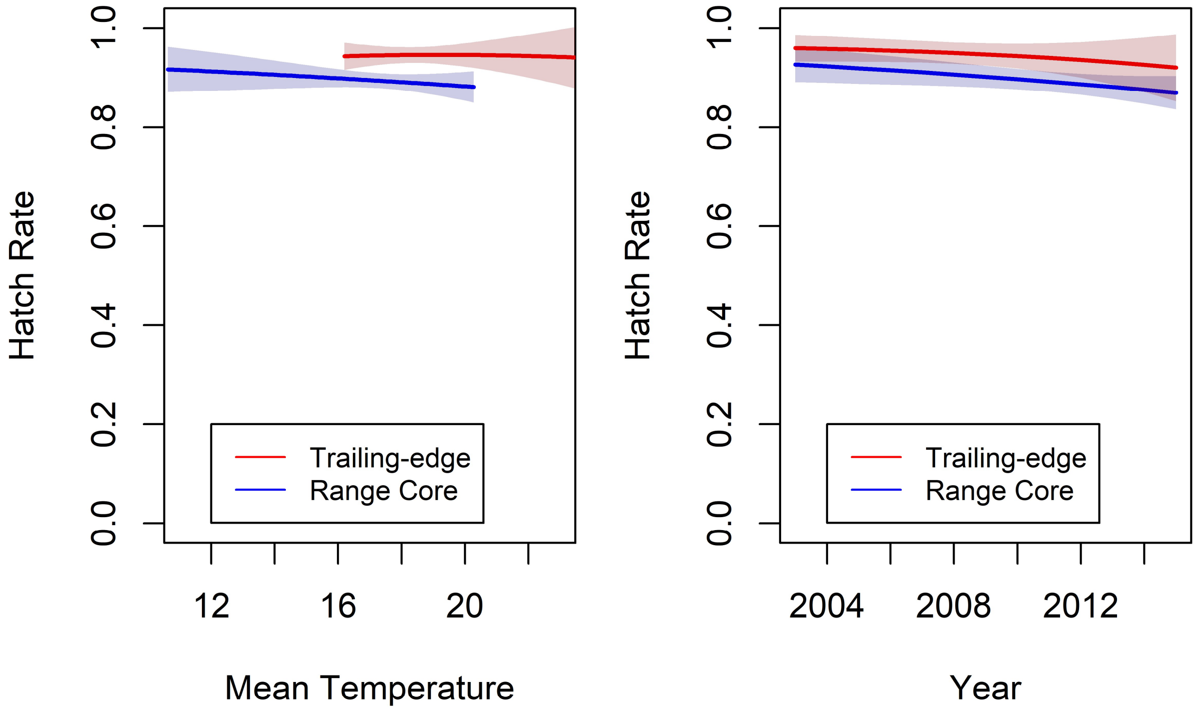

Figure 5.11. Hatch rates of black-throated blue warbler eggs averaged across all years at the core and trailing-edge of the species breeding range. Hatch rates of black-throated blue warblers at average regional temperatures over the entire study period in at the core and trailing-edge of the species breeding range.

CHAPTER 6

CONCLUSION

Efforts to understand the importance of abiotic factors and biotic interactions in limiting species distributions is older than the field of ecology itself. The urgency in understanding the forces shaping species distributions is growing as the Earth's climate changes and causes species' ranges to shift. Many hypotheses predict that biotic interactions are more important at low latitudes than abiotic factors and that this relationship reverses at high latitudes. However, there is growing evidence that abiotic factors limit species at their low-latitude range margin, leading to increased extinction risk as the climate continues to change. Populations at the trailing-edge of a shifting distribution are predicted to be at high risk of climate-induced extinction. Conservation of these populations is essential because they often harbor high genetic diversity and make up a large portion of regional biodiversity.

I identified potential hotspots of avian trailing-edge population diversity using a global database of bird distributions. I focused on one of the identified hotspots, the southern Appalachian Mountains of the eastern United States. Consistent with the definition of trailing-edge populations, I found that a large proportion of bird species in this region were declining. However, trend data were sparse as few Breeding Bird Survey routes occurred at high elevations, indicating that confirmation of the potential trailing-edge hotspots will require more focused long-term research. Nonetheless, this represents a first attempt at describing the global distribution of trailing-edge populations, and the distribution maps should benefit conservation efforts aimed at protecting these important populations

I addressed multiple hypotheses on the effects of biotic interactions such as Allee effects and pathogens on species distributions. In Chapter 3, I tested the Allee effect range limitation hypothesis using a playback experiment and found no evidence of Allee effects, socially-mediated or otherwise. Rather, I found support for the hypothesis that abiotic factors limit trailing-edge population growth rates of a cool-adapted songbird. This experiment, paired with observational data like point surveys, allowed me to link temperature and precipitation to population growth rates. This work aligns with the recommendation of Hampe and Petit (2005) regarding the need to assess the performance of trailing-edge populations and to understand the factors influencing spatial and temporal population dynamics.

Although Chapter 3 indicated that climate can influence population growth rates, the underlying mechanism were not revealed. It has been hypothesized that host-pathogen dynamics can be an important biotic interaction that can influence species range limits. Using hemoparasite infection data, point count surveys, and host-pathogen occupancy models, I tested the pathogen range limitation hypothesis. Cool-adapted songbirds avoided areas of high infection risk, whereas species at the core of their range did not. The possibility that pathogens influence range boundaries has important implications for understanding the mechanisms influencing climate-driven range shifts and adds a new complication to wildlife conservation in the face of climate change. Specifically, conservation efforts may need to account for the spread of vectors into cooler climates that currently serve as a refuge for trailing-edge populations, which are often genetically distinct and sensitive to environmental change. However, because this result only pertained to two species, more detailed and comprehensive investigation into the pathogen dynamics of this ecological community is required.

In Chapter 5, I used a reciprocal translocation experiment to test the hypothesis that abiotic factors like temperature and relative humidity affect hatch rates, nestling growth rates, and female behavior of a cool-adapted songbird. Egg hatch rates of the cool-adapted species were reduced when moved to warmer conditions at low elevations. To compliment this experiment, I compared hatch rates between the core and trailing-edge of the cool-adapted species breeding range and found no effect of temperature on hatch rates. However, I did find a decline in hatch rates over the entire study period, indicating that an unobserved factor is causing a long-term decline in hatch rates. Results from the reciprocal translocation experiment suggest that eggs and behavior are adapted to local climate conditions, and species at their physiological limit may be negatively affected by encroaching climate conditions. This poses a challenge to conservation efforts because phenotypic plasticity may not be sufficient for coping with novel conditions.

While this dissertation has advanced knowledge about the factors influencing trailing-edge populations, there is a great deal left to discover. Many hypotheses remain regarding competition, predation, and other biotic interactions, all of which can limit trailing-edge populations. Chief among these is the need to understand how climate change influences arthropod prey abundance, distribution, and phenology – all of which can impact the dynamics of trailing-edge populations of avian insectivores. Additionally, many more hypotheses pertaining to abiotic factors remain, particularly regarding influence of temperature and precipitation on reproductive output, survival, emigration, and immigration. Finally, detailed demographic studies of these phenomena are needed at other diversity hotspots where trailing-edge populations have received far less attention.

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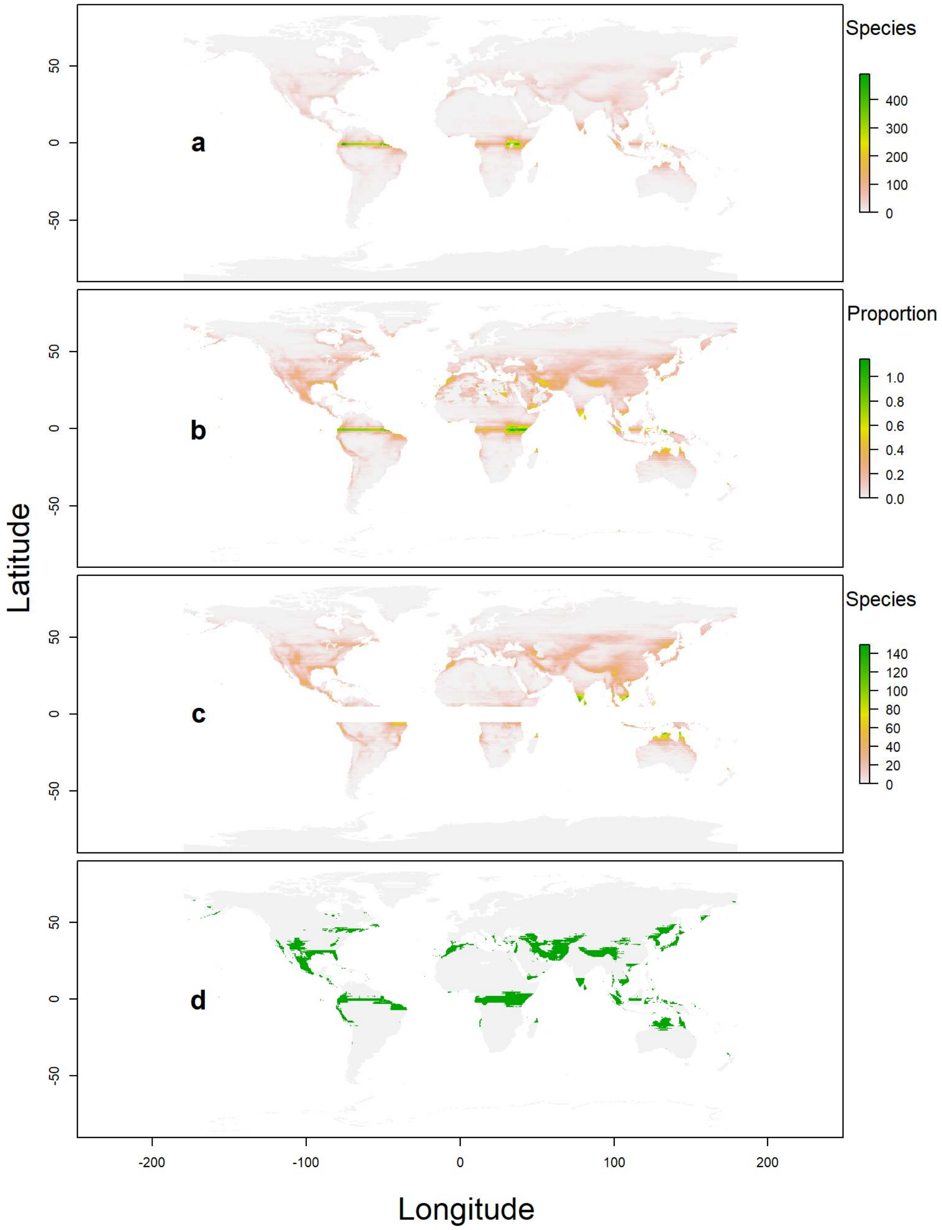
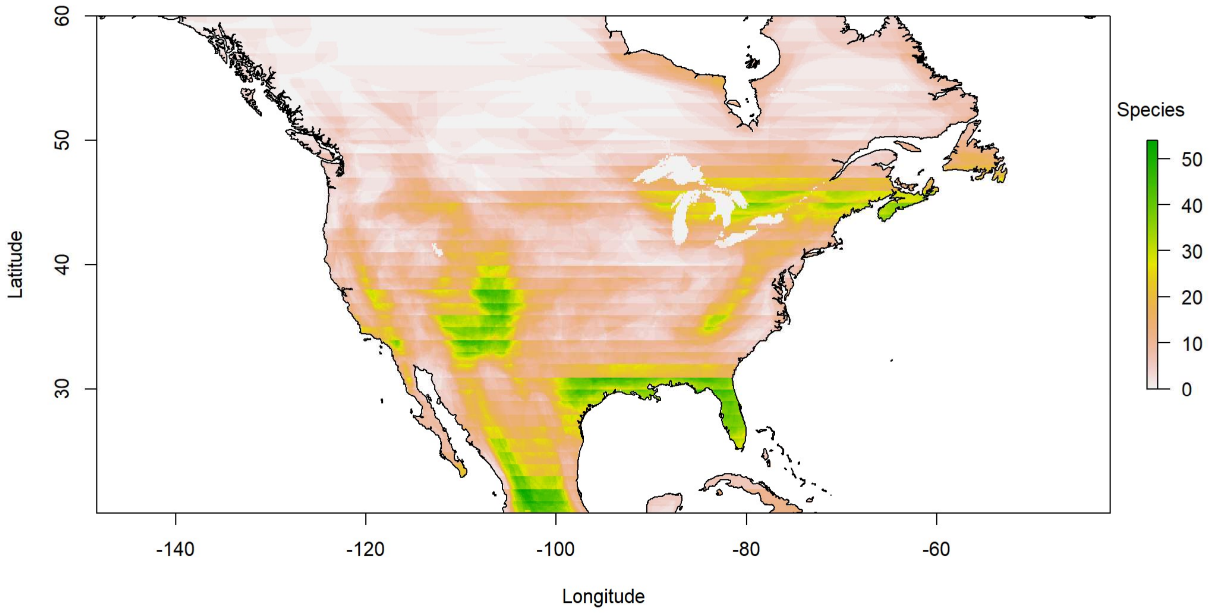
APPENDICES

Appendix A: Global diversity and distribution of potential trailing-edge populations (10%).



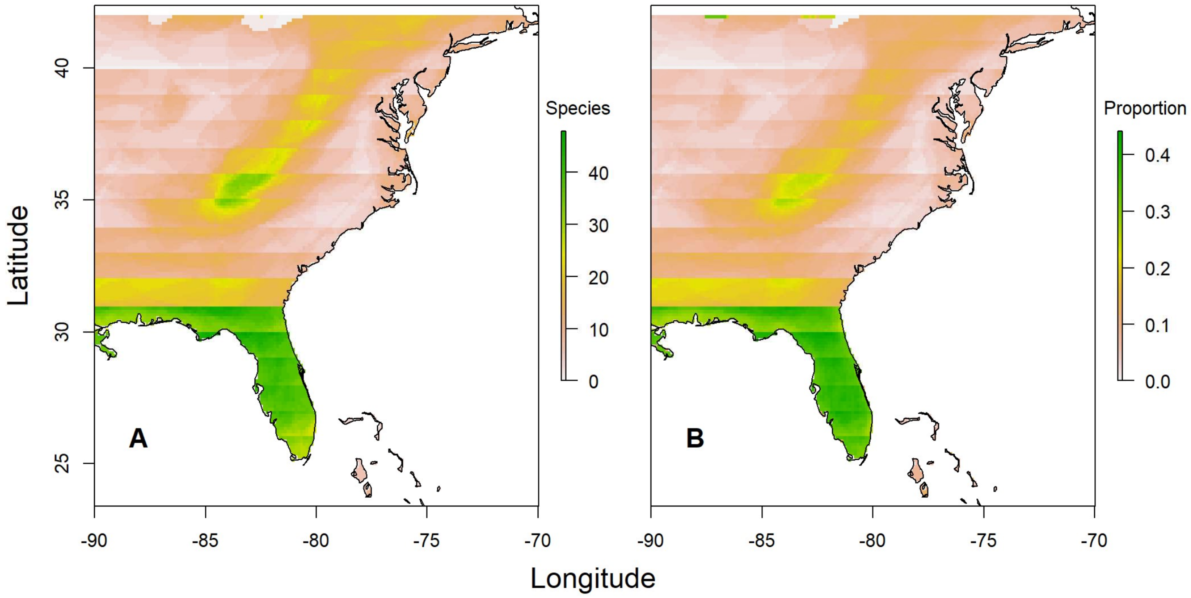
Global diversity and distribution of potential trailing-edge populations of bird species represented by(a) species richness and (b) proportional richness of local avifauna. Regions within five degrees of latitude north or south of the equator are removed in panel (c). Panel (d) indicates regions where ≥15% of the local avifauna is comprised of potential trailing-edge populations, excluding areas with fewer than 10 species. Low-latitude range segments were defined as the lower 10th percentile of each species' range.

Appendix B: Distribution of potential avian trailing-edge populations in North America (10%).



Distribution of potential avian trailing-edge populations in North America.Colors indicate the number of species with low-latitude range segments at each terrestrial location. Low-latitude range segments were defined as the lower 10th percentile of each species' range.

Appendix C: Diversity and distribution of trailing-edge populations in the Southeastern United States (10%).



Diversity and distribution of trailing-edge populations in the Southeastern United States, represented by (a) species richness and (b) the proportion of the local avifauna comprised of potential trailing-edge populations. Both figures used the lower 10th percentile to designate low-latitude range segments for each species.

Appendix D: Breeding Bird Survey trend estimates.

Breeding Bird Survey trend estimates, 95% credible intervals, and regional credibility measure codes (*G – representing the highest quality data, described as having at least 14 samples over the entire study period; Y – Data with a deficiency, such as low abundance estimates, fewer than 14 routes sampled, or imprecise results; R – Data where regional abundance estimates are very low, fewer than 5 routes sampled, or results are extremely imprecise*) for bird trailing-edge populations in the southern Appalachian Mountains. For all species a trend estimate is available for the entire Appalachian Mountain range. For some species, state-level trend estimates are also available (Sauer *et al.* 2015).

Species	Region	1966-2015 Trend Est. (CI)	2005-2015 Trend Est. (CI)	Regional Credibility Measure
sharp-shinned hawk	Appalachian Mtns	1.51 (0.40, 2.44)	1.94 (-0.92, 4.66)	R
(*Accipter striatus*)	Alabama	1.22 (-1.25, 3.46)	1.82 (-3.76, 9.15)	R
	Georgia	2.24 (-2.43, 7.25)	2.75 (-10.60, 14.61)	R
	North Carolina	-0.84 (-5.15, 2.46)	0.43 (-7.13, 12.27)	R
	Tennessee	2.80 (0.14, 5.62)	4.06 (-5.16, 10.78)	R
	Virginia	1.22 (-2.31, 4.53)	0.98 (-12.01, 9.48)	R
	West Virginia	1.29 (-1.88, 4.05)	1.49 (-9.59, 12.98)	R
ruffed grouse	Appalachian Mtns	-1.55 (-3.09, -0.11)	-0.83 (-4.91, 3.05)	R
(*Bonasa umbellus*)	Virginia	-5.55 (-10.61, -0.62)	-5.43 (-19.84, 9.88)	R
	West Virginia	-3.34 (-6.69, -0.27)	-3.55 (-14.82, 5.25)	R
yellow-bellied sapsucker	Appalachian Mtns	5.81 (4.30, 7.20)	1.02 (-1.92, 3.91)	Y
(*Sphyrapicus varius*)	West Virginia	3.97 (-4.91, 18.64)	1.30 (-28.75, 19.80)	R
alder flycatcher	Appalachian Mtns	2.77 (1.62, 3.99)	-0.31 (-3.46, 2.65)	Y
(*Empidonax alnorum*)	West Virginia	0.09 (-4.72, 4.54)	0.08 (-9.54, 13.56)	R
least flycatcher	Appalachian Mtns	-2.46 (-3.04, -1.93)	-2.49 (-4.15, -0.85)	G
(*Empidonax minimus*)	North Carolina	-4.11 (-6.62, -1.55)	-4.13 (-8.06, -0.28)	Y
	Tennessee	-1.13 (-5.09, 2.83)	-1.35 (-10.14, 5.11)	R
	Virginia	-8.56 (-14.30, -3.14)	-10.12 (-26.79, 5.05)	R
	West Virginia	-0.41 (-1.64, 0.93)	0.14 (-2.62, 4.31)	Y
blue-headed vireo	Appalachian Mtns	3.16 (2.15, 4.09)	1.42 (-0.32, 3.20)	Y
(*Vireo solitarius*)	Alabama	6.37 (1.93, 10.92)	6.56 (-0.48, 14.11)	R
	Georgia	7.11 (4.06, 10.45)	6.69 (-0.96, 12.39)	R
	North Carolina	2.29 (0.42, 4.02)	2.47 (-0.27, 5.73)	Y
	Tennessee	0.09 (-2.11, 2.28)	0.03 (-4.49, 4.18)	Y
	Virginia	5.51 (3.38,7.56)	4.74 (-1.86, 9.03)	Y
	West Virginia	4.11 (2.44, 5.93)	4.77 (0.61, 9.37)	Y
common raven	Appalachian Mtns	4.48 (3.37, 5.45)	5.59 (3.11, 7.97)	Y
(*Corvus corax*)	North Carolina	4.00 (0.25, 7.98)	6.44 (-1.49, 16.88)	R
	Virginia	0.56 (-1.37, 2.47)	2.23 (-3.11, 9.05)	Y
	West Virginia	6.21 (4.37, 8.10)	5.72 (1.03, 10.48)	Y
black-capped chickadee	Appalachian Mtns	0.65 (0.19, 1.11)	-0.97 (-2.39, 0.36)	G

(*Poecile atricapillus*)	Virginia	-0.03 (-2.39, 2.41)	-0.23 (-7.22, 6.41)	Y
	West Virginia	0.41 (-0.70, 1.49)	0.93 (-2.06, 4.32)	G
red-breasted nuthatch	Appalachian Mtns	4.10 (2.71, 5.47)	3.89 (-0.33, 8.03)	R
(*Sitta canadensis*)	West Virginia	5.40 (1.63, 9.54)	6.02 (0.65, 17.14)	R
brown creeper	Appalachian Mtns	0.47 (-0.90, 1.81)	0.93 (-2.72, 4.05)	Y
(*Certhia Americana*)	West Virginia	0.28 (-5.52, 6.51)	-0.62 (-13.22, 7.72)	R
winter wren	Appalachian Mtns	2.74 (1.16, 4.30)	-3.50 (-7.83, 0.19)	Y
(*Troglodytes hiemalis*)	West Virginia	1.52 (-0.84, 3.61)	1.32 (-5.95, 6.67)	R
golden-crowned kinglet	Appalachian Mtns	1.13 (-0.83, 3.12)	0.36 (-5.99, 5.42)	R
(*Regulus satrapa*)	West Virginia	1.67 (-1.28, 4.73)	1.65 (-4.89, 8.17)	R
veery	Appalachian Mtns	-0.32 (-0.68, 0.04)	0.34 (-0.54, 1.36)	G
(*Catharus fuscescens*)	North Carolina	0.89 (-1.75, 3.52)	0.88 (-2.84, 4.26)	Y
	Virginia	1.34 (-3.15, 7.00)	1.87 (-4.23, 10.48)	R
	West Virginia	3.81 2.60, 5.10)	3.90 (0.58, 7.46)	Y
hermit thrush	Appalachian Mtns	2.31 (1.28, 3.39)	0.19 (-2.44, 2.85)	Y
(*Catharus guttatus*)	West Virginia	4.62 (1.74, 7.69)	5.50 (-1.09, 14.88)	R
Swainson's thrush	Appalachian Mtns	2.04 (-0.63, 4.94)	1.27 (-7.15, 6.98)	R
(*Catharus ustulatus*)				
cedar waxwing	Appalachian Mtns	1.64 (1.00, 2.24)	1.31 (-0.49, 3.13)	G
(*Bombcilla cedrorum*)	Alabama	6.93 (1.24, 13.65)	-0.16 (-13.59, 15.47)	R
	Georgia	6.80 (1.67, 12.81)	-5.58 (-17.76, 10.58)	R
	North Carolina	2.04 (-0.10, 4.23)	-3.00 (-7.71, 1.48)	Y
	Tennessee	5.13 (2.67, 7.89)	-7.31 (-13.14, -1.25)	Y
	Virginia	3.78 (1.47, 6.20)	-0.89 (-6.70, 5.26)	Y
	West Virginia	2.6 (1.36, 3.93)	1.29 (-2.47, 5.10)	G
golden-winged warbler	Appalachian Mtns	-8.56 (-9.77, -7.29)	-7.65 (-10.95, -3.05)	Y
(*Vermivora Chrysoptera*)	North Carolina	-11.48 (-16.23, -6.62)	-11.68 (-18.50, -4.87)	Y
	Tennessee	-8.43 (-12.10, -5.37)	-7.99 (-18.21, 2.96)	Y
	Virginia	-8.67 (-12.11, -5.12)	-8.61 (-15.47, -1.89)	R
	West Virginia	-8.59 (-10.34, -6.53)	-7.84 (-12.90, 0.64)	Y
chestnut-sided warbler	Appalachian Mtns	0.00 (-0.68, 0.58)	-0.63 (-1.89, 0.55)	G
(*Setophaga pensylvanica*)	North Carolina	-3.63 (-5.27, -2.02)	-4.16 (-8.18, -1.28)	G
	Tennessee	-4.86 (-7.30, -2.55)	-5.35 (-12.79, -1.16)	Y
	Virginia	-4.27 (-7.02, -1.20)	-3.22 (-9.24, 11.36)	Y
	West Virginia	1.79 (0.41, 3.19)	-0.06 (-4.25, 3.83)	Y
magnolia warbler	Appalachian Mtns	2.39 (1.63, 3.15)	2.65 (0.26, 4.62)	Y
(*Setophaga magnolia*)	West Virginia	6.22 (4.06, 8.13)	5.41 (-2.76, 9.16)	Y
black-throated blue warbler	Appalachian Mtns	0.22 (-0.93, 1.22)	-0.25 (-2.09, 1.46)	Y
(*Setophaga caerulescens*)	North Carolina	-1.12 (-2.99, 0.81)	-0.69 (-3.39, 3.03)	Y
	Virginia	-3.45 (-6.71, -0.01)	-2.70 (-8.62, 9.69)	Y
	West Virginia	1.70 (0.10, 3.16)	1.46 (-2.44, 4.37)	Y
blackburnian warbler	Appalachian Mtns	-0.16 (-1.31, 0.84)	-3.01 (-5.39, -0.68)	Y

(*Setophaga fusca*)	North Carolina	-0.47 (-4.69, 3.90)	-0.74 (-6.98, 5.79)	Y
	Virginia	-7.72 (-10.37, -4.76)	-7.95 (-13.41, -2.47)	Y
	West Virginia	1.25 (-1.13, 3.59)	1.44 (-2.47, 6.28)	R
yellow-rumped warbler (*Setophaga coronate*)	Appalachian Mtns	2.13 (0.23, 4.00)	-5.86 (-10.50, -1.19)	Y
black-throated green warbler	Appalachian Mtns	1.19 (0.53, 1.82)	0.3 (-1.10, 1.71)	G
(*Setophaga virens*)	Alabama	-1.10 (-3.57, 1.20)	-1.89 (-7.69, 2.40)	Y
	Georgia	4.10 (1.30, 7.31)	2.11 (-6.49, 7.58)	Y
	North Carolina	1.54 (-0.45, 3.45)	1.18 (-1.94, 4.22)	Y
	Tennessee	-1.86 (-3.41, -0.40)	-1.85 (-6.13, 2.22)	Y
	Virginia	2.13 (-0.23, 4.79)	1.69 (-4.29, 7.98)	Y
	West Virginia	2.70 (1.27, 4.00)	2.91 (-0.98, 6.74)	Y
northern waterthrush	Appalachian Mtns	-1.52 (-3.27, 0.28)	-0.62 (-4.97, 4.94)	R
(*Parkesia noveboracensis*)	West Virginia	-4.4 (-11.27, 1.93)	-6.25 (-28.52, 8.07)	R
mourning warbler	Appalachian Mtns	-0.38 (-2.58, 1.21)	0.13 (-3.76, 3.63)	Y
(*Geothlypis philadelphia*)	West Virginia	-3.46 (-7.15, -0.01)	-4.48 (-15.81, 6.39)	Y
Canada warbler	Appalachian Mtns	-1.00 (-2.32, 0.16)	-0.19 (-2.20, 1.85)	Y
(*Cardellina canadensis*)	North Carolina	-1.6 (-4.86, 1.73)	-1.56 (-5.74, 2.70)	Y
	West Virginia	2.81 (0.33, 5.15)	2.91 (-2.53, 8.59)	Y
rose-breasted grosbeak	Appalachian Mtns	-0.82 (-1.35, -0.28)	-2.64 (-4.37, -1.03)	G
(*Pheucticus ludovicianus*)	North Carolina	-3.39 (-6.05, -0.66)	-2.27 (-7.28, 8.52)	Y
	Virginia	-1.85 (-4.38, 0.38)	-2.03 (-9.29, 3.11)	Y
	West Virginia	1.72 (0.32, 3.41)	1.30 (-3.13, 5.76)	Y
dark-eyed junco	Appalachian Mtns	1.36 (0.62, 2.06)	1.36 (-0.27, 2.93)	G
(*Junco hyemalis*)	North Carolina	0.94 (-1.19, 3.11)	0.69 (-2.38, 3.35)	Y
	Virginia	2.54 (-0.30, 5.64)	2.62 (-3.18, 10.20)	Y
	West Virginia	3.15 (1.54, 4.62)	3.01 (-0.97, 6.21)	Y
purple finch	Appalachian Mtns	0.02 (-0.73, 0.74)	-1.03 (-3.37, 1.13)	Y
(*Haemorhous purpureus*)	West Virginia	0.96 (-4.05, 7.11)	0.55 (-13.61, 17.37)	R

Appendix E: Global model for chapter 3

JAGS code for the dynamic N-mixture model including an interaction of climate and treatment effects on Canada warbler density and growth rate in the southern Appalachian Mountains of the United States.

```
model {

  ## Coefficients of model for initial abundance
  beta0 ~ dnorm(0, 1)
  beta1 ~ dnorm(0, 0.1)
  ## Coefficients of model for detection probability
  alpha0 ~ dnorm(0, 0.5)
  alpha1 ~ dnorm(0, 0.1)
  alpha2 ~ dnorm(0, 0.1)
  alpha3 ~ dnorm(0, 0.1)
  alpha4 ~ dnorm(0, 0.1)
  ## Coefficients of model for growth rate
  lambda0 ~ dnorm(0, 1)
  lambda1 ~ dnorm(0, 0.1)
  lambda2 ~ dnorm(0, 0.1)
  lambda3 ~ dnorm(0, 0.1)
  lambda4 ~ dnorm(0, 0.1)
  lambda5 ~ dnorm(0, 0.1)
  lambda6 ~ dnorm(0, 0.1)
  for(i in 1:nSites) {
   ## Model for year 1
   log(psi[i,1]) <- beta0 + beta1*climate[i]  ## psi is the expected value of N
   D[i,1] <- psi[i,1] / plotArea             ## D is the expected value of density
   DS[i,1] <- (D[i,1]-0.15)/0.25             ## Density (roughly) standardized
   N[i,1] ~ dpois(psi[i,1])                  ## Realized value of abundance
   ld.N.site.year[i,1] <- logdensity.pois(N[i,1], psi[i,1]) ## for WAIC
   for(j in 1:4) {
    ## Detection Probability
    logit(p[i,j,1]) <- alpha0 + alpha1*wind[i,j,1] + alpha2*noise[i,j,1] +
        alpha3*date[i,j,1] + alpha4*time[i,j,1]
    ## Count Data
    y[i,j,1] ~ dbin(p[i,j,1], N[i,1])
    ## Residuals
    resid[i,j,1] <- y[i,j,1]-N[i,1]*p[i,j,1]
    ## Log-densities to be used for WAIC
    ld.y.site.year.visit[i,j,1] <- logdensity.bin(y[i,j,1], p[i,j,1], N[i,1])
    ld.yN.site.year.visit[i,j,1] <- ld.y.site.year.visit[i,j,1]+ld.N.site.year[i,1]
```

```
    }
    ld.yN.site.year[i,1] <- ld.N.site.year[i,1]+sum(ld.y.site.year.visit[i,,1])
    resid.site.yr[i,1] <- mean(resid[i,1:4,1]) ## Average residuals at each site

    ## Model for years 2, 3, 4
    for(t in 2:T) {
      ## Growth Rate
      log(lambda[i,t-1]) <- lambda0 + lambda1*climate[i] + lambda2*treatment[i,1,t] +
         lambda3*DS[i,t-1] + lambda4*DS[i,t-1]^2 + lambda5*DS[i,t-1]*climate[i] +
         lambda6*DS[i,t-1]^2*climate[i]
      psi[i,t] <- psi[i,t-1]*lambda[i,t-1]
      D[i,t] <- psi[i,t] / plotArea
      DS[i,t] <- (D[i,t]-0.15)/0.25
      N[i,t] ~ dpois(psi[i,t])
      ld.N.site.year[i,t] <- logdensity.pois(N[i,t], psi[i,t])
      for(j in 1:nIntervals[t]) {
        logit(p[i,j,t]) <- alpha0 + alpha1*wind[i,j,t] + alpha2*noise[i,j,t] +
             alpha3*date[i,j,t] + alpha4*time[i,j,t]
        y[i,j,t] ~ dbin(p[i,j,t], N[i,t])
        resid[i,j,t] <- y[i,j,t]-N[i,t]*p[i,j,t]
        ld.y.site.year.visit[i,j,t] <- logdensity.bin(y[i,j,t], p[i,j,t], N[i,t])
        ld.yN.site.year.visit[i,j,t] <- ld.y.site.year.visit[i,j,t]+ld.N.site.year[i,t]
      }
      ld.yN.site.year[i,t] <- ld.N.site.year[i,t]+sum(ld.y.site.year.visit[i,,t])
      resid.site.yr[i,t] <- mean(resid[i,1:4,t])
    }
    ld.yN.site[i] <- sum(ld.yN.site.year[i,])
  }
  for(t in 1:T) {
    Ntotal[t] <- sum(N[,t])
  }
}
```

Appendix F: An assessment of spatial autocorrelation in the residuals using Moran's I.

Moran's I

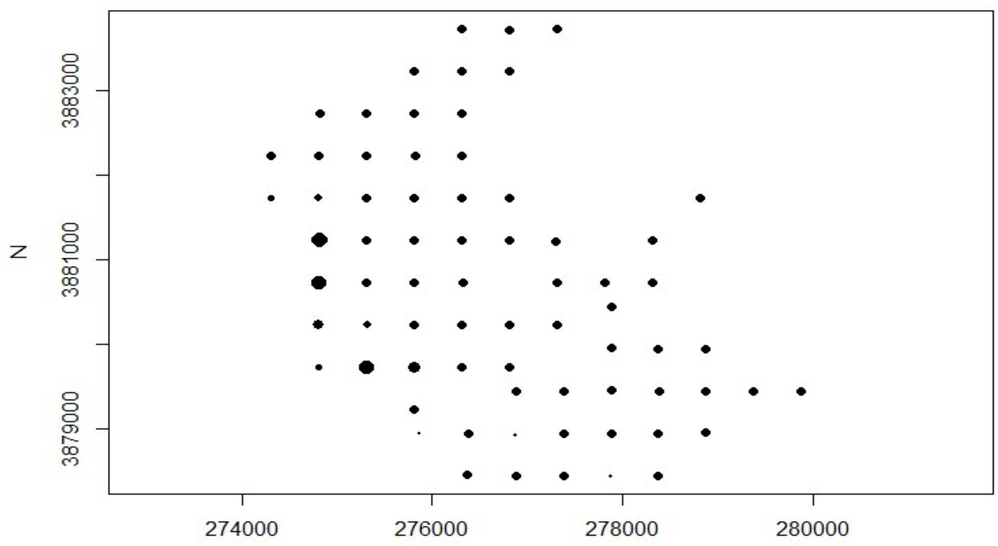
```
library(spdep)

## Loading required package: sp

## Loading required package: spData

## To access larger datasets in this package, install the spDataLarge
## package with: `install.packages('spDataLarge',
## repos='https://nowosad.github.io/drat/', type='source')`

## Loading required package: sf

## Linking to GEOS 3.8.0, GDAL 3.0.4, PROJ 6.3.1

cawa.resids <- read.csv("cawa-pb-resid.csv", row.names=1)
load("points.R")
## Coordinates (in the same site-order as resids)
coords <- as.matrix(all.points.xy)
dist.mat <- as.matrix(dist(coords))    # Distance matrix
weights <- ifelse(dist.mat)

1000, 0, 1) # Neighbors defined as sites within 1 km
diag(weights) <- 0                     # Weight=1 for neighbors, 0 otherwise
weight.list <- mat2listw(weights)      # create neighbor list for spdep
Mi.1 <- moran.test(cawa.resids[,1], weight.list) #test of year 1 resids
Mi.2 <- moran.test(cawa.resids[,2], weight.list) #test of year 2 resids
Mi.3 <- moran.test(cawa.resids[,3], weight.list) #test of year 3 resids
Mi.4 <- moran.test(cawa.resids[,4], weight.list) #test of year 4 resids
```

Table 1. Moran's I for each year shows no indication of spatial autocorrelation in the model residuals.

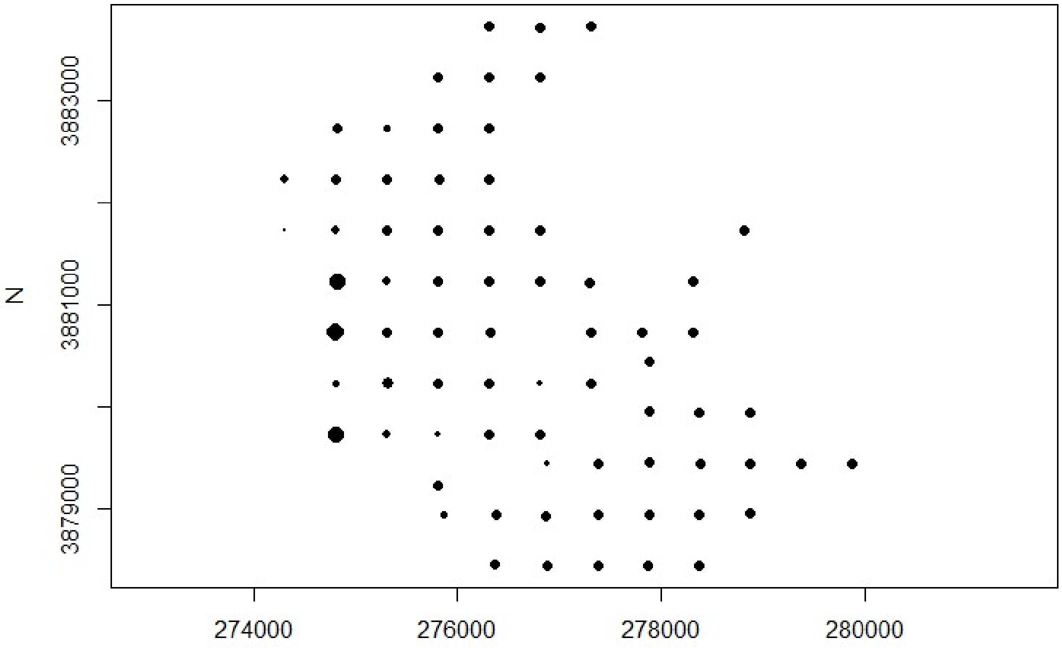
Year	Moran's I	p-value
1	-1.343	0.910
2	0.250	0.401
3	-2.349	0.991
4	-1.762	0.961

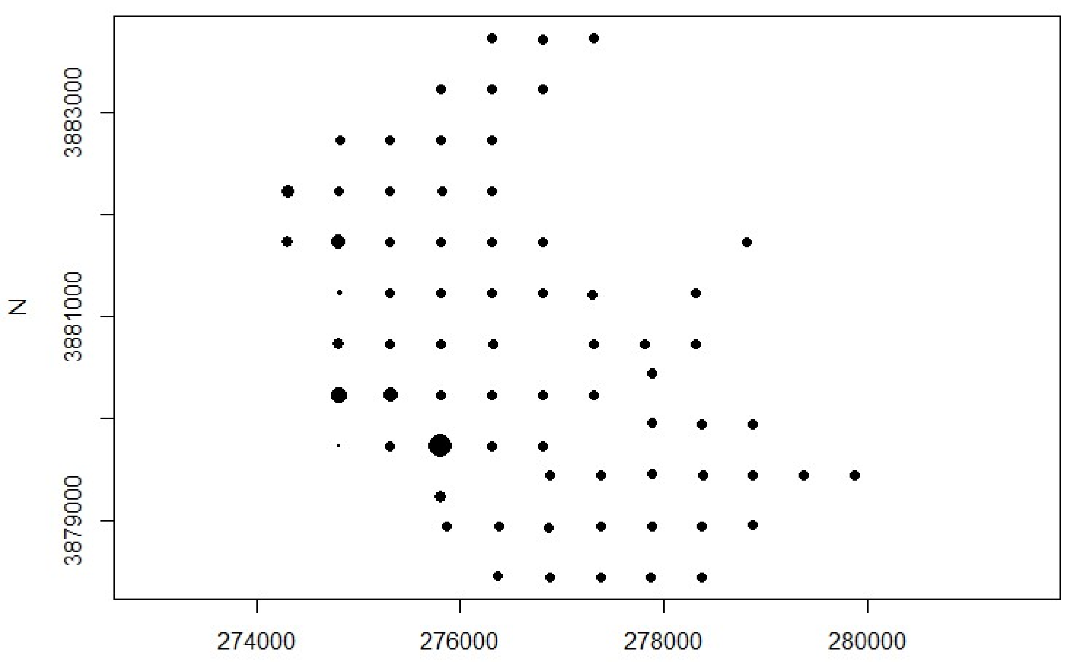
Appendix G: Model residuals at each survey point. The size of the point is proportional to the residual.

2014

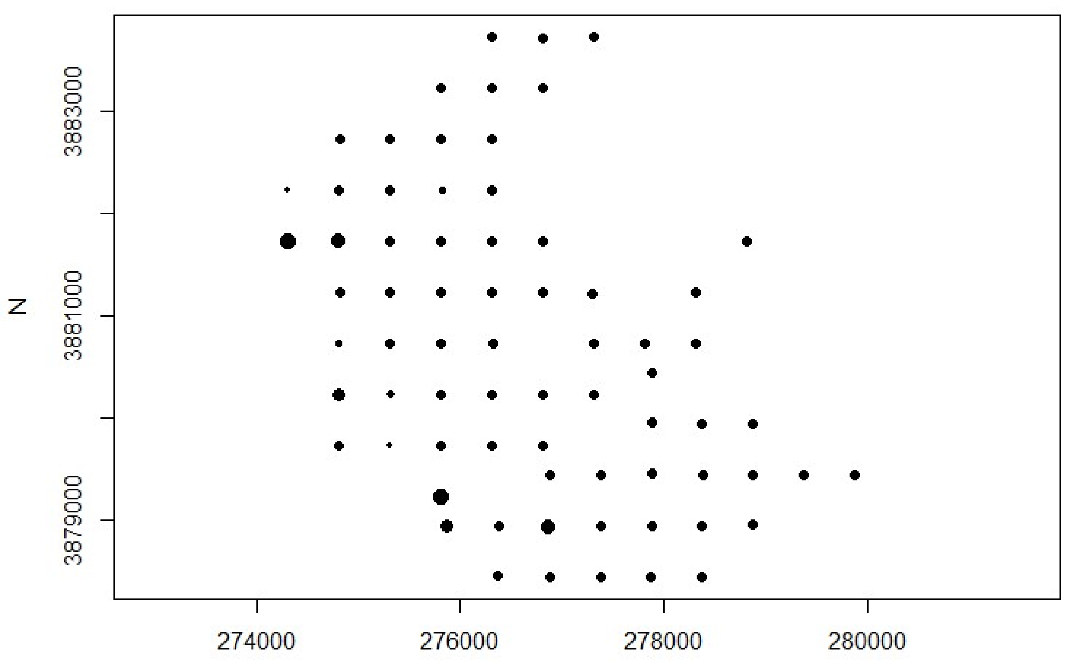


2015



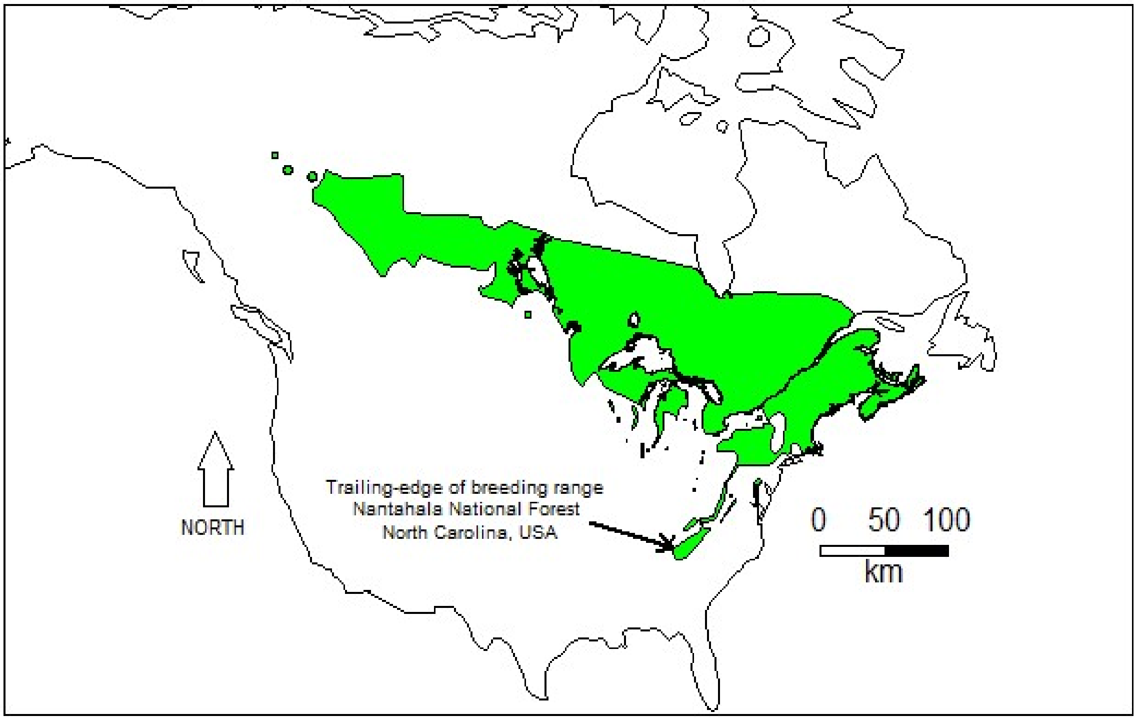

2016

N
3879000
3881000
3883000
274000
276000
278000
280000


2017

N
3879000
3881000
3883000
274000
276000
278000
280000

Appendix H: Breeding range of Canada Warbler



Appendix I: Playback units and Canada warbler

Appendix J. Haemoparasite infections in songbird species captured in the Nantahala National Forest, North Carolina, USA.

Species	Migration Strategy	*Haemoproteus*	*Leucocytozoon*	Microfilaria	Trypanosoma	Negative	Co-infection
Black-and-white warbler (*Mniotilta varia*)	Medium	0	0	0	0	20	0
Blue-headed vireo (*Vireo solitaries*)	Short	2	1	0	0	1	1
Black-throated blue warbler (*Setophaga caerulescens*)	Medium	3	0	0	0	49	0
Carolina chickadee (*Poecile carolinensis*)	Resident	0	0	0	0	6	0
Canada warbler (*Cardellina canadensis*)	Long	0	0	0	0	55	0
Gray catbird (*Dumetella carolinensis*)	Short	0	0	0	0	6	0
Hooded warbler (*Setophaga citrina*)	Medium	0	0	2	0	25	0
Louisiana waterthrush (*Parkesia motacilla*)	Long	0	0	0	0	2	0
Northern cardinal (*Cardinalis cardinalis*)	Resident	0	0	0	0	0	0
Ovenbird (*Seiurus aurocapilla*)	Medium	1	0	1	0	26	0
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	Long	1	0	0	0	1	0
Slate-colored junco (*Junco Hyemalis*)	Short	0	0	0	0	5	0
Scarlet tanager (*Piranga olivacea*)	Long	2	0	0	0	0	0
Tufted titmouse (*Baeolophus bicolor*)	Resident	0	0	0	0	2	0
Veery (*Catharus fuscescens*)	Long	0	0	0	0	40	0
Worm-eating warbler (*Helmitheros vermivorum*)	Long	1	0	0	0	3	0
Wood thrush (*Hylocichla mustelina*)	Medium	0	10	0	1	14	0

Appendix K: Transportation times for eggs in treatment groups and positive control groups.

Species	Test	df	Control time (min)	Swap time (min)	t-stat	p.value
BTBW	swap vs control	20	38.2	38.33	-0.036	0.971
HOWA	swap vs control	9	47.33	44.75	0.262	0.799
Both	Both	31	38.27	45.45	-1.864	0.072