LONG-TERM DEMOGRAPHIC DECLINES IN BLACK-THROATED BLUE WARBLERS (SETOPHAGA CAERULESCENS) FROM ACROSS THE BREEDING RANGE

by

WILLIAM BAGLEY LEWIS

(Under the Direction of Robert J. Cooper)

ABSTRACT

Climate change is leading to range shifts in many species, including range contractions at the low-latitude and low-elevation trailing edges. Little is known about the proximate mechanisms through which climate change causes spatial variation in demographic rates, population declines, and range contractions. I assessed the proximate mechanisms underlying trailing edge range contractions by analyzing long-term trends in an 18-year dataset on the demography of black-throated blue warblers (*Setophaga caerulescens*) breeding across an elevational climate gradient at the trailing edge of the range in North Carolina and the core of the range in New Hampshire. Populations remained stable at the range core; however, warming temperatures were correlated with population declines at the trailing edge. Trailing edge declines started at the lowest, warmest breeding elevations and gradually moved upslope. The demographic drivers of decline varied by study plot. Productivity, nestling mass, and late-season food abundance all declined at both the trailing edge and the range core; however, food abundance was negatively affected by warming temperatures and matched the elevational pattern of warbler population decline. Furthermore, food abundance was an important driver of population dynamics in areas with observed or projected population declines. I also deployed geolocators to determine migratory connectivity and the potential effect of non-breeding threats on breeding declines. Trailing edge populations overwintered in a restricted area of the Caribbean, which has experienced significant habitat loss over the past 2 decades. The results of my dissertation suggest that warming temperatures on the breeding grounds are a primary driver of trailing edge population declines, potentially exacerbated by overwintering habitat loss. The mechanistic pathways linking warming temperature and population declines, however, appear to be complex and involving multiple interacting pathways. Population declines at the trailing edge do not seem to be directly caused by declining productivity. Instead, declining food abundance, and its interactions with nestling mass, is a likely mechanism through which climate change is affecting trailing edge populations.

INDEX WORDS: Climate change, Demographics, Population dynamics, Range shifts, Trailing edge, Black-throated blue warbler, Migratory connectivity

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by

WILLIAM BAGLEY LEWIS

BA, Albion College, 2008

MS, University of Southern Mississippi, 2015

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WILLIAM BAGLEY LEWIS

Major Professor:	Robert J. Cooper
Committee:	Richard B. Chandler
	Jeff Hepinstall-Cymerman
	T. Scott Sillett

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
August 2021

DEDICATION

I dedicate this dissertation to my son, Kai Watkins Lewis. I hope that when you grow up you will love birds as much as I do.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Anthropogenic climate change is one of the largest environmental problems facing ecosystems worldwide. Atmospheric carbon dioxide levels have steadily increased since the industrial revolution, leading to a 0.85°C increase in global temperatures since 1880 (IPCC 2014, Melillo et al. 2014). Global temperatures are expected to increase 0.3-0.7°C by 2035, and up to 4.8°C by 2100 if greenhouse gas emissions continue to increase (IPCC 2014). Climate change has led to pronounced changes in natural ecosystems, including morphological and phenological shifts (Visser et al. 1998, Parmesan & Yohe 2003, Guerin et al. 2012, Radchuck et al. 2019), modification of life history traits (Musolin 2007, Isaac 2009, Clark et al. 2021), expanding spread of disease (Harvell et al. 2002, Rohr & Raffel 2010, Garamszegi 2011), novel biotic interactions (Montoya & Raefelli 2010, Blois et al. 2013) and even extinctions (Thomas et al. 2006); however, geographic range shifts are one of the most frequently documented responses to climate change (e.g., Parmesan et al. 1999, Tingley et al. 2009, Chen et al. 2011). Though species have shown variable responses in the direction and magnitude of range shifts (Tingley et al. 2012, Vanderwal et al. 2013), the general pattern is for ranges shifting towards higher latitudes and higher elevations (Hickling et al. 2006, Chen et al. 2011, Auer & King 2014, Rushing et al. 2020). Range shifts are frequently associated with expansion at the cool, leading edge of the range (Parmesan et al. 1999, Hickling et al. 2006, Parmesan 2006, Chen et al. 2011), but also with trailing edge range contraction at low latitudes and elevations (Moritz et al. 2008, Coristine & Kerr 2015, Rushing et al. 2020, Taheri et al. 2020).

Climate change causes range shifts by geographically shifting the factors which set range margins (Martínez-Meyer et al. 2004, Tingley et al. 2009, Wiens et al. 2009). Historically, range margins were hypothesized to be set by abiotic factors at the cool edge and biotic factors at the warm edge (e.g., MacArthur 1972, Kaufman 1995); however, recent tests of this hypothesis indicate that range limits at both edges can be set by abiotic and biotic factors (Wethey 2002, Cahill et al. 2014, Coristine & Kerr 2015, Merker & Chandler 2021). Geographic ranges can be viewed as broadly representing the ecological niche of a species, with populations near the range core being near the niche center and populations at the range margins being near the abiotic and biotic limits of the species (Hutchinson 1957, Brown 1984, Holt et al. 2005, Sexton et al. 2009, Lee-Yaw et al. 2016). Climate change is therefore likely to have the greatest effect on populations near their ecological tolerance at the range margins (Anderson et al. 2009, Jiguet et al. 2010), either through direct physiological effects or indirect biological interactions (Thomas 2010, Cahill et al. 2014). In particular, the strongest negative effects of climate change are likely to occur at the trailing edge of the range, where climate change will push populations past their ecological tolerance (Deutsch et al. 2008, Cahill et al. 2014, Coristine & Kerr 2015). Trailing edge populations may be able to adapt behaviorally or physiologically to being pushed past their ecological tolerance (Davis & Shaw 2001, Chown et al. 2010, Hoffman & Sgrò 2011); however, adaptive responses will likely be insufficient to keep pace with rapid climate change (Both & Visser 2001, Radchuck et al. 2019). Whether through dispersal or extirpation, climate change is likely to cause population declines and range contractions at the trailing edge.

Despite the multitude of studies documenting range contractions at the trailing edge, relatively little is known about the proximate mechanisms through which climate change brings about trailing edge declines (Cahill et al. 2013, Desforges et al. 2021). Climate change may directly affect organisms through physiological stress; direct effects are more likely in sessile organisms, ectotherms, and life history stages with limited thermoregulatory ability, such as eggs or nestlings (Deutsch et al. 2008, Aragón et al. 2010, Huey et al. 2012, Cunningham et al. 2013). Climate change is likely to indirectly affect many organisms through biological interactions (Thomas 2010, Cahill et al. 2013). While population-level effects of climate change are likely to be multifaceted and occurring through multiple mechanistic pathways (McLean et al. 2016), many studies have cited changes in the distribution, availability, and phenology of food resources as a primary mechanism through which climate change affects populations (Both et al. 2006, van de Pol et al. 2010, Cahill et al. 2013, Desforges et al. 2021). In addition to food, climate change may also affect habitat (Martin 2007, Trape 2009), competitive interactions (Heegard & Vandvick 2004, Alexander et al. 2015), vectors of disease (Garamszegi 2011), and predator-prey dynamics (Weatherhead et al. 2010, Laws 2017). Understanding the mechanistic pathways through which climate change causes population declines and range shifts is critically important for predicting future responses to climate change (Doak & Morris 2010, Urban et al. 2016, Desforges et al. 2021).

Determining the proximate mechanisms through which climate change causes range shifts requires long-term climate and demographic data from across the range. Studies investigating the proximate mechanisms through which climate change affects natural systems frequently correlate climate to life history traits or demographic rates, and then assume that this effect carries over to population dynamics (reviewed in McLean et al. 2016). This is not a safe assumption, however, as climate-induced changes in one metric may have little effect on population growth rates if demographic compensation occurs (Newton 1998, Miller-Rushing et al. 2010, van de Pol et al. 2010). For example, Franks et al. (2017) found that warming springs were correlated with breeding asynchrony and population declines; however, they concluded that declining productivity was unlikely to be the proximate driver because it did not affect population dynamics. Several studies have mechanistically linked climate change to population fluctuations at local scales (e.g., Doak & Morris 2010, van de Pol et al. 2010, Desforges et al. 2021); however, range shifts occur when climate change creates broad-scale spatial variation in demographic rates and population dynamics (Gaston 2009, Schurr et al. 2012). Determining the drivers of trailing edge range contractions requires understanding how the mechanistic pathways between climate and population dynamics vary across species' ranges.

Birds frequently have been used to assess the effects of climate change on natural systems due to the availability of broad-scale and historical monitoring data (e.g., Parmesan & Yohe 2003, Chen et al. 2011, Şekercioğlu et al. 2012, Stephens et al. 2016). Furthermore, birds are reliable bioindicators of ecosystem health (O'Connell et al. 2000, Burger & Gochfeld 2004, Padoa-Schioppa et al. 2006). Understanding the causes of avian population declines is of critical importance, as the abundance of the North American avifauna has declined by almost 3 billion over the past 50 years (Rosenberg et al. 2019). Population declines vary by habitat and have occurred in most taxonomic groups, but some of the strongest declines have occurred in long-distance migratory birds (Robbins et al. 1989, Ballard et al. 2003, Sanderson et al. 2006, Rosenberg et al. 2019). Long-distance migrants may suffer the most pronounced effects of anthropogenic change because they are exposed to a wide range of threats between the breeding grounds, non-breeding grounds, and along their migratory journeys (Coppack & Both 2002, Webster & Marra 2005, Newton 2008, Culp et al. 2017). Climate change has been linked to population declines in some species of long-distance migrants (e.g., Both et al. 2006, Møller et al. 2008, Illán et al. 2014, Pearce-Higgins 2015), and likely exacerbates other anthropogenic threats such as land use change (Mac Nally et al. 2009, Mantyka-Pringle et al. 2012, Rosenberg et al. 2019). Furthermore, prolonged migratory journeys may constrain the ability of many species to adapt to climate change (Both et al. 2005, Rubolini et al. 2010, Cohen et al. 2015, Källander et al. 2017), particularly at the trailing edge of the breeding range (Rushing et al. 2020).

The breeding ranges of many species of long-distance migrants in eastern North America exhibit a trailing edge distribution in the southern Appalachian Mountains (Merker & Chandler 2020). Trailing edge populations are generally restricted to the high-elevation forests near the tops of the mountains, where conditions more closely resemble the climate and habitat further north in the core of the species' ranges (Merker & Chandler 2020). The Southern Appalachians provide an ideal setting for assessing the proximate mechanisms behind trailing edge declines, as low-elevation populations in this region are near both their latitudinal and elevational warm edge. Furthermore, trailing edge populations are of high conservation value, as they compose a major portion of regional biodiversity and are frequently genetically distinct from populations in other parts of the range (Hampe & Petit 2005, Grus et al. 2009, Merker & Chandler 2020). Many trailing-edge species have been declining in the Southern Appalachians while remaining relatively stable, or even increasing, further north in the core of their breeding range (Sauer et al. 2017). These declines are generally associated with abandonment of low-elevation breeding habitats and upslope range shifts (Stodola et al. 2013, Merker 2017). The pattern of decline at the trailing edge suggests that range contractions may be caused by climate change, but the mechanistic drivers of population declines are currently unclear.

I used a long-term dataset on the demography of a model species, the black-throated blue warbler (*Setophaga caerulescens,* hereafter BTBW), from across the breeding range to determine the mechanistic pathways through which climate change is causing trailing edge range contractions. BTBW are small, sexually-dimorphic songbirds, and are one of the most well-studied species in North America (Holmes et al. 2017). BTBW winter primarily in the Greater Antilles and breed primarily in the Northeastern/Northcentral United States and southern Canada, with a trailing edge distribution along the Appalachian Mountains into Georgia (Holmes et al. 2017). Since 2002, BTBW breeding demography data have been collected across a range of elevations within the trailing edge (Nantahala National Forest, NC) and the core of the range (Hubbard Brook Experimental Forest, NH). Temperatures have been increasing at both range positions (Ford et al. 2011, Townsend et al. 2016), while precipitation has become more variable at the trailing edge (Laseter et al. 2012). The paired, long-term demographic data allowed me to examine the mechanisms potentially underlying range contractions by directly comparing declining trailing-edge populations with stable range-core populations.

The dissertation consists of this introductory chapter, 4 data chapters, and a concluding chapter. In chapter 2, I document the demographic drivers of long-term population declines at the trailing edge. I use a Bayesian hierarchical model (Kéry & Schaub 2011) to estimate long-term trends in female BTBW population dynamics and demographic rates across elevations at each range position. I then project population dynamics into the future to assess population viability over the next decade. Finally, I incorporate direct effects of temperature and precipitation into the population models to determine if climate change on the breeding grounds is driving population declines.

In chapter 3, I investigate the proximate mechanisms through which climate change is causing trailing edge population declines. Proximate mechanisms must be affected by climate and have a direct effect on population dynamics (McLean et al. 2016), and in chapter 3 I determine what breeding-ground effects are the primary drivers of population dynamics across elevations at each range position. I assess the population-level effects of three potential mechanisms, per-capita productivity, average nestling mass, and average late-season food abundance. These three breeding-ground effects likely have interacting, but not completely overlapping, effects on apparent survival and recruitment (Ringsby et al. 1998, Sillett et al. 2000, Doligez et al. 2002, Nagy & Holmes 2004, Dybala et al. 2013, Hatt 2013, Townsend et al. 2016). I also assess potential source-sink dynamics (Pulliam 1988) to determine if recruitment to the low elevations is driven by productivity at the most productive habitats at the high elevations. I assess the effects of potential mechanisms on population dynamics using the hierarchical population model from chapter 2.

In chapter 4, I examine the long-term trends in the three potential mechanisms to determine which is most likely to be the mechanistic link between climate change and population declines. I investigate trends in nest survival, probability of successfully fledging broods, nestling mass, and food biomass to determine if any show the same temporal pattern of decline across range positions and elevations as have BTBW. I also incorporate temperature and precipitation into the analyses to determine the direct effect of climate change on potential mechanisms.

In chapter 5, I assess the spatial distribution of overwintering birds from each range position and determine if habitat loss on the non-breeding grounds could be exacerbating trailing edge population declines. BTBW populations, at least at the range core, can be regulated by breeding conditions (Holmes et al. 1992, Sillett et al. 2000, Rodenhouse et al. 2003); however, conditions on the non-breeding grounds and migratory routes may interact with breeding-ground threats to drive population declines (Robbins et al. 1989, Newton 2006, Ilán et al. 2014, Hewson et al. 2016). Determining the mechanisms underlying breeding-ground declines in migratory species requires understanding the threats faced by birds over the entire annual cycle (Webster et al. 2002, Webster & Marra 2005). Threats experienced during the non-breeding season are most likely to exacerbate breeding declines if individuals from declining populations overwinter in broadly different areas or migrate along different pathways from individuals in stable populations (Finch et al. 2017, Kramer et al. 2018). Archival light-level geolocators were deployed on adult BTBW at each range position to determine the migratory routes and degree of migratory connectivity between breeding and overwintering areas.

In chapter 6, I summarize and synthesize the major findings of chapters 2-5. I discuss the effects of climate change on BTBW populations at the trailing edge and range core, and which breeding-ground effects are most likely to be the proximate mechanisms through which climate change is affecting population dynamics. I also discuss the relative importance of breeding vs. overwintering conditions on trailing edge declines. Finally, I discuss conservation implications and recommendations for future research involving the long-term BTBW monitoring project.

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CHAPTER 2

DEMOGRAPHIC DRIVERS OF TRAILING EDGE RANGE CONTRACTIONS IN A MIGRATORY SONGBIRD[1]

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[1] Lewis, W.L., R.J. Cooper, R.B. Chandler, T.S. Sillett, R.W. Chitwood, K.W. Stodola, M.H. Cline, J.L. Hatt, M.T. Hallworth, S.A. Kaiser, and N.L. Rodenhouse. To be submitted to *Global Change Biology*.

Abstract

Climate change causes trailing edge range contractions by creating spatial variation in demographic rates and population dynamics. Understanding the demographic drivers of range contractions is important for predicting species' responses to climate change; however, few studies have examined the effects of climate change on demographic rates and population dynamics across species' ranges. I assessed the demographic drivers of trailing edge population declines using a long-term breeding demography dataset of the black-throated blue warbler (*Setophaga caerulescens*) collected across an elevational climate gradient at the trailing edge of the range and at the range core. I used a Bayesian hierarchical model to estimate the effect of climate change on demographic rates and population dynamics. Warming temperatures led to population declines and extirpation at the lower elevation plots at the trailing edge, suggesting that these populations are most vulnerable to climate change by being near their ecological tolerance. Populations remained stable at the range core, though warming temperatures are predicted to cause population declines over the next decade at the lowest, warmest elevation plot. Demographic drivers of decline varied by study plot, with local population declines variably associated with reduced recruitment and increasing adult emigration away from poor-quality habitats. My results suggest that emigration may be an important process through which mobile species can behaviorally respond to climate change.

Introduction

Anthropogenic climate change has caused range shifts across a wide range of taxonomic groups (Chen et al., 2011; Hickling et al., 2006; Parmesan & Yohe, 2003; Root et al., 2003). The long-term consequences of such widespread range shifts are uncertain, though predicted effects include loss of biodiversity and degradation of ecosystem function (Bellard et al., 2012; Pecl et al., 2017). Individual species show a large degree of heterogeneity in the direction and magnitude of range shifts (Tingley et al., 2012; Vanderwal et al., 2013), but most shifts have been towards higher latitudes and elevations (Chen et al., 2011; Freeman et al., 2017; Hastings et al., 2020; Hickling et al., 2006; Parmesan et al., 1999). Among species' ranges which have shifted towards cooler areas, some have expanded at the leading edge (increasing range size), some have contracted at the trailing edge (decreasing range size), and some have done both (maintaining similar range size) (Freeman et al., 2018; Coristine & Kerr, 2015; Parmesan et al., 1999; Rushing et al., 2020). Gaining a better understanding of the mechanisms driving range shifts would help elucidate the drivers of these heterogeneous responses to climate change.

Climate-induced range shifts occur at the population level through spatial variation in demographic rates (Gaston, 2009; Schurr et al., 2012; Sexton et al. 2009). Peripheral populations are nearest to the biotic and abiotic conditions setting range limits, and so are nearer to their ecological tolerance compared to populations in the range core (Brown, 1984; Holt et al., 2005; Lee-Yaw et al., 2016). Climate is an important determinant of range boundaries at both the cool and warm edges of the range, either directly (e.g., thermal stress) or indirectly through biotic interactions (e.g., competition, food) (Cahill et al., 2014; Coristine & Kerr, 2016; Cunningham et al., 2016, MacArthur 1972, Wiens 2011). Climate change causes range shifts by shifting the geographic distribution of the factors setting range limits (Cahill et al., 2014); this leads to spatial variation in demographic rates in peripheral populations, which drives local colonization and range expansion at the leading edge and local extinction and range contraction at the trailing edge (Gaston, 2009; Schurr et al., 2012).

Understanding the demographic drivers of range shifts is especially important at the trailing edge of the range. Climate change is affecting populations throughout the range, but the strongest negative effects are frequently observed at the trailing edge (Anderson et al., 2009; Jiguet et al., 2010). Trailing edge populations are forced to adapt or decline to extinction as climate change pushes past their ecological tolerance (Cahill et al., 2013; Chown et al., 2010; Coristine & Kerr, 2015). Loss of trailing edge populations is likely to decrease regional biodiversity, potentially leading to changes in ecosystem function (Hampe & Petit, 2005; Merker & Chandler, 2020). Trailing edge populations are also frequently genetically distinct from other parts of the range, so their loss may negatively affect species-wide genetic diversity (Hampe & Petit, 2005; Parisod & Joost, 2010). Predicting the effects of climate change on trailing edge population is therefore of critical importance.

Incorporating demographic estimates into predictive models will increase forecasting ability for trailing edge range contractions (Normand et al., 2014; Schurr et al., 2012, Urban et al. 2016), but few studies have examined spatial and temporal variation in demographic rates at the trailing edge. Several factors have impeded study of the demographic drivers of trailing edge range contractions. First, change in one demographic rate may have little effect on range dynamics due to demographic compensation (Aikens & Roach, 2014; Doak & Morris, 2010; Villellas et al., 2015). Studies investigating the demographic drivers of range shifts must incorporate all relevant demographic rates and establish a direct link between climate change, demographic rates, and spatial variation in population dynamics (McLean et al., 2016; Pironen et al., 2018). Second, demographic studies are often restricted to small spatial areas or short time periods (Clutton-Brock & Sheldon, 2010). Range shifts occur through spatial variation in demographic rates (Gaston, 2009; Schurr et al., 2012), necessitating demographic data from across the geographic range (e.g., trailing edge and range core) (Ehrlén & Morris, 2015; Oldfather & Ackerly, 2019; Purves, 2009). Currently, studies documenting trailing edge demographic responses to climate change have mostly focused on plants (e.g., Doak & Morris, 2010; Oldfather & Ackerly, 2019; Sheth & Angert, 2018). Demographic responses to climate change likely differ between plants and mobile animals, which can respond to climate change through movement or other changes in behavior (Charmantier et al., 2008; Refsnider & Janzen, 2012; Rushing et al., 2015).

The goal of this chapter is to determine the demographic drivers of climate-induced trailing edge range contractions in mobile species. I assessed two hypotheses using long-term demographic data from two range positions: the trailing edge and the range core. First, I hypothesized that demographic rates are sensitive to climate. Within each range position, local demographic rates should be correlated with spatial variation in temperature and precipitation. Second, I hypothesized that populations at the trailing edge are nearer to their ecological tolerance than populations at the range core. Trailing edge populations should therefore be more sensitive to climate change, leading to local extinctions and trailing edge range contractions. If trailing edge populations are more sensitive to climate, then changes in temperature and precipitation at the trailing edge should have led to declining recruitment, apparent survival, and population density compared to populations in the range core. Furthermore, negative effects of climate should be strongest, and first observed, at the warmest and driest habitats within the trailing edge. I assessed these hypotheses using an 18-year dataset on the breeding demography of the black-throated blue warbler (*Setophaga caerulescens*) collected across a range of elevations at the trailing edge and core of the range.

Methods

Study species

Black-throated blue warblers are small (9-10g) migratory songbirds which have frequently been used as a model species for studying demographics and population regulation (reviewed in Holmes 2007, Holmes 2011, Holmes et al. 2017). The breeding range consists of forests in the northern United States and southern Canada, with trailing edge populations in the southern Appalachian Mountains (Holmes et al. 2017). Adult birds are sexually dimorphic, territorial, and socially monogamous, though 4-16% of males may be bigamous (Holmes et al., 1992). Little is known about juvenile dispersal, but studies from other species of songbirds indicate that natal dispersal distances are usually <100 km (Paradis et al., 1998; Tittler et al., 2009). In addition, recruitment of yearling warblers at the range core is significantly and positively correlated with per capita fecundity in the previous summer (Sillett & Holmes, 2005; Sillett et al., 2000). I therefore assumed that most yearlings recruiting to the study plots were born in the same general area. Populations have been declining at the trailing edge of the range while remaining stable in the range core (Sauer et al., 2017); however, the drivers of these declines are not well understood.

Study sites

Demographic data were collected from 2002-2019 at two range positions: the trailing edge of the range in the Nantahala National Forest in the Appalachian Mountains of North Carolina (35.1°N, 83.4°W) and the core of the range at the Hubbard Brook Experimental Forest in New Hampshire (43°56′N, 71°45′W). Both sites were composed of contiguous, northern hardwood forest (Bormann & Likens, 2012; Day & Monk; 1974). The range core was characterized by an overstory of sugar maple (*Acer saccharum*), American beech (*Fagus* *grandifolia*), and yellow birch (*Betula alleghaniensis*), with an understory of hobblebush (*Viburnum lantanoides*) and saplings of striped maple (*Acer pensylvanicum*) and the major canopy species (Cline et al., 2013; Holmes et al., 1992). Vegetation at the trailing edge was more diverse than at the range core. The canopy was composed mainly of oak (*Quercus* spp.), hickory (*Carya* spp.), and red maple (*Acer rubrum*), though all major tree species at the range core were also present. Understory at the trailing edge was predominantly rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) (Day & Monk, 1974). Within both range positions, three large plots were arranged across an elevation gradient roughly spanning the breeding elevation range of BTBW (Table 2.1). This sampling design enabled collection of demographic data near the warm-edge elevational range limit at both range positions, but birds breeding at the low-elevation plot at the trailing edge were near both the elevational and latitudinal warm-edge of the range. All study plots were separated by at least 1 km.

The mid-elevation plot at the trailing edge was expanded by 11ha in 2006. The original section contained much poor-quality habitat, being dry with a predominantly open understory and scattered clumps of the preferred nesting substrate. The expanded section was predominantly higher-quality habitat, being wetter with abundant cover of the preferred nesting substrate. Unless otherwise indicated, references to the mid-elevation plot at the trailing edge refer to the original section of the study plot.

Field methods

Study plots were surveyed at least every other day during the breeding season each year to locate warblers and their nests. The coordinates of all encountered individuals were recorded either using handheld GPS or on gridded maps, which were subsequently digitized. Territory boundaries were delineated using coordinates from the encounter locations; territories were visited, on average, every other day. Females were captured by flushing them off their nests into mist-nets. Individuals were marked with a USGS aluminum leg-band and a unique combination of three colored leg-bands to allow for individual identification at a distance without need for recapture. Age and location data were recorded for each captured individual. Black-throated blue warblers can be classified into two age classes based on plumage characteristics (Pyle, 1997): second-year individuals (first-time breeders, hereafter SY) or after-second-year individuals (at least second breeding year, hereafter ASY). The age class of some females could not be determined because they possessed intermediate plumage characteristics; these individuals were classified into a non-specific age class (first-time breeder or older, hereafter AHY). A few females were not captured in each year; however, unmarked females could be individually identified within a year based on the location of their territories. Individuals were excluded from the analysis if more than half of their territories were outside the plot boundaries. These survey methods resulted in two types of data: individual encounter histories and counts of unmarked individuals.

Climate data

Climate data were collected from a series of USDA Forest Service climate stations situated across a range of elevations near each study site (Miniat et al., 2015; Miniat et al., 2017; USDA Forest Service 2020 a,b). Only climate stations within 175m in elevation of the study plots at each range position were included, leaving 9 stations at the trailing edge (3 temperature, 6 precipitation) and 16 stations at the range core (6 temperature, 10 precipitation). Summer temperature and annual precipitation were both higher at the trailing edge (Figure 2.1). Temperatures during the early-breeding season increased across elevations at both range positions over the study period (Figure 2.2), while annual precipitation became more variable at the trailing edge (Figure 2.3).

I incorporated two climate variables in the analysis: thermal sums during the early-breeding period and annual precipitation. Early-breeding thermal sums were calculated from the average laying date (day of year 127 (trailing) and 143 (core)) to the average fledge date (day of year 159 (trailing) and 175 (core)) of first nesting attempts at each range position. Thermal sums were calculated as in Cesaraccio et al. (2001) and represent the heat accumulation experienced in the nest by warblers during a critical part of the breeding season (Lany et al. 2016). Rates of nestling starvation are higher in wetter years at the range core (Rodenhouse & Holmes, 1992), but the main food source of warblers, caterpillars (order Lepidoptera), are more abundant in wetter years at the trailing edge (R. Cooper, unpub. data). Annual precipitation was used in the analysis, as it roughly corresponds to wet vs. dry years at the trailing edge (less or more than 2100-2200 mm/year depending on elevation). Furthermore, the critical time period during which precipitation may affect warbler demography is unclear. Although climate stations were not located at the actual study plots, climate is broadly correlated with elevation at each range position (Figure 2.1). For each climate variable at each range position, I fit a linear model to data from the climate stations and then predicted climate conditions at the study plots. I specified a trend effect of elevation and a separate intercept for each year in the linear models.

Statistical models of population dynamics

I used a Bayesian hierarchical model to draw inferences on black-throated blue warbler population dynamics. Model structure was based on the Jolly-Seber model (Jolly, 1965; Kéry & Schaub, 2011; Seber, 1965), but modified to integrate both individual capture histories from marked individuals and counts of unmarked individuals. Models were female-specific and estimated processes of population growth, recruitment, age-specific apparent survival, capture probability, and temporary emigration. Models were run separately for each study plot.

Female abundance in each year is represented by N_t. Abundance is a state variable that is not directly observed, so I adopted a data augmentation approach (Royle et al., 2007). Data augmentation sets an upper limit (M) on the number of individuals which could have entered the population over the study period; I set M at 600 to ensure that it was much larger than the actual number of individuals entering the population. Yearly abundance is then given by $N_t = \sum_{i=1}^{M} z_{i,t}$, where $z_{i,t}$ is a binary state indicating if female i is alive in time t. Change in abundance between t and $t+1$ was modeled based on recruitment rate (γ) and age-specific apparent survival (ϕ_j).

Initial abundance and recruitment

Abundance in the first year (N_1) was defined based on the year that a female entered the population (b_i). Entry year for females was modeled as: $b_i \sim Categorical(\pi_1, \ldots, \pi_{T+1})$ where T is the number of years of data at the study plot. A female was alive in the first year according to $z_{i,1} = I(b_i = 1)$. Female age ($a_{i,t}$) was given as 0 for SY and 1 for ASY. Age in the first year was modeled as $a_{i,1} \sim Bern(\tau)$, where τ is an age-ratio parameter representing the probability of a female being in the ASY age class. First-year abundance was calculated as the sum of SY and ASY abundance in the first year, which were given by $n_{1,1} = \sum_{i=1}^{M} z_{i,1} (1 - a_{i,1})$ and $n_{2,1} = \sum_{i=1}^{M} z_{i,1}\, a_{i,1}$, respectively.

Entry of females into the population in subsequent years ($t = 2, \ldots, T$) was modeled based on the recruitment rate. Recruitment rate was defined by a log-linear model with either a temporal trend or a trend for one of the two climate variables (denoted w): $\log(\gamma_t) = \beta_0^{(\gamma)} + \beta_1^{(\gamma)} w$. Probability of entering a population in a year beyond the first was given by:

$$\pi_t = Pr(b_i = t) = \frac{E(n_{1,t})}{M} = \frac{E(n_{1,t-1})\gamma_{t-1} + E(n_{2,t-1})\gamma_{t-1}}{M}$$

where $E(n_{1,t-1})$ represents the expected abundance of SY females in time $t-1$ and $E(n_{2,t-1})$ represents the expected abundance of ASY females in time $t-1$. The probability of an individual not entering the population over the course of the study is given by $\pi_{T+1} = 1 - \sum_{t=1}^{T} \pi_t$. Female age beyond the first year is fully specified by b_i, such that:

$$a_{i,t} = \begin{cases} 0 \text{ (SY)} & \text{if} \quad b_i \geq t \\ 1 \text{ (ASY)} & \text{otherwise} \end{cases}$$

Apparent survival

Apparent survival is the probability of surviving and not permanently emigrating from the population. Age-specific apparent survival was given by a logistic model with either a temporal trend or a trend for one of the two climate variables: $\text{logit}(\phi_{j,t}) = \beta_{j,0}^{(\phi)} + \beta_1^{(\phi)} w$, where subscript j represents age class. Beyond the first year, females are alive in time t if they recruited in t or were alive in $t-1$ and returned in t:

$$z_{it} \sim \begin{cases} 0 & \text{if} \quad b_i > t \\ 1 & \text{if} \quad b_i = t \\ \text{Bern}(z_{i,t-1}\phi_{a_{it},t-1}) & \text{if} \quad b_i < t \end{cases}$$

Mark-resight process

Individuals were typically only captured once, after which they were marked and resighted without capture. Unmarked females were captured with probability $p_t^{(c)}$, and marked females were resighted on the study plots with probability $p^{(\eta)}$. Temporal variation in capture probability was modeled with a logit-linear function that included a temporal trend: $\text{logit}(p_t^{(c)}) = \beta_0^{(c)} + \beta_1^{(c)} t$. Upon capture, unmarked females were classified into a specific age class (SY/ASY) rather than the non-specific age class (AHY) with probability k. Age-specific capture data were modeled as:

$$capture_{i,t} \sim \begin{cases} \text{Bern}\left(z_{i,t} \times p_t^{(c)} \times k\right) & \text{if} \quad \text{classified into a specific age class} \\ \text{Bern}\left(z_{i,t} \times p_t^{(c)} \times (1-k)\right) & \text{if} \quad \text{classified into a non} - \text{specific age class} \end{cases}$$

Based on within-season daily resighting data collected from 2011-2019 at the mid and high elevation plots at the trailing edge, the average detection probability per visit for marked females was 0.61 (SD 0.27, data not shown). This calculation excluded detections from females at the nest, as repeatedly detecting females at a previously-located nest would bias the detection estimate high. Territories were visited 10-44 times over the course of a breeding season (median: 27), therefore the probability of not detecting a female over the course of the entire season was likely extremely low (i.e., 9.1 * 10^{-12}). Instead, $p^{(\eta)}$ largely represents the probability that a female was breeding on the study plot rather than having temporarily emigrated off plot. Resight history data from marked females were therefore modeled as: $y_{i,t} \sim \text{Bern}\left(z_{i,t} \times p^{(\eta)}\right)$.

I also integrated yearly counts of unmarked females into estimates of N_t. The number of unmarked females in the population at time t is given by: $U_t = \sum_{i=1}^{M} z_{i,t}\,(1 - m_{i,t})$, where $m_{i,t}$ is a binary variable representing if female i is marked in time t. Yearly counts of unmarked females are then given by: $u_t \sim Bin\left(U_t, p^{(\eta)}\right)$.

The low-elevation plot at the trailing edge was not sampled after 2008 (see results); however, I incorporated follow-up surveys performed in 2017 and 2018. The plot was intensively searched by 1-3 observers during the middle of the breeding season. To account for detection bias in years when the plot was only surveyed once, I incorporated a detection probability term ($p^{(r)}$) in the estimate of $y_{i,t}$ and u_t. Specifically, encounter history data were modeled as $y_{i,t} \sim Bern(z_{i,t} \times p^{(\eta)} \times p^{(r)})$ and counts of unmarked females were modeled as

$u_t \sim Bin(U_t, p^{(\eta)} \times p^{(r)})$. An informative prior was placed on $p^{(r)}$ based on the estimated mean and SD of the 2011-2019 within-season resight data.

Population viability and forecasting

I used statistical forecasting to assess population viability through 2030 (Clark et al., 2001; Desforges et al., 2018; Hooker et al., 2020; Howell et al., 2020). Statistical forecasting accounts for process variance (i.e., demographic stochasticity and environmental change) as well as parameter uncertainty (Zylstra & Zipkin, 2021). I performed statistical forecasting using the population model with a temporal trend for γ and ϕ. Recruitment rate was modified as a logistic function with an additional term for density-dependence:

$$\gamma_t = \alpha/(1 + \exp(-(\beta_0^{(\gamma)} + \beta_1^{(\gamma)} t - \beta_2^{(\gamma)} E(D_{t-1})\,)\,))$$

where α is a bounding parameter and $E(D_{t-1})$ is the expected density in $t - 1$. Density-dependence was included to prevent exponential growth during forecasts. I only considered negative density dependence because breeding-season Allee effects do not seem to be important in this system (Merker & Chandler, 2021). To assess sensitivity of quasi-extinction risk to vital rates, I varied γ and age-specific ϕ in increments of 5%, up to a maximum of 20%. Quasi-extinction risk was assessed for each plot as the proportion of forecasts that fell to 0 density.

Model fitting

Posterior samples were drawn from Markov Chain Monte Carlo (MCMC) simulations in JAGS (Plummer 2003), called using the 'rjags' package in program R v. 4.0.4 (Plummer, 2016; R-Core-Team, 2020). Models were implemented with an adaptive phase of 1000 iterations, and inferences were drawn from another 35,000 samples from each of 3 MCMC chains. Convergence was assessed by visually inspecting the MCMC chains (see Appendix A for JAGS code). Temperatures increased over time at both study periods; therefore, I visually examined the residuals between expected and realized estimates of γ and ϕ to test for temporal autocorrelation in early-breeding thermal sums models.

Results

Temporal trends

Consistent with my first hypothesis, density was negatively associated with the elevational temperature gradient at each range position (Figure 2.4 A-B). The highest density was observed at the trailing edge high-elevation plot, being ~ 2-2.5x higher than at the range core. Female density remained relatively stable over time across all three elevations at the range core (Figure 2.4 B). Density fluctuated annually but did not show any long-term trend at the high-elevation plot at the trailing edge; however, population declines occurred at both the low and mid elevation plots (Figure 2.4 A). Population density at the low-elevation plot declined steadily from 11 females in 2002 (95% credible interval 8 - 16) to 6 females in 2008 (95% credible interval 5 - 8). The monitoring effort ceased at the low-elevation plot after 2008 due to low female density and associated difficulty in studying demography (Stodola et al., 2013), but follow-up surveys in 2017 and 2018 detected no female black-throated blue warblers. In 2018, I detected one male at the low-elevation plot. This bird appeared to be SY based on prominent brown tinge on the flight feathers, and thus was likely to have recruited that year. The bird was observed traveling around a broad area broadcast singing, and no evidence was detected of a paired female. The population at the mid-elevation plot was stable until about 2012, after which it declined from 11 females in 2012 (95% credible interval 10 - 13) to 4 females in 2019 (95% credible interval 4 - 5).

Uncertainty around many demographic estimates was unavoidably high, especially at the trailing edge, and 95% credible intervals for most parameter estimates overlapped zero

(Appendix B). Uncertainty was highest at the low-elevation plot at the trailing edge, in part because the plot was only sampled intensively for seven years. Furthermore, only a few individuals were estimated to be present in the population in the latter years, such that loss or gain of even one individual had a substantial effect on per-capita demographic rates.

Temporal trends in demographic rates varied by study plot at the trailing edge. Both per-capita recruitment rate and apparent survival declined during the period of population decline at the low-elevation plot at the trailing edge (Figure 2.4 C, E). Uncertainty in estimates was high (recruitment: med = -0.09, 95% credible interval -0.94 – 0.44; survival: med = -1.16, 95% credible interval -3.44 – 0.55), so the exact demographic drivers of extirpation at this plot are unclear. Population decline at the mid-elevation plot at the trailing edge was driven by declining apparent survival (Figure 2.4 E, med = -0.38, 95% credible interval -0.84 - -0.004). During the period of population decline (2012-2019), 1-3 SY females recruited to the plot each year, but few returned to breed in subsequent years. In contrast to this temporal trend on the original section of the mid-elevation plot, breeding density and apparent survival only showed minor declines in the expanded section (Figure 2.5). At the range core, apparent survival declined over time at both the low (med = -0.38, 95% credible interval -0.72 - -0.06) and high (med = -0.25, 95% credible interval -0.48 - -0.01) elevation plots (Figure 2.4 F). The declining apparent survival at the high-elevation plot was, at least partially, offset by increasing per-capita recruitment rate (Figure 4 D, med = 0.10, 95% credible interval -0.03 – 0.23).

Statistical forecasting through 2030 indicated that density will remain at 0 at the low-elevation plot at the trailing edge. Density is also projected to remain relatively stable at the mid-elevation plot at the range core and at both high elevation plots (Figure 2.6). Many simulations led to population extirpation at the mid-elevation at the trailing edge by 2030. Despite showing relatively stable populations until 2015, declining apparent survival at the low-elevation plot at the range core is projected to lead to population declines in the future. Of the five extant plots, only the mid-elevation plot at the trailing edge and the low-elevation plot at the range core are projected to have quasi-extinction risk by 2030 (28% and 7% risk, respectively, Figure 2.7). Quasi-extinction risk at both plots was more sensitive to recruitment rate than to age-specific apparent survival.

Climate Effects

Warming temperatures had a negative effect on demographic rates and population dynamics. Population growth rate was negatively correlated with warmer early-breeding thermal sums at the low elevation plots at both range positions (Figure 2.8 A-B). Warmer temperatures led to lower per-capita recruitment at the trailing edge (Figure 2.8 C, med = -0.5, 95% credible interval -1.25 – 0.17) and lower apparent survival at the range core (Figure 2.8 D, med = -0.19, 95% credible interval -0.51 – 0.12). I found no effect of early-breeding thermal sums over the entire study period at the mid-elevation plot at the trailing edge; however, warmer temperatures negatively affected apparent survival during the period of population decline (2012-2019, med = -0.7, 95% credible interval -1.76 – 0.17). I used a linear model to determine if temperatures increased more during the period of population decline than during the period of stability. The model was fit using an interaction between year (trend effect) and period (before and after 2012) to explain variation in early-breeding thermal sums. The warming trend at this plot was not significantly different before and after 2012 (interaction term: t = 0.75, p = 0.47); therefore, the observed response to warming temperatures seem to represent a shift in how birds respond to climate.

The effect of annual precipitation on demographic rates and population growth varied by range position (Figure 2.9 A, B). At the range core, apparent survival was lower at the low-elevation plot following higher rainfall years (Figure 2.9 D, med = -0.32, 95% credible interval -0.65 - -0.01). At the trailing edge, per-capita recruitment tended to be positively correlated with rainfall at the mid and high elevation plots (Figure 2.9 C; mid-elevation: med = 0.14, 95% credible interval -0.15 – 0.41; high-elevation: med = 0.15, 95% credible interval -0.06 – 0.36).

Discussion

Warming temperatures have led to long-term population declines in black-throated blue warblers breeding at the trailing edge of the range in the southern Appalachian Mountains. Long-term demographic trends supported both climate-change hypotheses: breeding density and demographic rates were correlated with the climate gradient at each range position, and the strongest negative effects occurred at the warmest breeding areas at the trailing edge. Populations remained stable at the range core; however, warming early-breeding temperatures led to population declines and eventual extirpation at the lowest, warmest breeding habitats at the trailing edge. My results add to the rapidly growing body of literature documenting climate-change-induced range contractions at the low-latitude and low-elevation range edges (Coristine & Kerr, 2015; Moritz et al., 2008; Rushing et al., 2020; Taheri et al., 2020; Wilson et al., 2005). Population declines were first observed at the lowest, warmest plot and were not observed at higher, cooler elevations until later in the study period. This pattern is consistent with climate change gradually pushing the factors setting the warm-edge range limit further and further upslope. Trailing edge population declines occurred despite only a minor warming trend in this region, supporting the hypothesis that trailing edge populations are near the ecological limit of the species (Brown, 1984; Holt et al., 2005). Trailing edge populations are therefore likely to be particularly vulnerable to minor degrees of climate change pushing them past their ecological tolerance (Deutsch et al., 2008), leading to population declines, local extirpation, and range shifts. Populations at the high-elevation plot at the trailing edge are projected to remain stable over the next decade, but statistical forecasting may not be accurate if demographic rates respond differently to future climate change. The gradual contraction of the low-elevation range limit over the past two decades indicates that further warming in this region could eventually lead to population declines at the highest elevations.

Climate change is also likely to cause population declines at the range core despite populations remaining stable over the study period. The substantial warming trend at the range core led to declining apparent survival at the low-elevation plot, which is projected to cause population declines and potential extirpation by 2030. Consistent with climate-change hypotheses, negative effects of climate change were first observed at the lowest, warmest breeding habitat at the range core. Populations within the core of species' ranges have historically been considered to have lower risk of extinction than those at range edges (e.g., Gaston, 1990; Lawton, 1993) however my results agree with more recent tests of this hypothesis (Boakes et al., 2017; Channell & Lomolino, 2000) that even core populations may be at risk.

The strong negative effect of warming temperatures on warbler demography suggests that climate change is driving trailing edge declines; however, this region also experienced extensive loss of one of the major canopy tree species, eastern hemlock (*Tsuga canadensis*), following spread of the introduced hemlock wooly adelgid (*Adelges tsugae*) (Webster et al., 2012). A previous analysis of the 2002-2008 trailing edge black-throated blue warbler data concluded that population declines at the low-elevation plot were attributable to hemlock loss, since warblers used hemlock as a secondary nesting substrate at the low-elevation plot but not at the higher elevations (Stodola et al., 2013). Recent warbler population declines at other study plots, however, suggest that hemlock loss is unlikely to be the major driver of declines. While hemlock was almost completely extirpated from the area by 2011 (Webster et al., 2012), the low-elevation plot still contains enough cover of the preferred nesting substrate to support several warbler breeding pairs (W. Lewis, pers. obs.). Moreover, population declines at the mid-elevation plot are well explained by climate change hypotheses; however, this plot historically had low density of hemlock, and thus was little affected by its loss (Appendix C). The ecosystem-level consequences of hemlock loss are uncertain, but decreasing canopy cover from hemlock loss has led to increased cover of the preferred nesting substrate (Ford et al. 2012, Appendix C). Furthermore, understory deciduous leaf cover is a good predictor of warbler habitat quality (Robinson & Holmes, 1982; Rodenhouse et al., 2003), but deciduous sapling density did not change over the study period (Appendix C). Climate change, therefore, is the most likely driver of warbler population declines at the trailing edge.

Warming temperatures showed a strong and consistent relationship with warbler population declines, but the demographic drivers of declines varied between study plots. Extirpation at the low-elevation plot at the trailing edge was associated with declining recruitment and apparent survival, though the model could not differentiate between the two due to the high uncertainty. Temperature had a strong negative effect on recruitment, and the age-ratio became very heavily skewed towards older birds during the period of decline (Stodola et al. 2013). These findings indicate that declining recruitment was the primary demographic driver of population declines at this plot. In contrast, observed and predicted declines at other study plots were driven by declining adult apparent survival. The few studies documenting demographic trends underlying avian trailing edge population declines have found conflicting results about whether recruitment (Neat-Clegg et al., 2021; Waite & Strickland, 2006) or apparent survival (Srinivasan & Wilcove, 2021) are the primary drivers of declines. Warblers showed heterogeneous demographic responses between study plots, suggesting that response to climate change are likely to vary by factors such as species traits, degree of climate change experienced, and habitat type (Srinivasan & Wilcove, 2021; Tingley et al., 2012; Wolfe et al., 2015).

True survival is frequently inseparable from permanent emigration; however, I hypothesize that population declines were driven by increasing permanent emigration. Apparent survival declined precipitously in the original section of the trailing edge, mid-elevation plot despite remaining relatively stable in the expanded section. True annual survival would be unlikely to vary so dramatically between females breeding in adjacent sections of a study plot; therefore, population declines in the original section likely arose from increasing rates of permanent emigration. Emigration rates are generally higher from poor-quality habitats than from high-quality habitats (Cline et al., 2013; Holmes et al., 1996), explaining why permanent emigration would be increasing in the poor-quality original section of the plot but not in the higher-quality expanded section. Several SY females recruited to the poor-quality original section of the plot each year, which may have arisen if younger, competitively subordinate birds are forced into poor-quality habitats through site-dependent processes (Rodenhouse et al., 1997; Rodenhouse et al., 2003). Comparable data are not available from the range core, but a similar mechanism may have occurred. Habitat quality is negatively correlated with elevation at the range core (Cline et al., 2013), and adults engaging in breeding dispersal generally shift to higher-quality territories (Holmes et al., 1996; Rodenhouse et al., 2003). Avian site-fidelity is often assumed to be high (Greenwood, 1980; Greenwood & Harvey, 1982); however, my results suggest that this may not always be the case. Instead, adult emigration from poor-quality habitats may be a common method by which birds can behaviorally respond to climate change.

Warbler demography also responded to variation in precipitation, but not to the same extent as temperature. Recruitment was positively related to precipitation at the mid and high-elevation plots at the trailing edge, likely through effects on food abundance. Caterpillar abundance is higher in wetter years (R. Cooper, unpub. data), and food abundance is correlated with fecundity and recruitment to the next year (Nagy & Holmes, 2004; Rodenhouse & Holmes, 1992; Sillett et al., 2000; Townsend et al., 2016). Precipitation had the opposite effect at the range core. Apparent survival declined in wetter years at the range core, but only at the low-elevation plot. Heavy rainfall events at the range core increase rates of nest failure and nestling mortality (Rodenhouse & Holmes 1992), which may lead to adult emigration following reproductive failure (Cline et al., 2013; Greenwood & Harvey, 1982). The reason why this effect would only be observed at the low-elevation plot is not clear. Annual precipitation did not show any long-term trend at the range core and had a positive effect on population dynamics at the trailing edge. Population declines in black-throated blue warblers therefore appear driven by changes in temperature rather than precipitation, but I may not have modeled the correct precipitation variables or time periods during which precipitation affects demography (Tamburini et al., 2013; van de Pol & Cockburn, 2011). For example, productivity may be more affected by extreme precipitation events than by annual precipitation (Martin et al., 2017; Sillett et al., 2004), or variation in precipitation may have a time-lagged effect on warbler populations (Pearce-Higgins et al. 2015). More detailed study is needed to determine the effects of changing precipitation on black-throated blue warbler population dynamics.

Future research should determine the proximate mechanisms through which warming temperatures are driving demographic changes and population declines in black-throated blue warblers. Climate change may have had direct effects on warblers, such as physiological stress causing egg or nestling mortality (Cunningham et al., 2013; Grant, 1982), but the main effects are likely to be indirect through biotic interactions (Cahill et al., 2013; Thomas, 2010). For example, warming temperatures may change the activity and distribution of nest predators (Cox et al., 2013; Myers et al., 2009) or the phenology and abundance of prey times (van de Pol et al., 2010; Visser et al., 2006). Climate change may also lead to novel competitive interactions or modify the strength of pre-existing competitive interactions (Heegard & Vandvick 2004, Stenseth et al. 2015). Climate change is likely affecting warbler populations through multiple interacting pathways (McLean et al., 2016). These potential mechanisms may directly affect recruitment by causing declines in productivity, nestling quality, or first-year survival (Ringsby et al., 1998; Sillett et al., 2000; Sillett & Holmes, 2005; Streby & Anderson, 2011; Townsend et al, 2016). They may also cause adult emigration away from habitats experiencing declining breeding conditions (Doligez et al. 2002; Cline et al., 2013; Greenwood & Harvey, 1992).

One unexpected finding from this chapter was that breeding density was highest at the high-elevation plot at the trailing edge. This is contrary to biogeography theory, which predicts that density should be highest near the core of the range and decrease towards the edges (Brown, 1984; Brown et al., 1995; Lawton, 1993). Conditions are much cooler at the higher elevations at the trailing edge and are reminiscent of conditions further north in the core of the range. High-elevation populations at the trailing edge may not be as close to the ecological limit of the species as their geographic position would indicate.

Conclusions

This chapter documents black-throated blue warbler population declines and range contractions at the low-latitude and low-elevation edges of the range. Population declines were driven by increasing temperatures during the early breeding season, as all plots with observed or predicted declines showed negative relationships between early-breeding thermal sums and population dynamics. My results strongly support the hypothesis that climate change on the breeding grounds is driving population declines, but population dynamics of migratory species are governed by threats encountered during the entire annual cycle (Runge & Marra, 2005; Sillett et al., 2000). More study is needed to determine potential effects of habitat loss and climate change during the non-breeding season, and how these threats may interact with breeding-season climate change to drive population declines. Demographic drivers varied between study plots, but emigration away from poor-quality habitats may be a common behavioral response to climate change. The data do not indicate whether birds are emigrating upslope to better-quality habitats (regional redistribution) or if they are making long-distance dispersal movements to new areas. This is a priority area for future research, but tracking dispersal movements of small birds across broad areas of contiguous forest is difficult. One avenue may be to monitor the number of unmarked ASY birds immigrating to high-elevation breeding habitats at the trailing edge, as this should increase if birds are regionally redistributing to higher-quality habitats at high elevations (Holmes et al., 1996). Many species of birds are declining at the trailing edge of their ranges in the Southern Appalachians (Sauer et al., 2017); for at least one species, the Canada warbler (*Cardellina canadensis*), apparent survival is also lowest at the lowest, warmest elevations (Chandler et al. 2018). This may indicate that many trailing edge species respond to climate change through emigration, and that the demographic results from black-throated blue warblers may be used in mechanistic models to predict effects of climate change for a range of species in the Southern Appalachians. Understanding the drivers of trailing edge range contractions is critically important, as ongoing climate change may push the factors setting the low-elevation range limit further and further upslope until eventually reaching the tops of the mountains (Şekercioğlu et al., 2008).

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Table 2.1. Description of black-throated blue warbler census/capture-recapture plots across an elevation gradient near the trailing edge (North Carolina) and core (New Hampshire) of the species' range. Average elevation and area of the study plots are shown, as well as the number of marked females used in the analysis (n) and the time period over which each plot was sampled.

Range	Elevation	Avg. Elev. (m)	Area (ha)	n	Sampling Period
Trailing edge	Low	1050	23	15	2002-2008, 2017-2018
	Mid	1200	18	61	2002-2019
	High	1350	15	102	2003-2019
Range core	Low	300	98	161	2002-2016
	Mid	550	125	428	2002-2016
	High	800	56	209	2002-2016

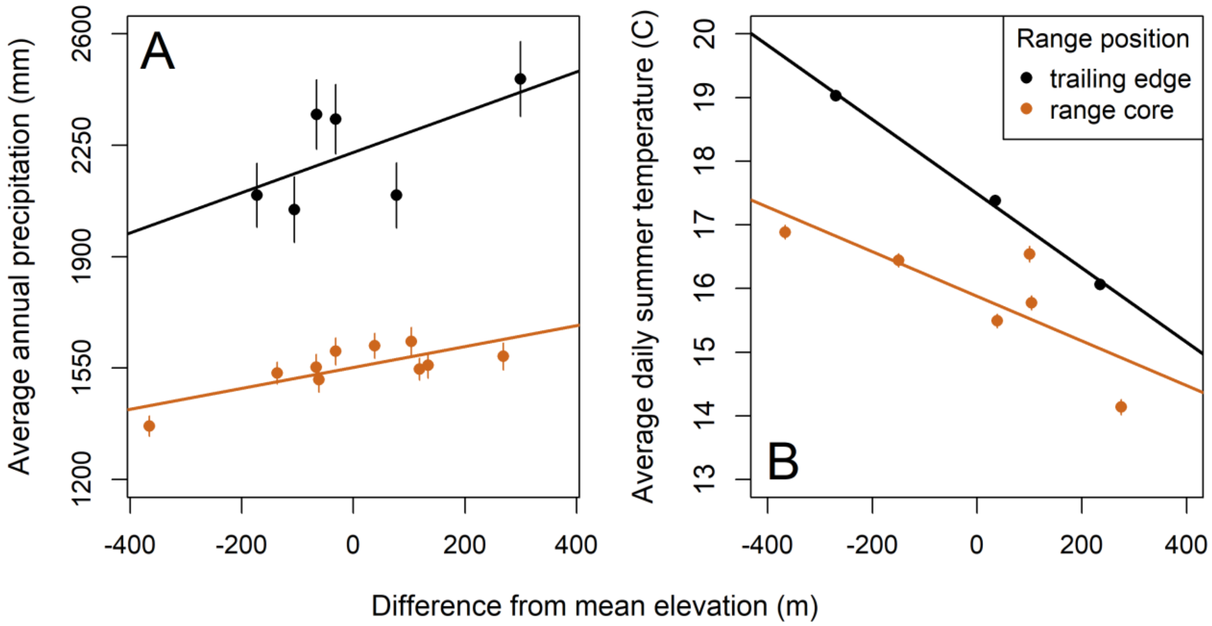

Figure 2.1. Average annual precipitation (A) and average daily summer temperature (B) in relation to elevation at each range position. Elevation breeding range of BTBW varied between range positions. To facilitate comparison across sites, elevation is shown as the difference from the mean elevation of climate stations at each range position (trailing edge mean: 1067m, range core mean: 627m). Climate data were provided by long-term climate stations run by the USDA Forest Service (see text for citations).

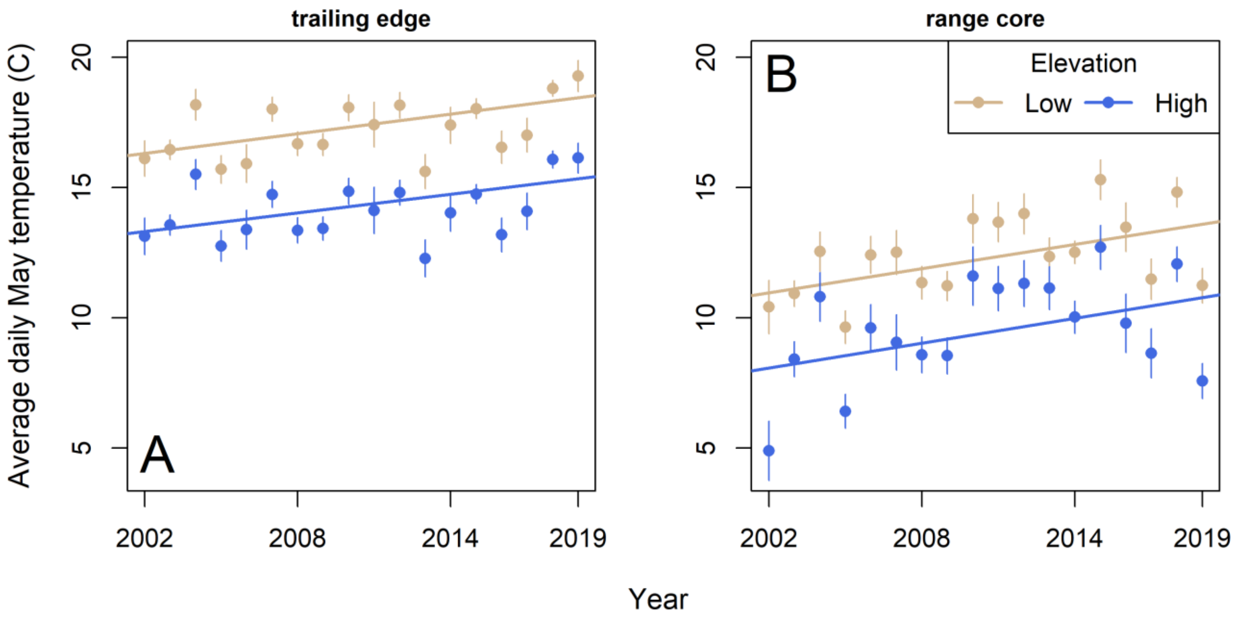

Figure 2.2. Change in average daily May temperature from 2002-2019 at the trailing edge (A) and range core (B). Climate data were provided by long-term climate stations run by the USDA Forest Service (see text for citations). The low-elevation data are from weather stations at elevations lower than the low-elevation plot at each range position (range core: 261 m, trailing edge: 884 m) while the high-elevation data are from weather stations at elevations higher than the high-elevation plot at each range position (range core: 903 m, trailing edge: 1389 m). Average daily May temperature increased significantly ($p<0.05$) across elevations at both range positions.

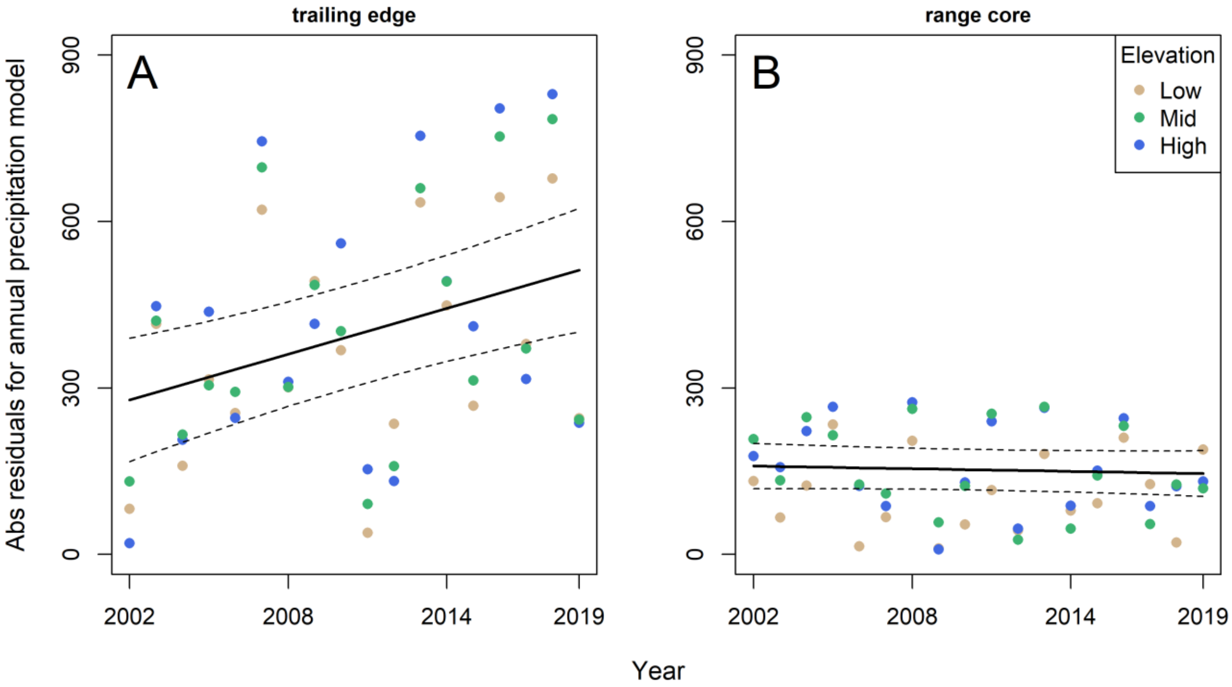

Figure 2.3. Variation in annual precipitation 2002-2019 at the trailing edge (A) and range core (B). Figures show absolute values of residuals from a linear model allowing for, at each range position, annual precipitation to vary by year (fixed effect) and elevation (trend effect). Absolute values of residuals are shown, as these were used as the dependent variable in an analysis to test if precipitation has become more variable over the study period. Climate data were provided by long-term weather stations run by the USDA Forest Service (see text for citations). The low-elevation data are from weather stations at elevations lower than the low-elevation plot at each range position (range core: 261 m, trailing edge: 894 m), mid-elevation data are from weather stations roughly in the middle of the elevation range (range core: 595 m, trailing edge: 1035 m), and the high-elevation data are from weather stations at elevations higher than the high-elevation plot at each range position (range core: 895 m, trailing edge: 1366 m).

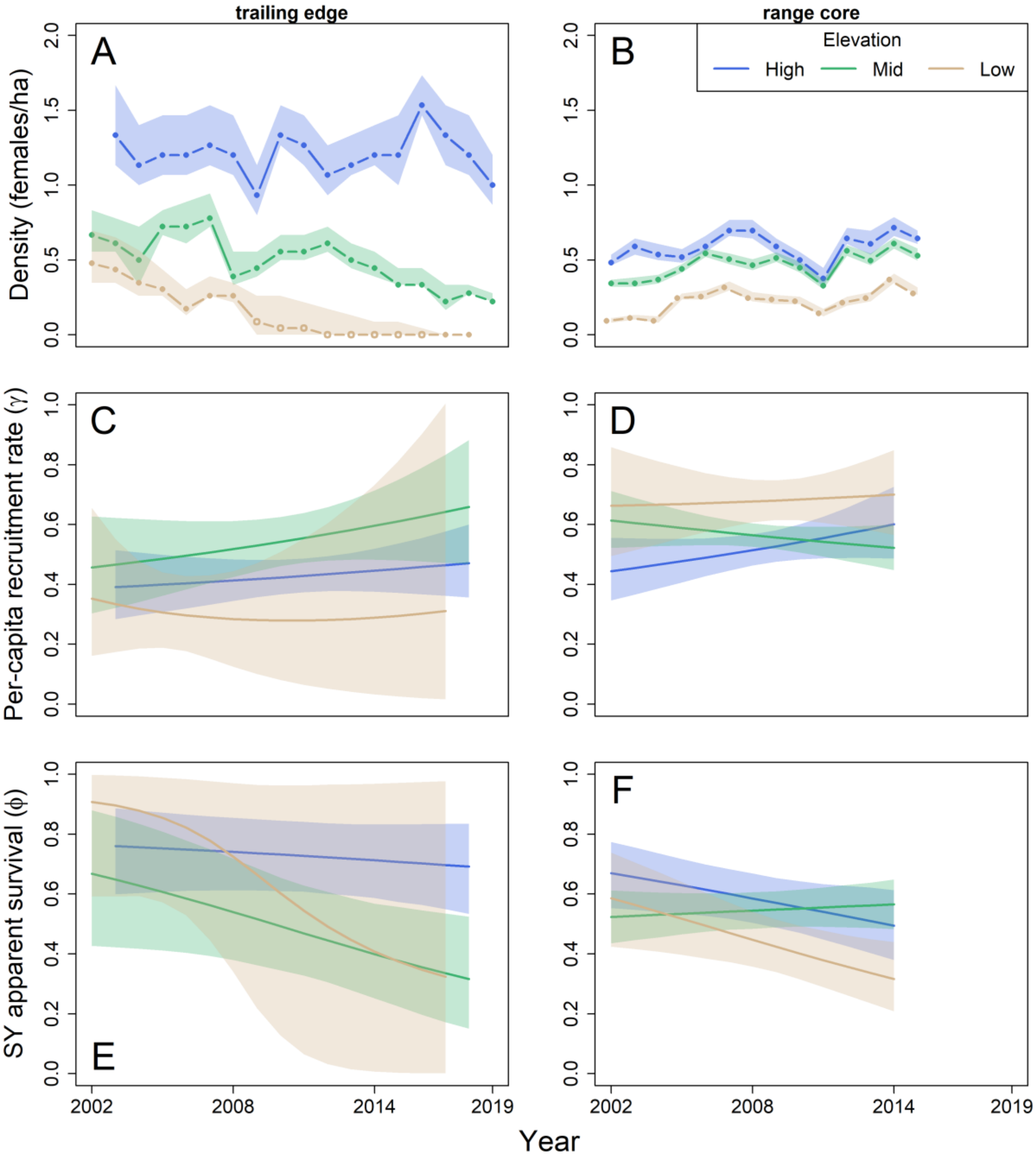

Figure 2.4. Estimates of annual density of female black-throated blue warblers (A, B) and predicted trends in per-capita recruitment (C, D) and SY apparent survival (E, F) from the Bayesian hierarchical analysis. ASY apparent survival showed a similar temporal trend, but the intercept was lower for all study plots. Model estimates are shown for the trailing edge (A, C, E) and range core (B, D, F). For the low-elevation plot at the trailing edge, filled circles represent years where the plot was surveyed. Mean values and 95% credible intervals are shown.

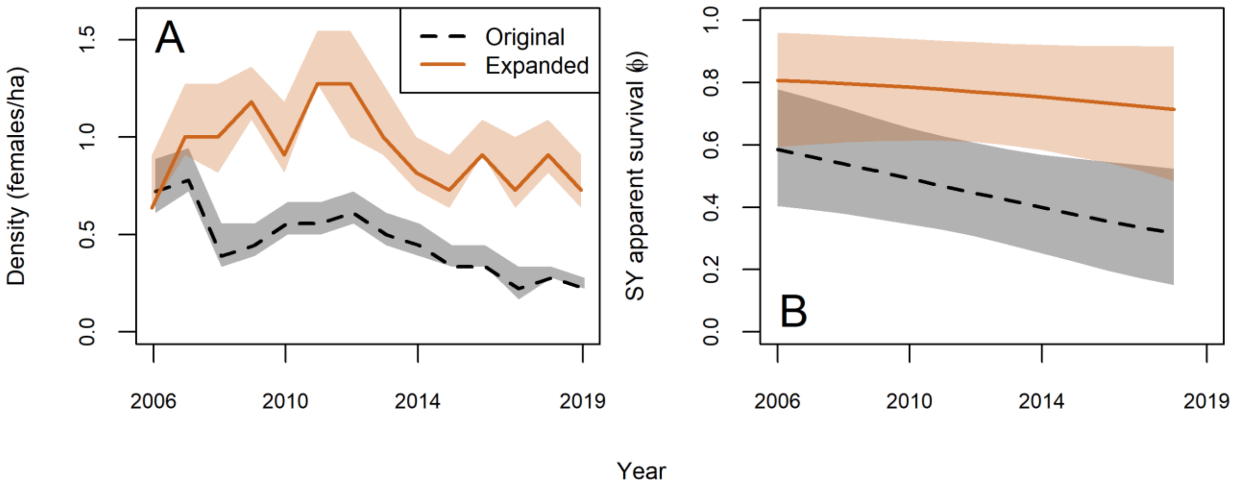

Figure 2.5. Estimates from the Bayesian hierarchical analysis of annual density (A) and predicted trends in SY apparent survival (B) of female black-throated blue warblers breeding on the original (dashed, black) and extended (solid, orange) sections of the mid-elevation plot at the trailing edge. Sections of the plot differed in habitat quality, with the extended section representing high-quality habitat and the original section representing low-quality habitat (see text for more details). ASY apparent survival showed a similar temporal trend, but the intercept was lower for both sections of the plot. Mean values and 95% credible intervals are shown.

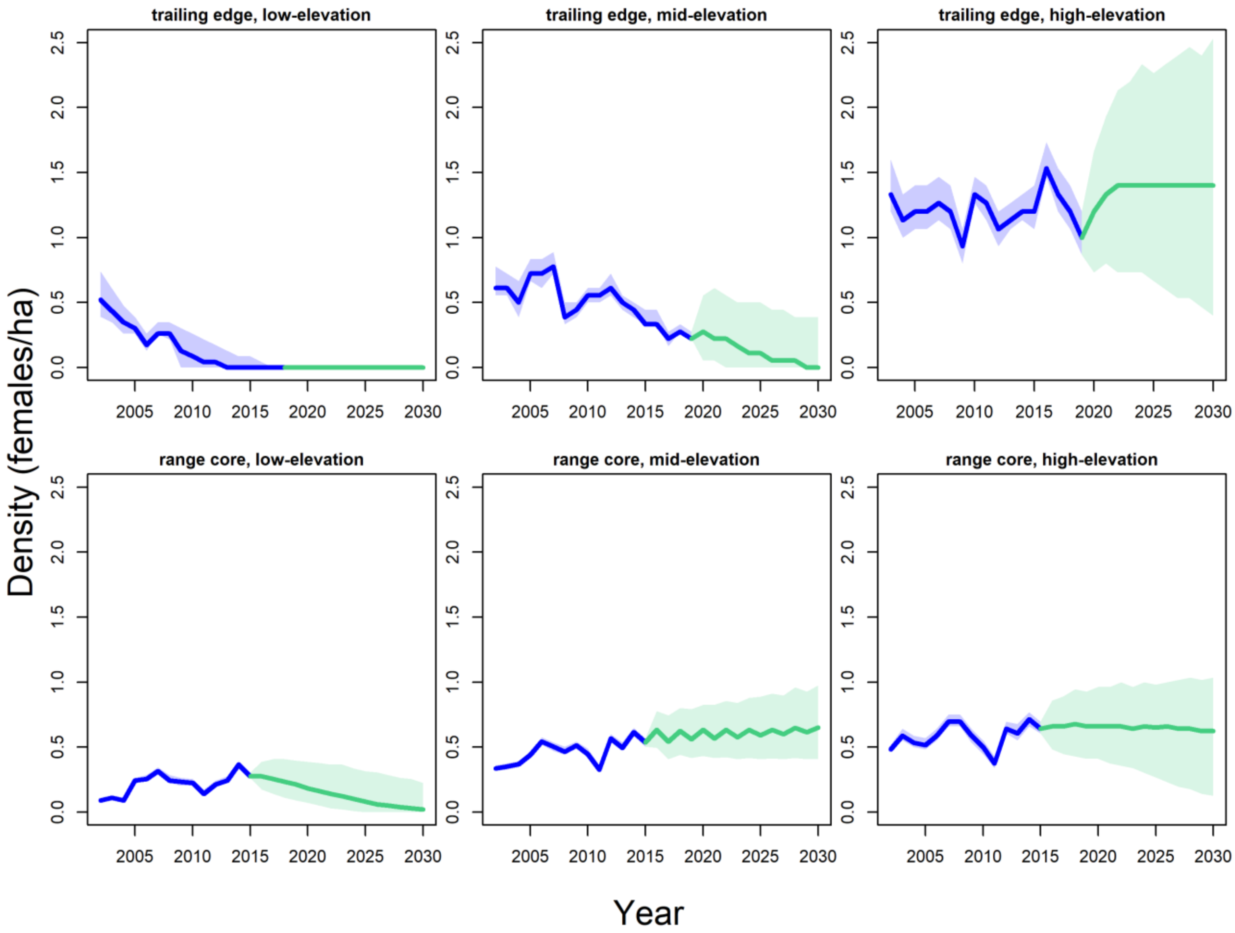

Figure 2.6. Forecasts of female black-throated blue warbler breeding density through 2030 at the trailing edge (top row) and range core (bottom row) under current trends in population dynamics. Estimates over the course of the study period (dark blue) and forecasts (green) are shown. Mean (solid line) and 95% credible intervals (shaded regions) are shown. See text for more details.

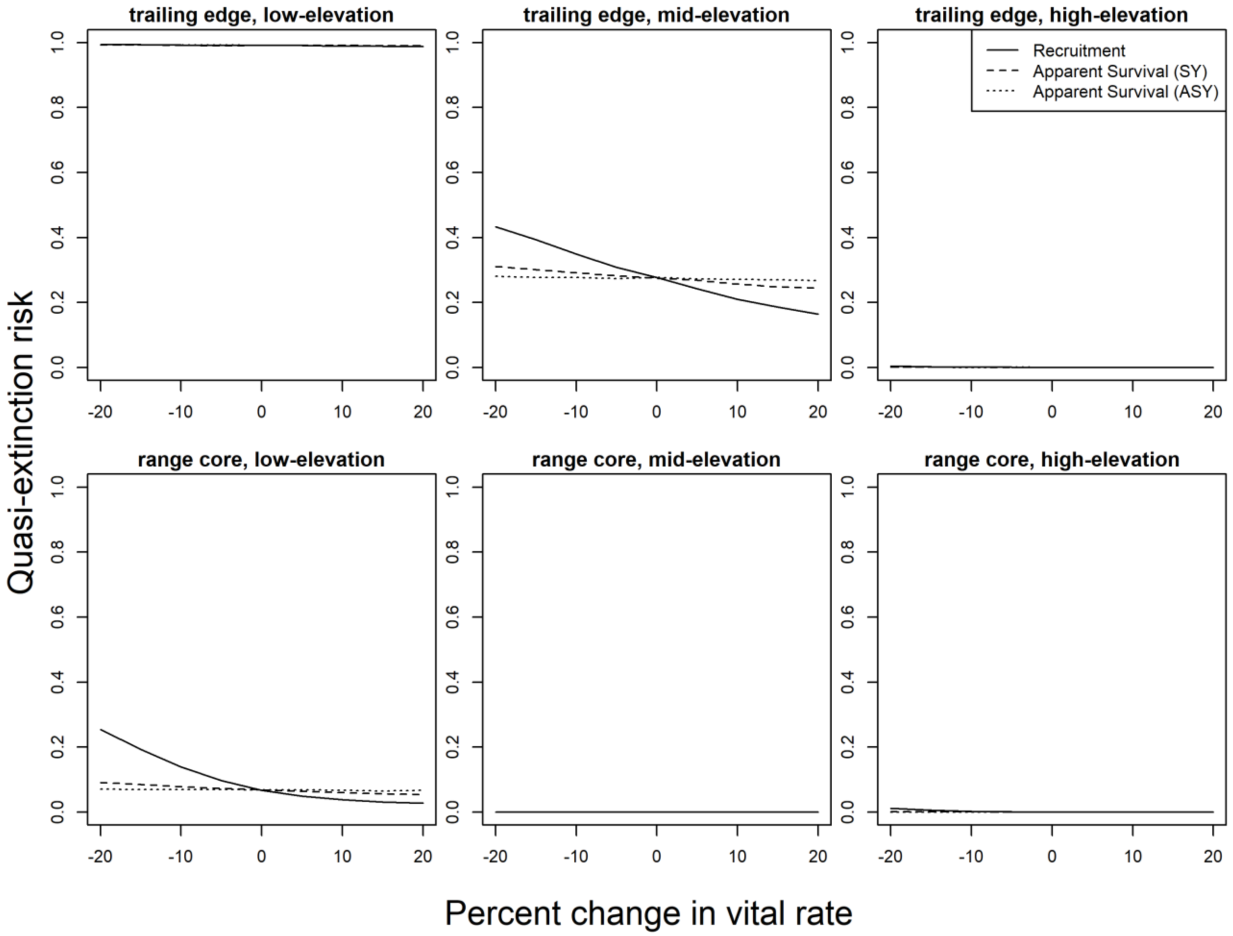

Figure 2.7. Sensitivity of quasi-extinction risk to proportional changes in per-capita recruitment rate (solid), SY apparent survival (dashed), and ASY apparent survival (dotted) of black-throated blue warbler populations at the trailing edge (top row) and range core (bottom row). Quasi-extinction risk is defined as the probability of population density falling to 0 females/ha when forecasting population dynamics through 2030. Quasi-extinction risk is shown to be at 1 for the low-elevation plot at the trailing edge, as this population was already locally extinct before the start of forecasting. See text for more details.

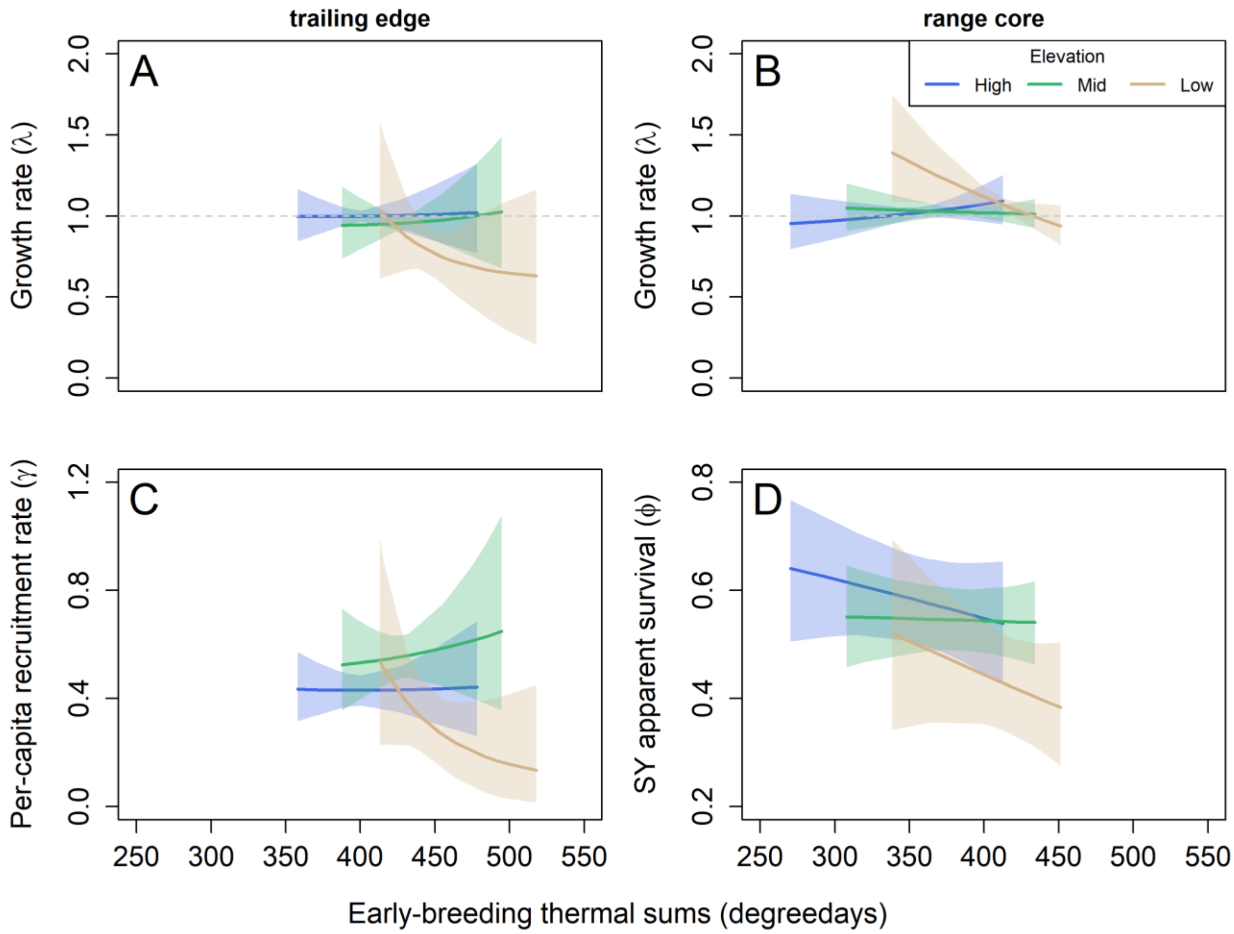

Figure 2.8. Predicted effect of thermal sums during the early-breeding period (average lay date to average fledge date of first broods, see text for more details) on the finite population growth rate at the trailing edge (A) and range core (B), per-capita recruitment rate at the trailing edge (C), and SY apparent survival at the range core (D) from the Bayesian hierarchical analysis. Figures show the population growth or demographic rate from year *t-1* to *t* in relation to early-breeding thermal sums in *t-1*. ASY apparent survival showed a similar trend, but the intercept was lower for all study plots. Per-capita recruitment (range core) and SY apparent survival (trailing edge) are not shown, as they did not show a relationship with early-breeding thermal sums. Mean values and 95% credible intervals are shown.

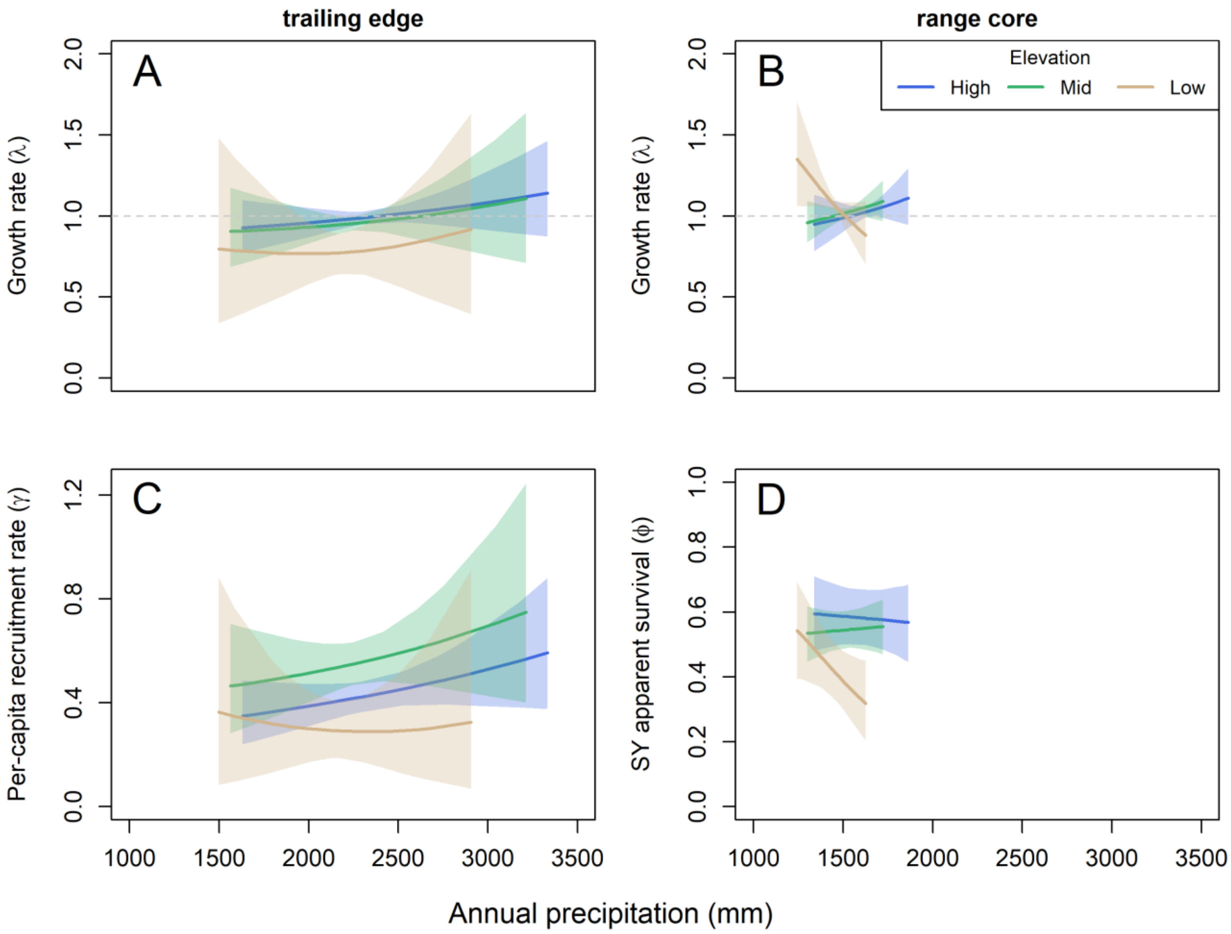

Figure 2.9. Predicted effect of annual precipitation on the finite population growth rate at the trailing edge (A) and range core (B), per-capita recruitment rate at the trailing edge (C), and SY apparent survival at the range core (D) from the Bayesian hierarchical analysis. Figures show the population growth or demographic rate from year *t-1* to *t* in relation to annual precipitation in *t-1*. ASY apparent survival showed a similar trend, but the intercept was lower for all study plots. Per-capita recruitment (range core) and SY apparent survival (trailing edge) are not shown, as they did not show a relationship with annual precipitation. Mean values and 95% credible intervals are shown.

CHAPTER 3

EFFECTS OF BREEDING CONDITIONS AND DEMOGRAPHICS ON LOCAL POPULATION DYNAMICS FROM ACROSS THE RANGE OF THE BLACK-THROATED BLUE WARBLER (SETOPHAGA CAERULESCENS)[1]

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[1] Lewis, W.L., R.J. Cooper, R.B. Chandler, T.S. Sillett, R.W. Chitwood, K.W. Stodola, M.H. Cline, J.L. Hatt, M.T. Hallworth, S.A. Kaiser, and N.L. Rodenhouse. To be submitted to *Ornithology*.

Abstract

Climate change is causing trailing-edge population declines and range contractions in many species, but the proximate mechanisms through which climate change affects populations remain poorly understood. Mechanisms must be sensitive to climate and directly affect population dynamics; therefore, a first step in identifying the mechanisms underlying range contractions is determining how the primary drivers of population dynamics vary across the geographic range. I investigated the drivers of population dynamics using a long-term dataset of black-throated blue warbler (*Setophaga caerulescens*) demography collected across a range of elevations at the trailing edge and core of the range. I used a Bayesian hierarchical model to assess the effects of three potential mechanisms on recruitment and apparent survival: per-capita productivity, nestling mass, and late-season food abundance. Drivers of population dynamics were highly variable between study plots but were not broadly different between the trailing edge and the range core. Variation in productivity had little effect on local population dynamics at the trailing edge, indicating that productivity may not be the mechanism behind trailing edge declines. Instead, population dynamics in lower-quality habitats were best explained by variation in late-season food abundance. These results suggest that food abundance is a likely mechanism through which climate change is causing trailing-edge declines, potentially through interacting effects on nestling mass.

Introduction

Global climate change is leading to changes in the geographic ranges, phenology, and biotic interactions of many species (Parmesan & Yohe 2003, Root et al. 2003, Visser & Both 2005, Chen et al. 2011, Alexander et al. 2015). The strongest negative effects of changing climate are frequently observed at the low-latitude and low-elevation trailing edges of the range, where changing temperature and precipitation regimes can lead to reduced population growth and latitudinal or elevational range contractions (Jiguet et al. 2010, Chen et al. 2011, Taheri et al. 2020, Neate-Clegg et al. 2021, Chapter 2). Trailing edge populations frequently harbor genetically distinct lineages from populations within the core of the range; therefore, loss of trailing edge populations may be detrimental for species-wide genetic diversity (Hampe & Petit 2005, Grus et al. 2009). Loss of trailing edge populations may also lead to a significant reduction in regional biodiversity (Hampe & Petit 2005, Merker & Chandler 2020). Range contractions occur through spatial changes in demographic rates (Gaston 2009), but the actual mechanisms by which climate change brings about spatial variation in demographic rates and population dynamics are often unclear. Understanding the mechanistic drivers underlying demographic rates and population dynamics is critically important for predicting population trends under future climate change (Urban 2016, Desforges et al. 2021).

One of the impediments to determining the mechanisms underlying climate-induced range shifts is that the effects of climate change can be multifaceted and affect demographic rates and population dynamics through multiple mechanistic pathways (Doak & Morris 2010, McLean et al. 2016). Climate can have direct physiological effects on organisms (Deutsch et al. 2008, Cunningham et al. 2013) or indirect effects on the distribution or phenology of habitat, food, predators, or competitors (Martin 2007, Pearce-Higgins et al. 2010, Alexander et al. 2015, DeGregorio et al. 2015). Each of the possible mechanistic pathways are unlikely to have an equal effect on populations, as population dynamics are generally more sensitive to some factors than to others. Effects of climate change will be greatest when climate change acts on the factor or factors to which demography and population dynamics are most sensitive (Miller-Rushing et al. 2010, Franks et al. 2017). Climate-induced changes in factors besides the ones primarily driving population dynamics may have little impact on growth rates due to demographic compensation (Newton 1998, Miller-Rushing et al. 2010, van de Pol et al. 2010). For example, climate-induced increases in predation pressure may have little effect on population dynamics in a food-limited population if increased mortality is compensated by lower competition for food among the surviving individuals. Determining the proximate mechanisms through which climate change causes population declines therefore requires understanding, not just how potential mechanisms are affected by climate change, but also how variation in mechanisms affects population dynamics (McLean et al. 2016).

Classic ecological theory predicts that population dynamics near the range margins may be driven by different factors compared to at the range core (MacArthur 1972, Brown 1984). Populations at range margins are nearest to the boundaries of the species' ecological niche and so are likely to be heavily influenced by the abiotic stressors and biotic interactions which set the boundaries of the geographic range (Brown 1984, Guo et al. 2005, but see Sangarin et al. 2006); however, little empirical work has been done to assess how the mechanistic drivers of population dynamics vary across a species' range. The few studies that have been performed on this topic support the hypothesis that driving factors can vary spatially based on local biotic and abiotic conditions (Baskauf 2003, Hoffman et al. 2010). The driving factors, and the mechanistic impacts of climate change, may therefore differ between populations at the trailing edge and populations within the range core.

Understanding the factors driving population dynamics is further complicated by the fact that populations in heterogeneous landscapes may be regulated over broad spatial extents (Hanski & Kuussaari 1995, Newton 1998, Pulliam 1988). An example of this broad-scale population regulation is source-sink dynamics, wherein sub-populations in poor-quality areas experience insufficient productivity to maintain local abundance and instead are maintained by dispersal of individuals from a limited number of highly productive areas (Pulliam 1988). Population growth in sink areas is driven largely by source areas producing many recruits rather than through local conditions in the sink areas (Pulliam 1988, Rushing et al. 2021). Landscape-scale effects need to be considered when investigating the mechanisms underlying climate-induced population declines. Landscape-scale population processes may be more pronounced at the latitudinal and elevational range edges due to generally lower population sizes with greater degree of population fluctuations (Thomas et al. 1994, Kanda et al. 2009, Seipel et al. 2016). For high-elevation species, lower elevation habitats may act as sink areas maintained by dispersal from higher-elevation source habitats (González-Megías et al. 2005).

In the eastern United States, many bird species exhibit trailing edge breeding distributions in the high elevation forests of the southern Appalachian Mountains (Merker & Chandler 2020). Many of these trailing edge populations have been declining in recent decades (Sauer et al. 2017), through extirpation from the lower elevations (Stodola et al. 2013, Chapter 2). One species exhibiting this pattern of trailing edge decline in the Southern Appalachians is the black-throated blue warbler (*Setophaga caerulescens*, hereafter BTBW), a small migratory songbird which has frequently been used as a model species for studying population dynamics (Holmes et al. 2017). Population densities have remained relatively stable within the core of the breeding range in New England but have declined at lower elevations in the Southern Appalachians in response to warming temperatures (Chapter 2). The process of decline at the trailing edge is complex and involves changes in both recruitment and adult emigration rates (Chapter 2). To better understand the mechanisms through which climate change is driving population declines at the trailing edge, we first need to understand what factors drive population dynamics at the different range positions.

I used an 18-year dataset on BTBW demography from across a range of elevations at the trailing edge and the range core to determine how population dynamics are affected by breeding-ground effects, and how this varies across the breeding range. While climate change on the breeding grounds may be affecting populations through many mechanistic pathways, I focused on three breeding-ground effects which likely have interacting, but not completely overlapping, effects on demographic rates and population growth: per-capita productivity, nestling mass, and food abundance during the late breeding season. Productivity accounts for variation due to predation pressure, clutch size, rate of double-brooding, and food abundance (Nagy & Holmes 2004). Many populations are food-limited (Martin 1987, Newton 1988), and food abundance is a key determinant of annual productivity in BTBW at the range core (Rodenhouse & Holmes 1992, Nagy & Holmes 2004, Sillett et al. 2000, Townsend et al. 2016). Nestling mass is affected by a variety of factors intrinsic to a habitat, such as predator abundance, food availability, and local climate (Naef-Daenzer & Keller 1999, Sillett et al. 2000, de Zwaan et al. 2019), and is often a good predictor of post-fledging and first-year survival (Ringsby et al. 1998, Monrós et al. 2002, Dybala et al. 2013). Outside of effects on productivity and nestling mass, late-season food abundance may also have direct effects on post-fledging survival of juvenile BTBW (Hatt 2013). Nestling mass and late-season food abundance may therefore impact recruitment independently of productivity. These breeding factors may also affect apparent survival either negatively, if adults invest heavily in reproduction when conditions are favorable at the expense of future survival (Roff 1993), or positively, if adults emigrate away from areas when breeding success or habitat quality are poor (Doligez et al. 2002, Cline et al. 2013). The goal of this chapter was not to determine all possible interacting pathways through which breeding-ground effects are affecting populations. Instead, my goal was to determine the relative strength of each breeding-ground effect for explaining variation in recruitment, apparent survival, and population growth.

Productivity at the range core is positively and significantly correlated with the number of recruiting birds in the next year (Sillett et al. 2000, Sillett & Holmes 2005); therefore, I hypothesized that populations at both range positions are most sensitive to changes in productivity. Additionally, low elevation populations at the trailing edge are near their elevational and latitudinal range limits; therefore, these areas have the highest likelihood of acting as sink populations maintained by recruitment from higher elevations. Source-sink dynamics have previously been theorized to be major drivers of BTBW distributions at the trailing edge (Graves 1997). I hypothesized that elevational source-sink dynamics are more pronounced at the trailing edge than at the range core. I predicted that the primary drivers of population dynamics would show more variation along the elevational gradient at the trailing edge compared to at the range core. I assessed how the three breeding-ground effects affected population growth rates using an age-structured Bayesian hierarchical model to directly estimate the effect of the potential mechanisms on recruitment and apparent survival.

Methods

Long-term BTBW demography data were collected at two range positions: the trailing edge and the range core. The trailing edge study site was in the Nantahala National Forest near the Coweeta Hydrologic Laboratory in western North Carolina (35.1°N, 83.4°W) while the range core study site was in the Hubbard Brook Experimental Forest in New Hampshire (43°56′N, 71°45′W). Both sites are in contiguous, northern hardwood forest. At both sites, BTBW demography was studied at study plots located at three different elevations (low, mid, and high) roughly spanning the elevational range in which BTBW breed. See Chapter 2 for a more detailed description of the study plots and study area at each range position. Habitat quality increases with elevation at both range positions, as temperature, precipitation, food abundance, and abundance of the preferred nesting substrate are all correlated with elevation (Chapter 2, Stodola et al. 2013, Cline et al. 2013, Kaiser et al. 2015). The high-elevation study plots may therefore act as source areas for the low-elevation study plot at each range position.

Breeding demography of BTBW was studied at the trailing edge from 2002-2019 and at the range core from 2002-2015. At the trailing edge, the high-elevation plot was not established until 2003 while the low-elevation plot was not sampled after 2008 due to the population declining to near extirpation (Stodola et al. 2013). Study plots were surveyed approximately every 2 days during the breeding season to assess breeding density and map territories of BTBW. Intensive nest-searching was undertaken in an endeavor to find all nests of BTBW breeding on the study plots. Once found, nests were monitored approximately every 1-4 days (average 2), moving to every day when close to the anticipated fledge date. Nests were monitored until either they failed or fledged young. Nestlings were weighed and banded with USGS aluminum leg bands 6 days after hatching, estimated to be the last day of the nesting cycle that nestlings can be safely handled without risk of force-fledging (Stodola et al. 2010). Unbanded females were captured by flushing them off nests and into mist-nets, whereupon they were banded with a USGS aluminum leg band and a unique combination of three plastic colored leg bands. Captured birds were aged based on plumage characteristics (Pyle 1997) as either second-year (SY) or after-second-year (ASY). Some females were classified as after-hatch-year (AHY) because they possessed intermediate plumage characteristics. A few females were not caught in each year, but

I used territory maps to estimate the number of unbanded females breeding on each study plot in each year.

Annual productivity was calculated by summing the total number of fledglings produced by each female in each year (Rodenhouse & Holmes 1992). In about 10% of instances where a nest was known to have fledged, the actual nest was not located but a family group of adults and dependent fledglings was found in the nearby area. Fledgling detections are likely to undercount the actual number of young fledged because fledglings have high mortality in the first few days post-fledging (Rush & Stutchbury 2008, Hatt 2013, Jones et al. 2016). Furthermore, adults frequently divide the brood for parental care (Holmes et al. 2017). I used the nesting data to simulate total brood size for family groups found after fledging. Brood size decreases throughout the season, as modal clutch size decreases from 4 eggs to 3 roughly around June 20th at both range positions (data not shown). Nests were therefore classified into one of two time periods: either "early" or "late" based on if laying started before this date. For each time period at each study plot, I calculated the probability of successful nests fledging 1-5 young and used this vector of probabilities in a categorical distribution to predict brood size for nests found after fledging. I used the larger of the simulated brood size and the actual number of fledglings observed in the calculation of annual productivity. Clutch reduction experiments were undertaken at the range core between 2013-2015, where 4.4% of successful nests had 1-2 eggs removed. In these cases, I calculated the probability of each young surviving from lay through fledge in unmanipulated nests. This probability was used in a binomial distribution to predict how many of the removed eggs would have hatched and fledged if the nest had not been manipulated. I averaged yearly values of fledglings/female to calculate yearly per-capita productivity at each study plot.

I fit a linear mixed-effects model at each study plot to predict average nestling mass in each year. Models were fit with a separate intercept for each year. I included random effects of day of season and nest ID to account for seasonal changes in nestling mass and correlation in mass among brood-mates (Hochachka & Smith 1991, Slagsvold 1984, McCarty & Winkler 1999, García-Navas & Sanz 2010). Models were used to predict average nestling mass at the midpoint of the breeding season in each year at each study plot. At the trailing edge, nestling mass was not recorded in 2002 and could not be measured in 2017 at the mid-elevation plot because no nests survived until nestling day 6. Nestling mass has declined over the study period at both range positions (Chapter 4), so I predicted nestling mass in years without data using a second linear mixed-effects model with a temporal trend.

The abundance of caterpillars (order Lepidoptera) was assessed bi-weekly during the summer, as caterpillars are the primary food source for BTBW during the breeding season (Robinson & Holmes 1982, Rodenhouse & Holmes 1992). Larval sawflies (order Hymenoptera) were also counted at the trailing edge, as they are functionally similar to caterpillars. Surveys were conducted over 5 consecutive 2-week sampling periods lasting from May 1 through mid-July at the trailing edge. Surveys were conducted over 4 consecutive 2-week sampling periods from late-May through late-July at the range core. Observers visited a series of grid points located along transects spanning the study plots and visually examined 50 leaves and petioles from two specimens each of common understory plant species. The length and number of caterpillars per 50-leaf sample was recorded. Plant species surveyed for caterpillars were northern/scarlet red oak (*Quercus* sp.), red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), and American chestnut (*Castanea dentate*) at the trailing edge. Species surveyed at the range core were American beech (*Fagus grandifolia*), sugar maple (*Acer* *saccharum*), striped maple, and hobblebush (*Viburnum lantanoides*). Biomass (mg) of caterpillars was calculated based on length-to-biomass equations from Rogers et al. (1977). BTBW forage predominantly in the understory (Holmes 1986); therefore, these surveys are representative of food abundance for BTBW.

Caterpillar sampling was varied slightly from 2003-2006 at the low and high elevation plots at the range core. Caterpillars were sampled at individual BTBW territories rather than at grid points along transects, which consisted of bi-weekly sampling of 50-leaves of the focal understory plant species 10m from the territory center in each of the four cardinal directions. Survey data are comparable between transect and territory-level counts, as they both involve counting and measuring the length of caterpillars on 50-leaf samples of the same plant species. The main difference was that each territory survey sampled each plant species 4 times (1 in each cardinal direction) rather than 2 times as in the transect surveys. To better match the transect surveys, I randomly subset the territory-level surveys to only include two 50-leaf samples from each of the focal plant species at each territory in each sampling period. I subset all caterpillar data to the late-breeding season, mid-June to mid-July at the trailing edge and late-June to late-July at the range core, and averaged biomass values in each year at each study plot.

I used an individual-based Bayesian hierarchical model to directly model the effects of the three breeding-ground effects on per-capita recruitment and apparent survival, which then infers effects on population growth. The population model has been described in detail in Chapter 2, so I only briefly summarize it here. The population model is based on the Jolly-Seber model (Kéry & Schaub 2011) but is modified to be age-structured and incorporate yearly counts of unbanded females and individual capture histories of banded females. Individual state at time *t* is represented by a binary variable, $z_{i,t}$, where alive birds are represented by $z_{i,t} = 1$.

Abundance in year t (N_t) is the sum of $z_{i,t}$, and represents the sum of the alive, unbanded females (U_t) and the alive, banded females ($marked_t$). Abundance is not directly observed, so I used a data augmentation approach (Royle et al. 2007). Beyond the first year, the number of SY birds entering the population in year t is given by the formula: $E(n_{t-1})\gamma$, where $E\left(n_{1,t-1}\right)$ is the expected female abundance in $t-1$ and γ is the per-capita recruitment rate. Individuals alive in time $t-1$ ($z_{i,t-1}=1$) survive and return to the study plot in time t based on the formula: $\text{Bernoulli}\left(z_{i,t-1}\phi_{a_{i,}}\right)$, where ϕ_{a_i} is age-specific apparent survival. Unbanded females are captured with probability $p_t^{(c)}$ and classified into a specific age class (SY/ASY) rather than AHY with probability k based on the formula: $\text{Bernoulli}\left(z_{i,t}\times p_t^{(c)}\times k\right)$. Marked females are resighted on the study plots with probability $p^{(\eta)}$, based on the formula: $\text{Bernoulli}\left(z_{i,t}\times p^{(\eta)}\right)$. The probability of not detecting a female breeding on the study plots over the course of the entire season is extremely low (Chapter 2), so $p^{(\eta)}$ largely represents the probability of breeding on the study plot. Yearly counts of unbanded females arise from a binomial distribution: $Binomial\left(U_t, p^{(\eta)}\right)$. Models were run separately for each of the six study plots.

For each of the three breeding-ground effects, I fit a separate model for a trend effect of the breeding-ground effect on γ and ϕ. Two additional models were fit at each study plot: a null model with constant γ and ϕ and, to account for temporal autocorrelation, a temporal model with a time-trend effect on γ and ϕ (Neate-Clegg et al. 2021). To test for potential source-sink dynamics, I fit an additional model for the low and mid elevation plots at both range positions (referred to as source models) allowing γ at the study plot to vary based on per-capita productivity at the high-elevation plot. No breeding-ground effects were correlated at a study plot (r<0.7), except for nestling mass and late-season food biomass at the low-elevation plot at the trailing edge. In this case, I only fit the model allowing for trend effects of late-season food on demographic rates. Competing models at each study plot were ranked via Watanabe–Akaike information criterion (WAIC, Watanabe 2010, Gelman et al. 2014).

Models were fit via Markov Chain Monte Carlo (MCMC) methods in JAGS (Plummer 2003), using 3 chains of 35000 iterations following an adaptive chain of 1000 iterations. Vague priors were used for all parameters, and model convergence was assessed through visual inspection of MCMC chains. All analyses were conducted in R version 4.0.3 (R Core Team 2020) using the 'nlme' (Pinheiro et al. 2017) and 'rjags' packages (Plummer 2016).

Results

A different model was supported with all of the WAIC weight at most study plots (Table 3.1). Each breeding-ground effect was supported as the top model, based on WAIC weight, for a least one study plot. One objective of this chapter was to determine the effect of breeding-ground effects on population dynamics, so I report results from all models which received more support than the null model (constant recruitment and apparent survival) and the temporal-trend model.

Of the three-breeding ground effects, nestling mass best explained variation in population dynamics at the high-elevation plots at both range positions. Nestling mass positively affected apparent survival at the trailing edge (Figure 3.1 B, med = 0.32, 95% credible interval 0.03 – 0.63) but tended to negatively affect recruitment (Figure 3.1 C, med = -0.07, 95% credible interval -0.23 – 0.08). The contrasting effects of nestling mass on recruitment and apparent survival led to a relatively small net effect on population growth at the high-elevation plot at the trailing edge (Figure 3.1 A). Though the top breeding-ground effect model at the high-elevation plot was also for an effect of nestling mass, no breeding-ground effect model performed better than the temporal trend model (Table 3.1).

Top models at the mid-elevation plots differed between range positions. The top model at the trailing edge was for an effect of late-season food abundance on population dynamics, which was mostly driven by the effect on recruitment. Uncertainty was high, but greater late-season food biomass generally led to higher recruitment and population growth (Figure 3; med = 0.14, 95% credible interval -0.11 – 0.38). Models for nestling mass and source productivity also performed better than the null and temporal models, though only nestling mass had a discernable effect on demographic and population growth rates. Nestling mass tended to be positively correlated with recruitment, apparent survival, and population growth at the mid-elevation plot at the trailing edge (recruitment: med = 0.13, 95% credible interval -0.11 – 0.42; apparent survival: med = 0.21, 95% credible interval -0.22 – 0.69), but credible intervals overlapped 0. In contrast, the effect of per-capita productivity was the top model at the range core. Similar to the top model at the trailing edge, this was mainly driven by a strong positive effect on recruitment (Figure 3.3; med = 0.20, 95% credible interval 0.07 – 0.35). The second-best model was for the effect of per-capita productivity at the high-elevation plot on recruitment (source model). Recruitment to the mid-elevation plot tended to be positively correlated with productivity at the high-elevation plot (recruitment: med = 0.06, 95% credible interval -0.02 – 0.14).

The top model at the low-elevation plots also differed between range positions. The top model at the range core was for an effect of late-season food abundance while the top model at the trailing edge was for an effect of per-capita productivity at the high-elevation plot on recruitment (source model). These results do not seem reliable, however, as they were largely driven by one outlier year at each range position with a high value of the breeding-ground effect and high population growth. No other model at either range position showed a discernable relationship between breeding-ground effects and population dynamics. The lack of fit at the low-elevation plots may be explained, at least partially, by the low population sizes at these plots; there were less than 10 females breeding on the plots in some years. WAIC scores of the population models seemed to be sensitive to outlier values at low population sizes, as loss or gain of 1 or 2 birds has a substantial effect on per-capita rates (Chapter 2). As an alternative to the population modelling at the low-elevation plots, I show the long-term trends in breeding-ground effects and female density (Chapter 2). Visually examining the temporal trends shows that some breeding-ground effects are more strongly correlated to population fluctuations than others. Only average nestling mass and late-season food abundance declined alongside female density at the trailing edge (Figure 3.4). Food abundance, in particular, sharply declined over the study period. All breeding parameters showed a similar temporal pattern to population density at the range core to some extent, though productivity and late-season food seemed to best track population fluctuations with a 1-year time lag (Figure 3.5).

Discussion

This chapter is one of the first to document spatial variation in the mechanistic drivers of population dynamics across a species' geographic range. Little is known about this topic due to the cost and effort required to collect long-term demographic data at multiple study sites; however, my results are consistent with the few other studies showing geographic variation in the drivers of population dynamics (e.g., Baskauf 2003, Hoffman et al. 2010). Other studies have shown broad-scale variation in the drivers of population dynamics between widely separated populations. My results show that this can also occur at much finer scales, and even between breeding areas as little as 1km apart. The drivers of population dynamics were broadly similar between range positions, and the differences among elevations were slight. Heterogeneity in responses to breeding-ground effects suggests that local population dynamics are influenced by local environmental conditions.

Contrary to my hypothesis, population dynamics at most study plots were not driven by per-capita productivity. This was especially evident at the trailing edge, where models incorporating local productivity received little support and were never supported above the null and temporal models. This result is surprising, as previous research from the range core has shown that recruitment rate in BTBW is significantly and positively correlated with productivity (Sillett et a. 2000, Sillett & Holmes 2005). The low support for productivity models at most study plots could have occurred if local population dynamics were more directly affected by conditions during the post-breeding period than by breeding-season productivity. For example, greater nestling mass and late-season food abundance often are correlated with higher survival of juveniles during the post-fledging period (Wiens et al. 2006, Vitz & Rodewald 2011, Dybala et al. 2013, Hatt 2013). Variation in juvenile survival may have a larger effect on population dynamics than does variation in productivity (Streby & Anderson 2011). Besides direct effects on juvenile survival, variation in nestling quality and late-season food may affect population dynamics by acting as a form of public information about habitat quality. During the post-breeding period, juveniles and adults of many species, including BTBW, prospect for future breeding sites to which they will return next year (Doligez et al. 2004, Betts et al. 2008). Birds can directly assess breeding conditions and nestling quality in prospective breeding areas (Doligez et al. 2002); therefore, variation between years in nestling mass and late-season food abundance may affect recruitment and adult emigration regardless of any effects on juvenile survival.

The top models at each study plot generally showed a positive correlation between the supported breeding-ground effect and demographic rates, except for the negative correlation between nestling mass and per-capita recruitment at the high-elevation plot at the trailing edge. This counterintuitive result may occur through site-dependent processes, such that high-quality habitats at the highest elevations are preferentially-selected by returning, dominant individuals (Rodenhouse et al. 1997, Rodenhouse et al. 2003). This hypothesis is supported by the strong positive correlation between nestling mass and apparent survival at this plot. True survival is often inseparable from permanent emigration when estimating apparent survival; however, adult emigration in BTBW may not be uncommon, especially from poor habitat conditions (Holmes et al. 1996, Cline et al. 2013, Chapter 2). Furthermore, adults are more likely to emigrate from areas producing poor-quality fledglings and to immigrate to areas producing high-quality fledglings (Doligez et al. 2002). Breeding philopatry, therefore, may be positively correlated with spatial and temporal variation in nestling quality, either by adults responding directly to variation in nestling quality or by responding indirectly to yearly variation in microclimate, nest predators, food abundance, and other factors that determine nestling mass. If high-quality habitat at the high elevations is limited at the trailing edge, then recruitment of young, subordinate birds to the highest-quality habitats may be limited by pre-emptive selection by returning, competitively dominant adults (Buston 2003, Sergio et al. 2007). Recruitment of young birds to the high-elevation habitats may be further limited through adult dispersal from lower, poorer-quality habitats to higher, better-quality habitats (Holmes et al. 1996, Rodenhouse et al. 2003), especially following years where high-quality young are produced at the high elevations (Doligez et al. 2002). Decreased philopatry or adult immigration following years of poor nestling condition may lead to more opportunities for young birds to recruit to the high elevations.

Recruitment at the high elevations may therefore only be indirectly related to nestling mass through being jointly correlated with adult apparent survival. In support of this hypothesis, nestling mass had a stronger effect on apparent survival than on recruitment.

In contrast to the higher elevations, late-season food abundance seemed to best explain population fluctuations at both low-elevation plots and at the mid-elevation plot at the trailing edge. Low elevation habitats at both range positions are generally poor quality, as they are the warmest, driest, and have the least amount of food and nesting substrate (Cline et al. 2013, Stodola et al. 2013, Kaiser et al. 2015, Chapter 2). The mid-elevation plot at the trailing edge can also be considered poor-quality habitat, as it is relatively dry with little in the way of suitable nesting substrate for BTBW (Chapter 2). Food is a major limiting factor for many populations (Newton 1980, Newton 1998), including in BTBW (Rodenhouse & Holmes 1992, Nagy & Holmes 2005), and fluctuations in food abundance are likely to have a greater effect on individuals in poor-quality habitats (Lin & Batzli 2001, Studds & Marra 2007, Kaiser et al. 2015). Yearly variation in food abundance can affect all populations across elevations and habitat types, but the strongest effects are likely to be observed in the food-poor habitats at the lower elevations.

Of the poor-quality study plots, the demographic link between late-season food abundance and population dynamics could only be determined at the mid-elevation plot at the trailing edge. Food abundance may have driven population fluctuations through a combination of direct effects and indirect effects on demographic metrics such as nestling mass (trailing edge) or productivity (range core) at the low-elevation plots, but late-season food drove population dynamics through a positive correlation with per-capita recruitment at the mid-elevation plot. Late-season food had little effect on apparent survival; however, BTBW population declines at this plot were driven by declining apparent survival (Chapter 2). I advise caution before interpreting this result to mean that late-season food abundance did not cause population declines. I only modeled the effects of average late-season food biomass on population dynamics; however, birds may instead be responding to changes in the size or spatial distribution of caterpillars (Naef-Daenzer & Keller 1999, Naef-Daenzer et al. 2000, Chapter 4). Though not the best-supported model, nestling mass was positively correlated with apparent survival at this study plot. Effects of food abundance on apparent survival may therefore be indirect through effects on nestling mass. More study is needed to determine the potential mechanisms underlying population declines at the low and mid elevation plots at the trailing edge.

I found little evidence that low-elevation plots acted as sink habitats maintained by higher-elevation source populations, especially at the trailing edge. This does not imply, however, that birds do not recruit to lower elevations. Breeding birds were extirpated from the low-elevation plot at the trailing edge before 2016, yet in 2017 a single male, apparently without a mated female, had recruited to the study plot (Chapter 2). The low-elevation breeding limit of BTBW in this region had shifted well upslope of the study plot by this time (R. Chandler unpub. data), so this bird must have recruited from a higher elevation. Following a particularly cold spring in 2020 at the trailing edge, many BTBW recruited, and even successfully reproduced, at low elevation habitats that had been vacated for years (R. Chandler unpub. data). These observations show that birds can successfully recruit from higher to lower elevations, especially if weather conditions at the high elevations are unfavorable. The results of this study, however, suggest that this elevational recruitment is not a major driver of population dynamics at low elevations. Changes in productivity at the high-elevations are unlikely to be the mechanistic drivers of low-elevation BTBW population declines.

The results of this chapter show that each of the three breeding-ground effects can have a strong effect on local population dynamics; however, population dynamics are also likely to be affected by a variety of factors that I did not include in the analysis. No breeding-ground effect adequately explained population fluctuations at the high-elevation plot at the range core, likely indicating that some other factor was principally driving population dynamics. Populations have remained stable at this study plot over the past 20 years; however, apparent survival has declined, and per-capita recruitment has increased (Chapter 2). The factors driving these changes are unclear. A potential explanation is that the boreal ecotone has been shifting downslope into the elevational range of the high-elevation plot at the range core (Foster & D'Amato 2015), which may have led to changes in vegetation structure or boreal-associated nest predators (Hallworth et al. in review). It seems surprising that changes in habitat or community interactions would not affect population dynamics through changes in the three breeding-ground effects, though birds could have based settlement and emigration decisions on direct assessment of vegetation or predator communities (Morton 2005, Buler et al. 2007, Pärt et al. 2011). Conditions experienced during the non-breeding season could have also affected breeding-ground population dynamics (Robbins et al. 1989, Sanderson et al. 2006, Hewson et al. 2016, Rushing et al. 2017). I found that breeding-ground effects had a strong effect on local population fluctuations at most study plots, but threats faced throughout the annual cycle likely interact to drive population dynamics (Sillett et al. 2000, Runge & Marra 2005, Rushing et al. 2017).

The results of this chapter show that the primary drivers of local BTBW population dynamics are highly variable between study plots in close proximity, but do not broadly differ between range positions. What environmental conditions may be driving the differential response at each study plot is not immediately clear, but potential drivers include spatial variation in microclimate, phenology, vegetation structure, and the distribution of prey, competitors, and predators (Both et al. 2006, Burgess et al. 2011, McNew et al. 2012, Gaynor et al. 2019, Oldfather & Ackerly 2019, Peterson et al. 2021). The degree of variability in driving factors implies that the mechanisms underlying BTBW population declines at the trailing edge are likely to be complex. Despite this variability, I observed little effect of productivity on local population dynamics at the trailing edge. This result does not imply that productivity is an unimportant determinant of population dynamics in this region; however, it may imply that productivity is not the primary mechanism through which climate change is causing trailing-edge population declines. Instead, late-season food abundance appeared to have the strongest total effect on population dynamics in poor-quality habitats at the lower-elevation study plots. The three poor-quality study plots are also the only ones where BTBW populations have declined, or are predicted to decline, in response to warming temperatures (Chapter 2). Climate change can indirectly affect populations through trophic interactions (Both et al. 2006, Pearce-Higgins et al. 2010) and has led to pronounced shifts in invertebrate communities and distributions (Parmesan et al. 1999, Kocsis & Hufnagel 2011, Pureswaran et al. 2018); therefore, I hypothesize that changes in caterpillar abundance is the mechanism through which climate change is affecting trailing-edge BTBW declines. Changing food abundance may cause BTBW population declines through multiple interacting pathways, such as changes in post-fledging survival, public information, and nestling condition. This study provides an important first step in identifying the mechanisms underlying climate-induced population declines by determining the effects of breeding-ground effects on population dynamics. Further research is needed studying long-term climate-induced changes in the breeding-ground effects to determine if they can explain the pattern of low elevation population declines for trailing edge populations in the Southern Appalachians.

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Table 3.1. WAIC model selection results for the effect of three breeding-ground effects on recruitment and apparent survival of black-throated blue warblers breeding across an elevational gradient at the trailing edge and range core. Results are shown for all 6 study plots, though models were run separately for each plot. Demographic rates were allowed to vary based on a linear trend in average nestling mass 6 days post-hatch (NestMass), average late-season food abundance (LSFood), or per-capita productivity (Prod). A null (Null) and temporal-trend (Time) model were also run at each study plot, with either constant or a time-trend on per-capita recruitment and apparent survival, respectively. To test for source-sink dynamics, an additional model was built at the low and mid elevation plots at each range position allowing for a linear trend in the per-capita productivity at the high-elevation plot (ProdSource). For each model other than ProdSource, both apparent survival and recruitment were allowed to vary with a trend-effect of the explanatory variable. The nestling mass model was not run at the low-elevation plot at the trailing edge, as nestling mass was correlated with late-season food. See text for more details.

Range Position	Elevation	Model	WAIC	ΔWAIC	w
Trailing edge	Low	ProdSource	12289.8	0	1
Trailing edge	Low	Time	12330.9	41.1	<0.001
Trailing edge	Low	Null	12667.3	377.5	<0.001
Trailing edge	Low	LSFood	12965.5	675.7	<0.001
Trailing edge	Low	Prod	13317.6	1027.8	<0.001
Trailing edge	Mid	LSFood	40008.3	0	1
Trailing edge	Mid	NestMass	40388.2	379.9	<0.001
Trailing edge	Mid	ProdSource	40407.7	399.4	<0.001
Trailing edge	Mid	Null	40466.7	458.4	<0.001
Trailing edge	Mid	Prod	40666.0	657.7	<0.001
Trailing edge	Mid	Time	42324.8	2250.1	<0.001
Trailing edge	High	NestMass	65287.9	0	1
Trailing edge	High	Time	66440.7	1152.8	<0.001
Trailing edge	High	Prod	66652.1	1364.2	<0.001
Trailing edge	High	Null	66917.7	1629.8	<0.001
Trailing edge	High	LSFood	67251.8	1963.8	<0.001

Range core	Low	LSFood	50573.1	0	1
Range core	Low	NestMass	51154.2	581.1	<0.001
Range core	Low	Null	51579.6	1006.5	<0.001
Range core	Low	Time	51801.1	1228.0	<0.001
Range core	Low	Prod	52083.5	1510.4	<0.001
Range core	Low	ProdSource	52458.8	1885.7	<0.001
Range core	Mid	Prod	130001.1	0	1
Range core	Mid	ProdSource	130931.7	930.6	<0.001
Range core	Mid	Null	131099.7	1098.6	<0.001
Range core	Mid	LSFood	131129.7	1128.6	<0.001
Range core	Mid	Time	131472.2	1471.2	<0.001
Range core	Mid	NestMass	131773.6	1772.6	<0.001
Range core	High	Time	74455.8	0	1
Range core	High	NestMass	74907.3	451.5	<0.001
Range core	High	LSFood	75023.7	567.9	<0.001
Range core	High	Prod	75255.7	800.0	<0.001
Range core	High	Null	75616.6	1160.8	<0.001

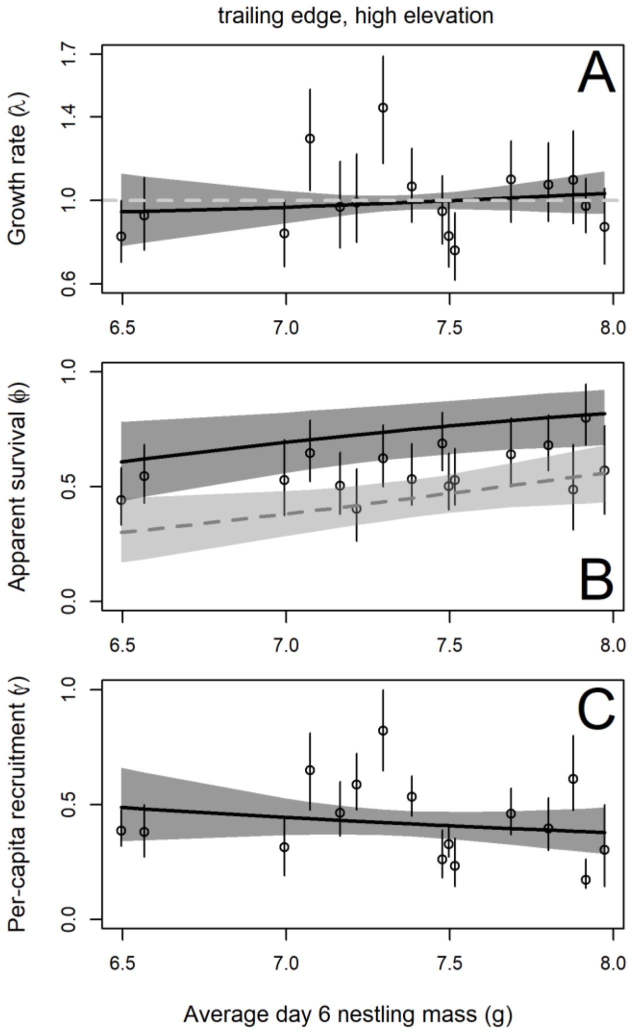

Figure 3.1. Model estimates for the effect of average black-throated blue warbler nestling mass on (A) population growth rate, (B) apparent survival, and (C) per-capita recruitment at the high-elevation study plot at the trailing edge. Nestling mass was measured 6 days post-hatch. The gray dashed line in panel A represent no change in population size. Median values (line) and 95% credible intervals (shaded) are shown. Open circles represent median predictions and 95% credible intervals at the observed values of average nestling mass in each year. Estimates of SY (solid black) and ASY (dashed gray) apparent survival are shown. Predictions at the observed values in panel B represent averaged predictions of apparent survival between age classes. See text for more details.

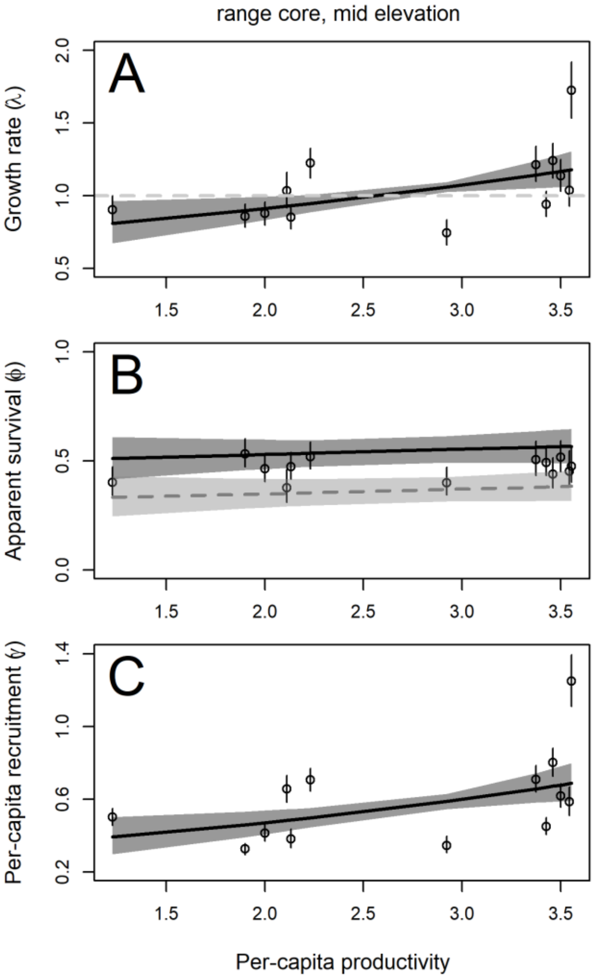

Figure 3.2. Model estimates for the effect of average late-season food abundance on black-throated blue warbler (A) population growth rate, (B) apparent survival, and (C) per-capita recruitment at the mid-elevation study plot at the trailing edge. The gray dashed line in panel A represents no change in population size. Median values (line) and 95% credible intervals (shaded) are shown. Estimates of SY apparent survival are shown, though estimates of ASY apparent survival showed a similar trend. Open circles represent median predictions and 95% credible intervals at the observed values of average late-season food abundance in each year. Estimates of SY (solid black) and ASY (dashed gray) apparent survival are shown. Predictions at the observed values in panel B represent averaged predictions of apparent survival between age classes. See text for more details.

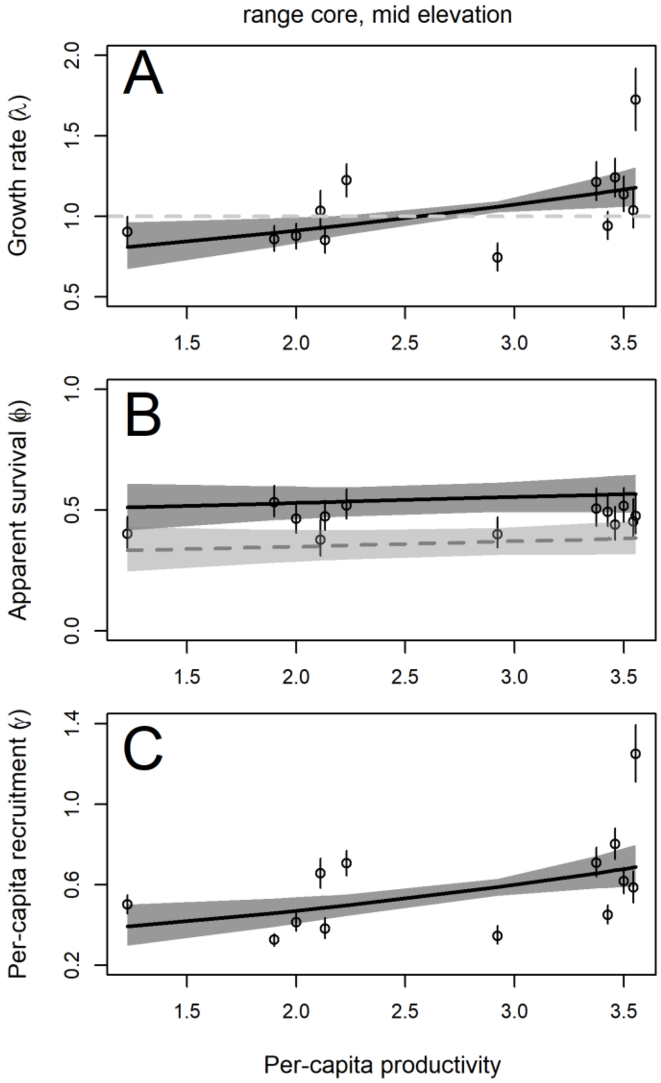

Figure 3.3. Model estimates for the effect of per-capita productivity on black-throated blue warbler (A) population growth rate, (B) apparent survival, and (C) per-capita recruitment (C) at the mid-elevation study plot at the range core. The gray dashed line in panel A represents no change in population size. Median values (line) and 95% credible intervals (shaded) are shown. Open circles represent median predictions and 95% credible intervals at the observed values of per-capita productivity in each year. Estimates of SY (solid black) and ASY (dashed gray) apparent survival are shown. Predictions at the observed values in panel B represent averaged predictions of apparent survival between age classes. See text for more details.

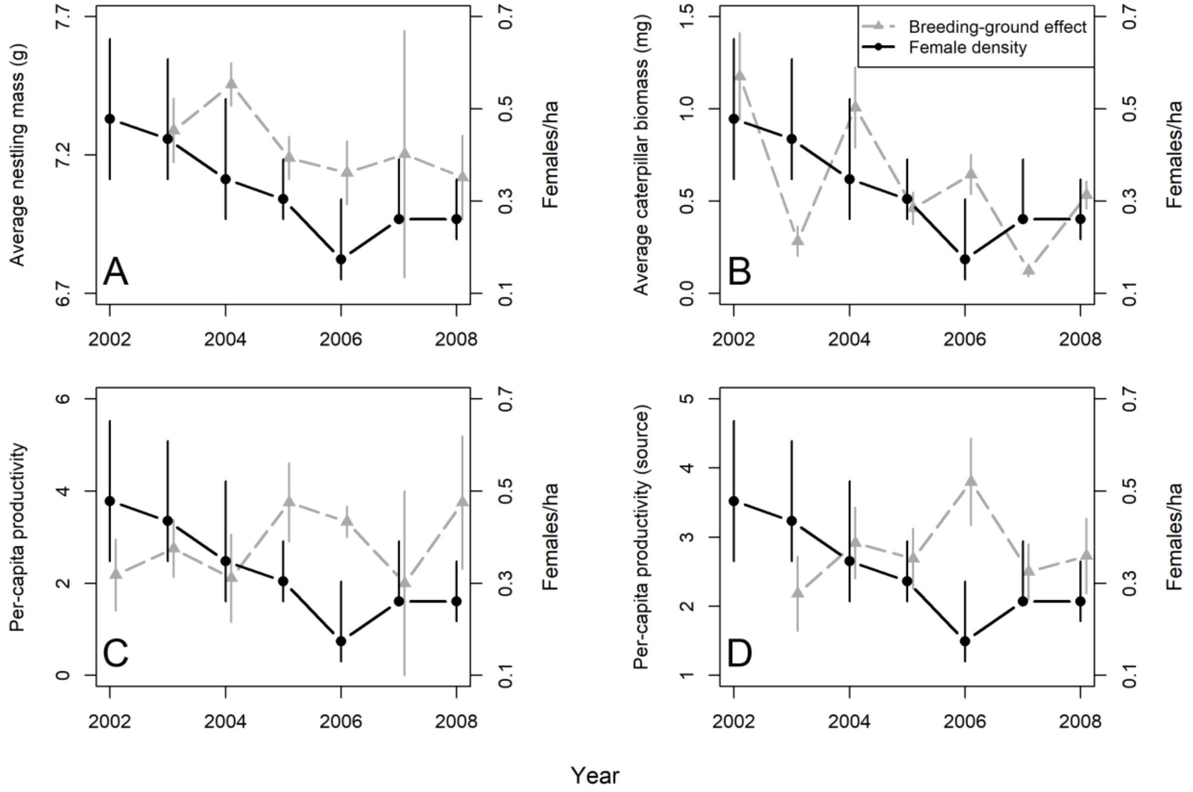

Figure 3.4. Temporal trends in female black-throated blue warbler density at the low-elevation study plot at the trailing edge (Chapter 2) in relation to temporal trends in average nestling mass 6 days post-hatch (A), average late-season food abundance (B), per-capita productivity at the low-elevation plot (C), and per-capita productivity in the potential source area at the high-elevation plot (D). Female density is denoted with black circles while breeding-ground effects are denoted with gray triangles. Note that nestling mass at the low-elevation plot and productivity at the high-elevation plot were not recorded before 2003. Median and 95% credible intervals are shown for female density, and mean and se bars are shown for breeding-ground effects. See text for more details.

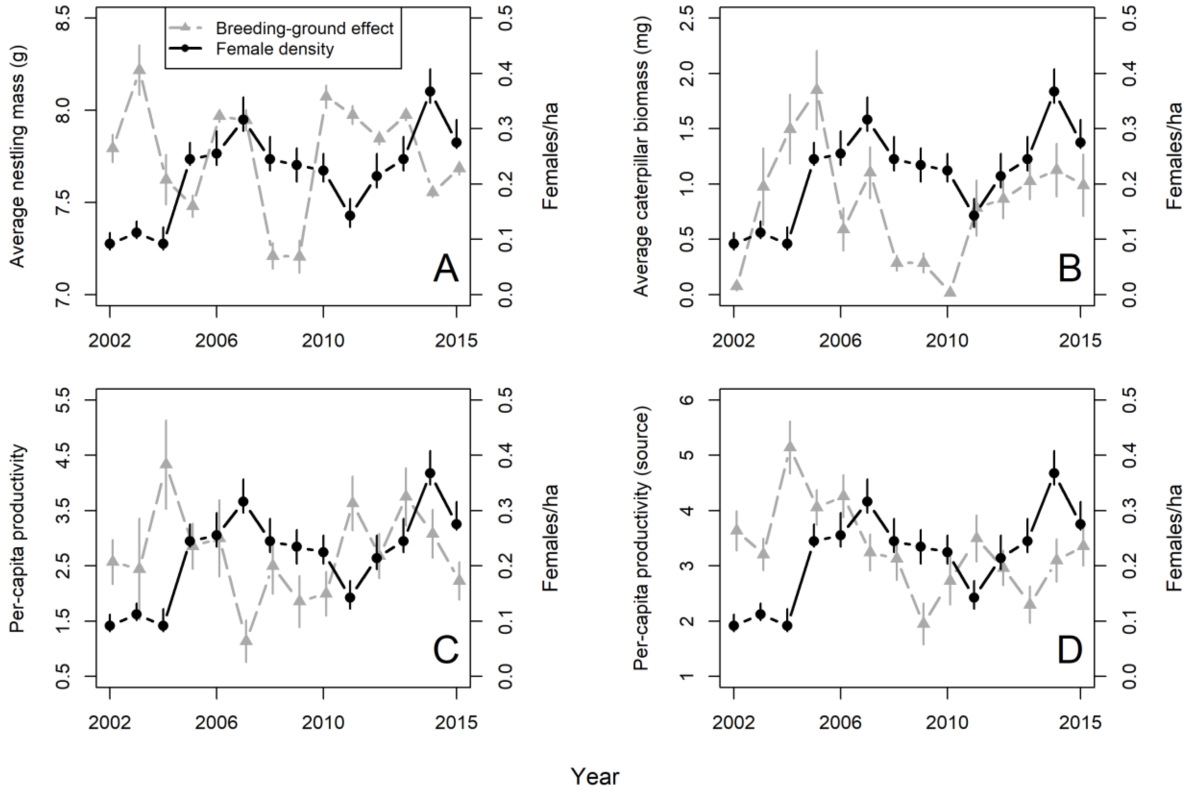

Figure 3.5. Temporal trend in female black-throated blue warbler density at the low-elevation study plot at the range core (Chapter 2) in relation to temporal trends in average nestling mass 6 days post-hatch (A), average late-season food abundance (B), per-capita productivity at the low-elevation plot (C), and per-capita productivity in the potential source area at the high-elevation plot (D). Female density is denoted with black circles while breeding-ground effects are denoted with gray triangles. Median and 95% credible intervals are shown for female density, and mean and se bars are shown for breeding-ground effects. See text for more details.

CHAPTER 4

ASSESSING PROXIMATE MECHANISMS OF TRAILING EDGE RANGE CONTRACTIONS: LONG-TERM DECLINES IN BREEDING-GROUND EFFECTS FROM ACROSS THE GEOGRAPHIC RANGE OF BLACK-THROATED BLUE WARBLERS (SETOPHAGA CAERULESCENS)[1]

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[1] Lewis, W.L., R.J. Cooper, R.B. Chandler, T.S. Sillett, R.W. Chitwood, K.W. Stodola, M.H. Cline, J.L. Hatt, M.T. Hallworth, S.A. Kaiser, and N.L. Rodenhouse. To be submitted to *Ecology*.

Abstract

Climate change is driving trailing edge range contractions in many species, but little is known about the proximate mechanisms through which climate change affects trailing edge populations. Determining the mechanistic drivers of climate change is important, not just for understanding how climate change affects populations, but also for predicting future responses to climate change. I used a long-term breeding demography dataset from the trailing edge and the range core of black-throated blue warblers (*Setophaga caerulescens*) to assess long-term trends and climate effects on three potential mechanisms: productivity, nestling quality, and food abundance. All breeding-ground effects declined over time at both range positions; however, none perfectly mirrored the spatial and temporal pattern of warbler population decline. Mechanistic effects of climate change at the trailing edge appear complex, including both top-down effects of nest predators and, especially, bottom-up effects of declining food abundance. The results of this chapter suggest that understanding the mechanisms through which climate change affects populations requires understanding how climate change is affecting communities.

Introduction

Anthropogenic climate change is widely recognized as one of the greatest threats facing ecosystems worldwide. Though climate change affects species throughout their geographic range, the strongest effects are frequently observed at the range margins (Anderson et al. 2009, Jiguet et al. 2010, Neate-Clegg et al. 2021). Range margins have been historically viewed as set by abiotic conditions at the cool edge and biotic conditions at the warm edge (e.g., MacArthur 1972, Kaufman 1995), but more recent evidence indicates that range limits at both warm and cold edges can be set by abiotic and biotic conditions (Wethey 2002, Cahill et al. 2014, Coristine & Kerr 2015, Merker & Chandler 2021). Populations at range margins are likely to be those most affected by climate change because they are closer to their ecological tolerance than populations within the core of the range (Sexton et al. 2009, Lee-Yaw et al. 2016). Climate change at the warm edge of the range is likely to push populations past their ecological tolerance (Deutsch et al. 2008, Cahill et al. 2014, Christine & Kerr 2015), explaining why many species' ranges have contracted at the low-latitude and low-elevation margins (Chen et al. 2011, Auer & King 2014, Taheri et al. 2020).

While many studies have documented population declines and range shifts at the trailing edge of ranges, few have determined the proximate mechanisms through which climate change brings about these declines (Cahill et al. 2013, Desforges et al. 2021). Climate change may have direct physiological effects on organisms (Deutsch et al. 2008, Cunningham et al. 2013); however, the main effect of climate change is frequently indirect through changes in habitat and biotic interactions (Martin 2007, Cahill et al. 2013, Thomas 2010). Climate change is likely to affect populations through multiple mechanistic pathways (McLean et al. 2016), but food availability is frequently cited as a primary mechanism (Both et al. 2006, van de Pol et al. 2010, Cahill et al. 2013, Desforges et al. 2021). In addition to food, climate change may bring about changes in habitat (Martin 2007, Trape 2009), competitive interactions (Alexander et al. 2015), disease (Garamszegi 2011), and predator communities or activity patterns (Weatherhead et al. 2010, Laws 2017). Understanding the proximate mechanisms through which climate affects populations is critically important for predicting how species will respond to ongoing climate change (Doak & Morris 2010, Urban et al. 2016, Desforges et al. 2021).

Due to the cost and effort associated with collecting long-term ecological data, studies investigating the proximate mechanisms behind climate-induced population declines are frequently constrained to a limited spatial extent and few study sites (e.g., Doak & Morris 2010, Desforges et al. 2021). Climate change brings about range shifts by creating spatial variation in proximate mechanisms, which in turn brings about spatial variation in demographic rates and population dynamics (Gaston 2009, McLean et al. 2016). Understanding the mechanisms behind range shifts, therefore, necessitates understanding how climate change affects demographics across broader spatial scales. Specifically, inferences on the mechanisms behind trailing edge range contractions would be strengthened by comparing declining populations from the trailing edge with stable or increasing populations from other parts of the range (e.g., Both et al. 2006).

Birds have frequently been used to assess the effects of climate change due to the availability of broad-scale and historical monitoring data (e.g., Parmesan & Yohe 2003, Auer & King 2014, Stephens et al. 2016). Birds are also highly mobile and have short generation times; therefore, they can rapidly respond to climate change (Maclean et al. 2008, Lindström et al. 2013). Many species of birds that breed in the northeastern United States and Canada reach the trailing edge of their breeding range in the southern Appalachian Mountains (Merker & Chandler 2020). Birds in these trailing edge populations are generally restricted to the high-elevation forests near the tops of the mountains, where conditions more closely resemble the climate and habitat further north in the range core. The Southern Appalachians provide an ideal setting for assessing the proximate mechanisms behind trailing edge declines, as low-elevation populations in this region are near both their latitudinal and elevational warm edge. Many trailing edge populations in this region are declining and shifting their ranges upslope (Stodola et al. 2013, Merker 2017, Sauer et al. 2017). Declines are likely driven by climate change on the breeding grounds (Chapter 2), but the proximate mechanisms underlying these declines are unknown.

The goal of this chapter is to assess the proximate drivers of trailing edge population declines by using a long-term breeding demography dataset from black-throated blue warblers

(*Setophaga caerulescens*, hereafter BTBW). BTBW are small, migratory songbirds which exhibit a trailing edge breeding distribution in the Southern Appalachians (Holmes et al. 2017). Populations have remained relatively stable over the past few decades within the core of the range but have been declining at low and mid elevations at the trailing edge (Chapter 2). Local BTBW population dynamics seem driven by local conditions rather than broad-scale latitudinal differences across the geographic range (Chapter 3); therefore, changes in breeding-ground effects may be assumed to have comparable effects on population dynamics at each range position. Previous research indicates that productivity, nestling mass, and food abundance all can affect BTBW population growth rates (Chapter 3); therefore, I hypothesized that these breeding-ground effects are acting as the proximate mechanisms driving trailing edge population declines.

The three breeding-ground effects likely have interacting, but not completely overlapping, positive effects on population dynamics. Food is a primary resource limiting BTBW populations and is an important determinant of both post-fledging survival and annual productivity (Rodenhouse & Holmes 1992, Sillett et al. 2000, Nagy & Holmes 2004, Hatt et al. 2013, Lany et al. 2016). In addition to food abundance, annual productivity is affected by nest survival rates and the length of the breeding season (Nagy & Holmes 2004, Lany et al. 2016, Townsend et al. 2013). Nestling condition is directly affected by nest microclimate and the amount of food provisioned by adults (Martin 1987, Stodola et al. 2010, Andreasson et al. 2018), though provisioning is dependent on food abundance and predation pressure in the surrounding environment (Van Balen 1973, Martin et al. 2011, de Zwaan et al. 2018). Nestling condition is frequently used as a proxy for first-year survival (Ringsby et al. 1998, Newton 1998, Sillett et al. 2000, Bouwhuis et al. 2015). Adults base emigration and immigration decisions on local breeding conditions (Holmes et al. 1996, Doligez et al. 2002, Cline et al. 2013); therefore, these breeding-ground effects may also affect apparent survival of adults. I predicted that breeding-ground effects acting as proximate mechanisms would be directly and negatively affected by climate variation. Furthermore, the temporal and spatial trends in the breeding-ground effect should mirror trends in BTBW population density. The strongest negative trends in the breeding-ground effect should, therefore, be observed at the lowest elevations at the trailing edge.

Methods

BTBW Data Collection

Long- term BTBW breeding demography data were collected at two range positions: the trailing edge study site was located near the Coweeta Hydrologic Laboratory (35.1°N, 83.4°W) in the Nantahala National Forest of western North Carolina and the range core site was located at the Hubbard Brook Experimental Forest (43°56′N, 71°45′W) in the White Mountain National Forest in New Hampshire. Both sites are in contiguous forest and have not experienced appreciable land use change over the past few decades. Temperature, precipitation, and habitat quality are correlated with the elevational gradient (Chapter 2, Stodola et al. 2009, Cline et al. 2013); therefore, at each range position breeding demography was studied at three plots (low, mid, and high elevations) roughly spanning the breeding elevation range of BTBW. See Chapter 2 for a further description of the study plots. I used breeding data from 2002-2019 at the trailing edge and 2002-2018 at the range core. The high elevation plot was not established until 2003 at the trailing edge, while the low elevation plot was not sampled after 2008 due to population declines almost to extirpation (Stodola et al. 2013, Chapter 2). The low and high elevation plots were not sampled after 2016 at the range core. Temperatures have increased at both range positions over the study period, while precipitation has also become more variable at the trailing edge (Chapter 2).

Each breeding season, intensive nest-searching was undertaken at each study plot to monitor BTBW breeding demography. Nests were monitored every 1-4 days (average 2) until failing or fledging young. Nests found after laying were backdated to determine lay date of the first egg. Backdating was based on average values of 13 days for incubation and 9 days for nestlings (Holmes et al. 1992). Nests found empty near the expected fledge date (~9 days after hatching) were confirmed to have fledged if fledglings were located or adults were observed carrying food. Otherwise, these nests were assumed to have fledged if parents were agitated at the presence of observers near nests or fecal sacs were observed underneath or on the rim of nests. Unbanded females were captured off nests using mist nets and banded with a USGS aluminum leg band and a unique combination of plastic colored leg bands. Several females could not be captured and banded in each year; however, unbanded females could still be identified within a year based on the location of their territories. Nestlings were weighed and banded with an aluminum leg band 6 days post-hatch. Nests and nestlings were only included in the analysis if at least 50% of the adult territory was located on the study plot.

Caterpillars (order Lepidoptera) are the primary food source for BTBW during the breeding season and are the predominant prey provisioned to nestlings (Goodbred & Holmes 1990, Rodenhouse & Holmes 1992). Caterpillar abundance was surveyed bi-weekly during the breeding season at all study plots to measure seasonal changes in food abundance. Caterpillar abundance was assessed at a series of sampling points located ~50m apart along transects crossing the study plots. At each survey point, observers visually inspected 50 leaves (leaf and petiole) from two specimens each of common sapling species in a 0.04ha circular area around the point. The number and length of caterpillars per 50-leaf sample was recorded. BTBW forage predominantly in the understory (Holmes 1986), so this survey method provides a reliable estimate of BTBW food abundance. I calculated caterpillar biomass based on length-to-biomass equations from Rogers et al. (1977). Sawfly larvae (order Hymenoptera) are functionally similar to caterpillars, so they were also recorded at the trailing edge. Surveys started in May (early May at the trailing edge and mid-May at the range core) and were repeated over 5 (trailing edge) or 4 (range core) 2-week sampling periods. From 2003-2006, surveys were performed at the center of BTBW territories on the low and high elevation plots at the range core rather than at transect points. These survey types are directly comparable, as they both involved the same methodology of counting and measuring caterpillars on 50-leaf samples of the same sapling species. See Chapter 3 for a more thorough description of the data collection methods.

Climate Data

The USDA Forest Service has maintained a series of long-term climate monitoring stations across the elevation gradient at each range position (Miniat et al., 2015; Miniat et al., 2017; USDA Forest Service 2020 a,b). Climate stations were not located at the actual BTBW study plots; instead, I used daily temperature and precipitation data from climate stations located within 175m elevation of the study plots. Daily thermal sums were calculated from daily temperature data as in Cesaraccio et al. (2001) to assess heat accumulation each day of the year (Lany et al. 2016). Temperature and precipitation are strongly correlated with elevation at both range positions (Chapter 2). For each of the climate variables used in the analysis (see below), I fit a linear model between elevation and the climate variable and predicted to the elevations of the study plots. Climate variables were predicted separately at each range position.

Statistical Analysis

All statistical analyses were conducted in R version 4.0.3 (R Core Team 2020). Nest survival was modelled using program MARK via ‘RMark’ (Laake and Rexstad 2008). Nests of uncertain fate were not included in analyses (Jehle et al. 2004), though inclusion did not affect the results (data not shown). I fit a series of 8 competing models to explain variation in nest daily survival rates (DSR): a null model with constant DSR and models allowing DSR to vary by a linear effect of year, range position, elevation, and all possible combinations of the three. Density of breeding females was included as a covariate in all models to account for potential density-dependent effects on nest survival (Schmidt & Whelan 1999, Gunnarsson & Elmberg 2008). Competing models were ranked via AIC (Burnham & Anderson 2002).

Nest survival may not be an accurate estimate of annual productivity, as birds can re-nest multiple times following nest failure (Holmes et al. 1992, Nagy & Holmes 2004). The distribution of female productivity is strongly multimodal based on how many successful broods the female raised in a year (data not shown). As an alternative measure of productivity, I analyzed the probability of a female fledging 0, 1, or 2 successful broods in a year using ordinal regression. In some cases, family groups of adults and fledglings were detected even though the nest had not been found; I counted these instances as a successful brood for the female. Competing models were fit with the same covariates as in the nest survival analysis via the 'MASS' package (Ripley et al. 2013).

Nestling mass was log-transformed and analyzed using linear-mixed effects models in package 'lme4' (Bates et al. 2007). I fit a series of 8 competing models to explain variation in log-mass: a null model and models allowing log-mass to vary by a linear effect of year, range position, elevation, and all possible combinations of the three. A fixed effect of female density and a random effect of brood ID were included as covariates in all models to account for density-dependent effects (Sillett et al. 2004, Sillett et al. 2005) and correlation in mass among brood mates (Slagsvold 1984, Nagy & Holmes 2005a, Martin et al. 2011). Competing models were ranked with AIC.

For both nest survival and nestling mass, I performed a second analysis by adding a series of models allowing the breeding-ground effect to vary based on four climate variables: early-breeding thermal sums (EBTS), annual precipitation (AP), average daily thermal sums during the nesting period (ATSN), and average daily precipitation during the nesting period (APN). These climate variables represent both year-specific climate (EBTS and AP) and nest specific climate (ATSN and APN). EBTS are negatively related to BTBW population dynamics (Chapter 2) and represent thermal accumulation from the average first lay date (day of year 127 (trailing) and 143 (core)) to average fledge date of first broods (day of year 159 (trailing) and 175 (core)). The two year-specific climate variables, EBTS and AP, generally represent warm vs. cold and wet vs. dry yearly conditions, respectively. The two nest-specific climate variables were calculated as the average of the daily thermal sums over the period from lay date to fledge/fail date (ATSN) and the average daily precipitation from hatch date to fledge/fail date (APN). ATSN increases throughout the breeding season; therefore, this measure was corrected for time of season prior to analysis. At each range position, I fit a linear model allowing ATSN to vary by study plot and a trend effect of time of season, defined as the last day of the season for which the nest was known to be active. Residuals from these linear models were used as detrended estimates of ATSN in subsequent analyses. Models were fit allowing DSR or log-mass to vary based on the four climate variables, as well as by interactions between the climate variables and the variables in the top ranked model from the first analysis.

Caterpillar communities likely differ between North Carolina and New Hampshire, so I ran analyses separately for each range position. Caterpillar biomass was aggregated prior to analysis based on transect/territory survey points; however, the data were still extremely zero-inflated. I used the Bayesian log-gamma hurdle model from Hilbe et al. (2017) for analysis. The hurdle model can handle zero-inflated datasets through at two-step modeling of presence of caterpillars and caterpillar biomass, conditional on presence. The likelihood of the model is based on occurrence probability *P* when caterpillars are absent and is based on the log-gamma biomass model conditional on *P* when caterpillars are present. The likelihood of the model does not fit a standard probability distribution, so the likelihood was maximized via the "zeros trick" (Lunn et al. 2012). A vector of zeros (z) is defined as: z_i ~ Poisson(-likelihood$_i$ + C), where C is some large constant (e.g., 10,000). Since z_i is set to 0, the likelihood is maximized to overcome C. Estimates of probability of occurrence and conditional biomass were then multiplied to estimate total biomass.

At each range position, I fit a null model and models allowing caterpillar biomass to vary by sampling period, year, elevation, and all possible combinations. In each model, I included the same covariate effects on presence and conditional biomass. I included an effect of survey point in all models to account for differences in microclimate and habitat between survey points; the effect of survey points was specified as arising from a normal distribution with mean of 0. To account for potential differences in biomass between territory and transect surveys, I included an effect of survey type in all range core models. Competing models were ranked via WAIC (Watanabe 2010, Gelman et al. 2014). Models were fit using Markov Chain Monte Carlo (MCMC) simulation with 3 chains of 5000 iterations implemented in JAGS (Plummer 2003) via the 'R2jags' package (Su et al. 2015). Vague priors were used for all parameters. Model convergence was assessed through visual examination of MCMC chains.

Like nest survival and nestling mass, a second analysis was performed adding climate variables to the top model from the first analysis. A large caterpillar outbreak occurred at the range core from 2002-2003 which, in some areas, caused ~20x increase in caterpillar biomass. These outbreak years did not affect the results of the first analysis; however, having 2 high biomass years at the beginning of the study did affect the climate trend analysis. I therefore removed years 2002-2003 from the climate analysis at the range core. In addition to EBTS and AP, I also fit models allowing caterpillar biomass to vary based on climate variables which have previously been found to affect caterpillar communities: spring precipitation (SpP, day of year 60-120, Tamburini et al. 2013), thermal sums during the growing season of the previous year (TSGrow, day of year 74-228, Reynolds et al. 2007), sum of daily max spring temperatures (MSpT, day of year 60-115, Charmantier et al. 2008), and average daily mean January temperatures (AJT, Kocsis & Hafnagel 2011). No climate variables used in analysis were correlated ($r<0.6$).

Results

Productivity

I used 2100 BTBW nests for the nest survival analyses (565 from the trailing edge and 1535 from the range core). The top-ranked nest survival model was for DSR to vary by year and elevation with 86% of the AIC weight (Table 4.1). The three-way interaction between year, elevation, and range position also received some support (Table 4.1), so I performed model-averaging on the nest survival models. Nest DSR declined precipitously at the high-elevation plots at both range positions. Nest DSR was much higher at the high-elevation plots than at lower-elevation plots at the at the start of the study but declined to be about equal to the low and mid elevation plots by the end of the study (Figure 4.1). In contrast to the high-elevation plots, DSR was relatively invariant over the study period at the low and mid elevation plots. Assuming a 25-day nesting period from laying-fledging (Holmes et al. 1992, Holmes et al. 2017), nest success at the high-elevation plot at the trailing edge is estimated to have declined from 68% (95% CI 60 - 75%) in 2003 to 35% (95% CI 24 - 46%) in 2019. Similarly, success at the high-elevation plot at the range core is estimated to have declined from 69% in 2002 (95% CI 62 - 75%) to 41% in 2016 (95% CI 34 - 48%).

I used 1373 female BTBW in the ordinal regression to assess probability of successfully raising 0, 1, or 2 successful clutches in a year (397 from the trailing edge and 976 from the range core). Estimates of productivity from the ordinal regression showed a similar pattern to nest survival. The top model was for the interaction between year and elevation (Table 4.2). This model received 97% of the weight, so I did not perform model-averaging. The probability of a female successfully fledging 1 brood in a year changed little at the high-elevation plots (Figure 4.2); however, the probability of successfully double-brooding declined from 21% in 2002 (95% CI 16% - 27%) to 8% in 2019 (95% CI 5 - 12%). The probability of not raising a successful brood also increased from 16% in 2002 (95% CI 12 - 21%) to 36% in 2019 (95% CI 27 - 45%) at the high-elevation plots. Assuming that productivity for double-brooded females is twice that for single-brooded females, productivity declined by about 45% at the high-elevation plots over the course of the study. Similar to nest survival, productivity at the high-elevation plots declined to about the level of the other elevations.

The similar trends in nest survival and probability of successful breeding indicates that nest survival in this system is largely reflective of annual productivity. I only assessed the impact of climate on nest survival, as I could incorporate both year-specific and nest-specific climate variables into the analysis. Nests which were found and failed during incubation could not be backdated to determine laying date; these nests were removed from analysis, as nest-specific climate variables could not be determined. I also removed nests which were active for less than 4 days, leaving 1814 nests for the climate analysis. Nest DSR was largely invariant to year-specific climate variables; instead, climate experienced by individual nests had a much stronger effect on DSR at both range positions. The top model was for an interaction between elevation and ATSN with 95% of the AIC weight (Table 4.3). Nests experiencing warmer temperatures had lower DSR at all elevations, though this effect was most pronounced at the high-elevation plots (Figure 4.3). This model performed better than the top-ranked temporal trend model from the first analysis (elevation * ATSN AICc: 5906.5, elevation * year AICc: 5918.6), indicating that these results are unlikely to be attributable to temporal autocorrelation (Neate-Clegg et al. 2021).

Nestling mass

I used 2947 BTBW nestlings (842 from the trailing edge and 2105 from the range core) from 913 nests in analyses. The top model was for nestling mass to vary based on an interaction between range position and year (Table 4.4). Day 6 nestling mass declined at both range positions, but this effect was particularly pronounced at the trailing edge (Figure 4.4). Average day 6 mass at the trailing edge was estimated to have declined from 7.6g in 2003 (95% CI 7.5 - 7.8g) to 6.7g in 2019 (6.7 - 7.1g). This corresponds to a decline of 11.8% in nestling mass over the course of the study period at the trailing edge. In contrast, nestling mass declined by about 4.9% at the range core (2002: mean = 7.9g, 95% CI 7.8 - 8.0g; 2018: mean = 7.5g, 95% CI 7.4 - 7.7g). The top climate model was for a negative effect of APN on nestling mass at the range core; however, no climate model performed better than top temporal model from the first analysis (range position * APN AICc: -4837.6, range position * year AICc: -4849.0).

Food abundance

The top model explaining caterpillar biomass at each range position was a three-way interaction between year, elevation, and sampling period with all of the WAIC weight (Table 4.5). For ease of interpretation, I hereafter analyze caterpillar biomass separately for “early” (sampling periods 1-2) and “late” (sampling periods 3-5 at the trailing edge, 3-4 at range core) seasons rather than by sampling period. Caterpillar biomass declined at the mid and high elevation plots at the range core in both the early (Figure 4.5B; mid: median = -0.04, 95% CI -0.06 - -0.02; high: median = -0.12, 95% CI -0.08 - -0.004) and late seasons (Figure 4.5D; mid: median = -0.02, 95% CI -0.05 - -0.003; high: median = -0.03, 95% CI -0.06 – 0.006). Trailing edge caterpillar biomass increased at the mid and high elevation plots during the early season (Figure 4.5A; mid: median = 0.07, 95% CI 0.02 - 0.12; high: median = 0.06, 95% CI 0.02 - 0.11). Late-season caterpillar biomass also increased at the high elevation plot at the trailing edge (median = 0.05, 95% CI 0.03 - 0.08), but declined at the low elevation plot (Figure 4.5C; median = -0.12, 95% CI -0.21 - -0.03).

Probability of caterpillar occurrence generally showed a similar temporal trend to conditional biomass at the range core. A different pattern was observed at the trailing edge, especially at the low and mid elevation plots during the late season (Figure 4.6). Late-season probability of occurrence trended upwards over time at the low and mid elevation plots (low: median = 0.07, 95% CI -0.01 – 0.15; mid: median = 0.05, 95% CI 0.02 – 0.08), but conditional biomass declined (low: median = -0.16, 95% CI -0.23 - -0.09; mid: median = -0.03, 95% CI -0.05 - -0.0002). These results indicate that caterpillars have become more widespread at the low and mid elevation plots at the trailing edge, but, when present, are smaller or are found in lower densities. The conflicting influence of probability of occurrence and conditional biomass resulted in no overall change in total caterpillar biomass being detected at the mid-elevation plot at the trailing edge.

No climate model performed better than the temporal-trend model for explaining caterpillar biomass in the early season at the range core; however, most climate models performed better than the temporal-trend model in the other seasons at both range position (Table 4.6). The top early-period model at the trailing edge was for an effect of AJT on caterpillar biomass (WAIC weight = 0.75). Early-season caterpillar biomass at the trailing edge declined at the low and mid elevation plots with higher AJT (Figure 4.7). The model allowing for an effect of TSGrow on caterpillar biomass was the top-ranked model for the late season at both range positions (WAIC weight = 1) and received support for the early season at the trailing edge as well (WAIC weight = 0.25). The effect of TSGrow differed between range positions (Figure 4.8). Trailing edge caterpillar biomass was negatively related to TSGrow at the low (median: -0.29, 95% CI -0.56 - -0.007) and mid (median: -0.28, 95% CI -0.48 - -0.07) elevation plots in the early season. TSGrow was negatively correlated with biomass across all elevations in the late season (low: median = -0.28, 95% CI -0.47 - -0.08; mid: median = -0.26, 95% CI -0.42 - -0.1; high: median = -0.37, 95% CI -0.48 - -0.27). At the range core, however, TSGrow was positively related to late-season caterpillar biomass at all elevations (low: median = 0.24, 95% CI 0.11 – 0.37; mid: median = 0.18, 95% CI 0.08 – 0.29; high: median = 0.23, 95% CI 0.11 – 0.36).

Discussion

Many studies have documented trailing edge range contractions in relation to climate change (e.g., Moritz et al. 2008, Coristine & Kerr 2015, Taheri et al. 2020), but few have used long-term demographic data from across the geographic range to determine the mechanisms behind these declines. I have shown that BTBW food abundance, productivity, and nestling mass all declined over the past 2 decades at both the trailing edge and the range core. BTBW populations have declined only at the low and mid elevation plots at the trailing edge; however, no breeding-ground effect showed this exact spatiotemporal pattern. This discrepancy indicates that trailing edge declines are probably not driven by a single mechanism; instead, the mechanistic effects of climate change in this system are likely complex and affecting trailing edge populations through multiple pathways (McLean et al. 2016). Climate change also may have affected populations through other pathways which I did not consider, such as through shifting competitive interactions, physiological stress on eggs or nestlings, or spread of disease (Heegard & Vandvick 2004, Garamszegi 2011, Cunningham et al. 2013, Alexander et al. 2015, S. Merker unpub. data).

Of the three potential mechanisms that I investigated, change in food abundance seems likely to be the most important driver of trailing edge declines. This finding is consistent with previous research documenting population-level effects of climate change acting on food abundance (e.g., van de Pol et al. 2010, Cahill et al. 2013, Desforges et al. 2021). Late-season caterpillar biomass at the trailing edge showed the predicted pattern of declining at the low elevation plot during the period of BTBW population decline; furthermore, caterpillar biomass increased at the high-elevation plot where BTBW populations were stable (Chapter 2). Food abundance at the end of the breeding season is critical for juvenile survival during the post-fledging period (Matin 1987, Hatt 2013), which can have a substantial effect on population growth rates (Streby and Anderson 2011). Declining food abundance may also have contributed to the decline in nestling mass at the trailing edge. Furthermore, declining food abundance may have non-lethal effects on low-elevation population dynamics. Many post-breeding birds prospect for future breeding sites to which they will return to breed next year (Doligez et al.

2002, Betts et al. 2008). Similarly, permanent emigration rates are higher from poor-quality habitat (Holmes et al. 1996, Cline et al. 2013). Declining late-season food abundance may thus have driven increased emigration and reduced recruitment independent of changes in first-year survival. BTBW populations are frequently food-limited (Rodenhouse & Holmes 1992 Sillett et al. 2000, Sillett & Holmes 2005) and fluctuations in food abundance are likely to have the greatest effect in the poor-food habitats at the low elevations (Kaiser et al. 2015, Chapter 3); therefore, declining late-season food abundance likely was a major driver of low-elevation population declines at the trailing edge.

Though total late-season caterpillar biomass at the mid-elevation plot at the trailing edge did not change over the course of the study, late-season caterpillars became smaller or more spatially dispersed. Provisioning adults focus their foraging efforts on small concentrations of caterpillars (Naef-Daenzer & Keller 1999). Adults also preferentially select larger caterpillars when provisioning young (Naef-Daenzer & Keller 1999) and may switch to alternate food when caterpillars are small, regardless of the abundance of small caterpillars (Naef-Daenzer et al. 2000). Alternate prey, such as arthropods with hard exoskeletons, are generally lower quality food for developing nestlings than are caterpillars (Tremblay et al. 2005, Arnold 2010). Changes in the size or spatial distribution of late-season caterpillar communities at the mid-elevation plot may have negatively affected BTBW populations at the trailing edge and contributed to the local population declines.

Caterpillar biomass was also the only breeding-ground effect that was differentially affected by climate at the two range positions. Thermal sums during the growing season had a strong effect on caterpillar biomass in the next year at both range positions; however, this effect was positive at the range core and negative at the trailing edge. The positive relationship between warm growing seasons and caterpillar biomass in the subsequent year has previously been reported from the range core (Reynolds et al. 2007), potentially by allowing more generations in a year or modifying biotic interactions with host plants and predators (Stireman et al. 2005, Zvereva & Kovlov 2006, Reynolds et al. 2007). Temperatures have been increasing at the trailing edge (Chapter 2), though the drivers of the negative relationship between growing season temperatures and caterpillar biomass are unclear. Caterpillars were not identified to species, but climate change could be shifting the caterpillar community towards smaller species or away from species that form large aggregations. Warmer temperatures may also produce smaller adults with lower fecundity (Miller 2005), thereby leading to fewer caterpillars in the next year. Alternatively, warm years at the trailing edge also tend to be dry (Pearson's correlation: $t = -1.93$, $df = 16$, $p = 0.07$, $r = -0.43$). Caterpillar abundance is often positively associated with precipitation, which could lead to population growth in the next year (Sillett et al. 2000, Karban & de Valpine 2010, Tamburini et al. 2013). Temperature had a greater effect on caterpillar biomass than did precipitation; however, I may not have modeled the correct time periods during which precipitation is affecting caterpillar populations (Tamburini et al. 2013). Precipitation at the trailing edge has become more variable with drier growing seasons (Ford et al. 2011, Chapter 2), which could have caused the decline in late-season caterpillar biomass at the low and mid elevation plots.

Caterpillar biomass declined alongside BTBW populations at the low and mid elevation plots at the trailing edge, but biomass also declined at the mid and high elevation plots at the range core. Food abundance is tightly correlated with BTBW productivity and recruitment at the range core (Rodenhouse & Holmes 1992, Sillett et al. 2000, Nagy & Holmes 2004, Lany et al. 2016); however, declining caterpillar abundance at the range core had little effect on long-term

BTBW population trajectories (Chapter 2). Why declining caterpillar biomass had little effect on BTBW population density at the mid and high elevation plots at the range core is unclear and requires further study. One potential explanation is that BTBW may have adapted to declining caterpillar biomass by switching to alternate prey, such as beetles or spiders (Robinson & Holmes 1982, Rodenhouse & Holmes 1992, Maley 2011). The declining caterpillar biomass at the range core is also surprising; temperatures have been increasing in the area (Chapter 2), and caterpillar biomass at the range core is positively related to summer temperatures. No climate model adequately explained the decline in caterpillar biomass in the early season at the range core, suggesting that the declining biomass in this region may not be wholly related to climate change. The boreal ecotone has shifted downslope at the range core over the past several decades (Foster & D'Amato 2015), and caterpillars may be responding to changes in forest structure and host plant communities. More study is needed to understand the causes of caterpillar declines at each range position, especially in light of widespread global patterns of insect declines (Dirzo et al. 2014, Hallmann et al. 2017, Wagner 2020).

Previous research has suggested that warming springs are causing a phenological mismatch between avian reproduction and seasonal peaks in food abundance (Visser & Both 2005, Both et al. 2006). Though population declines in relation to phenological mismatches have been documented in some species (e.g., Both et al. 2006), climate change does not seem to have led to a phenological mismatch in BTBW. The phenological mismatch hypothesis assumes that food abundance shows a predictable seasonal peak which birds time their reproduction around, but caterpillars at the range core do not show a predictable seasonal peak in biomass (Lany et al. 2016). Caterpillar biomass at the trailing edge generally peaks in early June, but caterpillar biomass should have increased in the early season and declined in the late season if this peak has advanced over time. Instead, the low and high elevation plots at the trailing edge showed the same temporal trends in biomass between the early and late seasons. Changes in caterpillar biomass, and their likely effect on BTBW populations, seem to reflect overall biomass declines rather than shifting phenology.

In contrast to caterpillar biomass, the trends in nest survival and productivity were in the opposite direction from predictions. Nest survival and productivity did not change at the low and mid elevation plots, where BTBW populations declined at the trailing edge, but declined precipitously in the stable populations at the high-elevation plots. Productivity was still highest at the high-elevation plots over most of the study period despite the declines, likely explaining why birds still recruited to these areas. Productivity in BTBW is dependent on nest survival rates and frequency of double-brooding, the latter of which is positively associated with late-season food abundance, conspecific density, and length of the breeding season (Nagy & Holmes 2004, Sillett et al. 2004, Nagy & Holmes 2005b, Sillett & Holmes 2005, Townsend et al. 2013, Lany et al. 2016). Declining productivity at the high-elevation plots is unlikely to have arisen from increased crowding, as the high-elevation study plots did not exhibit any long-term trends in breeding density over the study period (Chapter 2). Declining productivity is also unlikely to have been caused by changes in the length of the breeding season, as breeding season length varies between years but is unlikely to have driven the strong elevational pattern. Temperatures during the start of the breeding season have also been increasing at both range positions (Chapter 2), which would be expected to allow earlier breeding and higher rates of double-brooding (Townsend et al. 2013). Long-term changes in food abundance also did not match the elevational pattern of productivity decline. Declining food abundance at the range core may have contributed to the declining rates of double-brooding at the high-elevation plot; however, productivity did not decline at the mid-elevation plot despite a similar decline in food abundance. Furthermore, productivity declined at the high-elevation plot at the trailing edge despite late-season food abundance increasing. Only nest survival showed a similar elevational pattern to productivity, suggesting that declining productivity at the high-elevation plots is driven by changes in nest survival rather than by changes in food abundance.

The primary cause of BTBW nest failure is from depredation (Holmes et al. 1992, Nagy & Holmes 2004), so the decline in productivity likely reflects changes in the distribution or activity of nest predators at the high-elevation plots. A diverse community of mammals, reptiles, and birds can depredate BTBW nests, though small mammals, mainly squirrels and chipmunks (family Sciuridae), are the primary nest predators (Reitsma et al. 1990, Holmes et al. 1992). Currently, we have little quantitative data on how the distribution of nest predators has changed at the study sites, especially at the trailing edge. Climate change is expected to increase nest depredation rates by snakes (Cox et al. 2013, DeGregoio et al. 2015). Snakes are uncommon at the high-elevation plots at both range positions, and thus are unlikely to have caused the decline in nest survival. Instead, the declining nest survival at the high-elevation plots could be attributed to changes in the abundance of one of the major nest predators, red squirrels (*Tamiasciurus hudsonicus*). Red squirrel abundance at the range core is closely tied to the transition ecotone between northern hardwood and boreal forests (Hallworth et al. in review). The boreal ecotone has been shifting downslope at the range core into the elevational range of the high-elevation plot (Foster & D'Amato 2015), which may have increased red squirrel abundance in the area and led to increased nest depredation rates. Red squirrels also reach the trailing edge of their distribution in the high-elevation forests of the Southern Appalachians (Weigl & Hanson 1980). While we do not know how the spatial distribution of red squirrels has changed in the Southern

Appalachians, red squirrels may have shifted their ranges upslope in a manner similar to trailing edge birds. This effect may have concentrated red squirrels at the highest, coolest elevations and increased depredation rates for birds breeding there. More study is needed on the identities and distributions of nest predators at both range positions to test these hypotheses.

Nest survival was also directly influenced by climate, but the exact mechanism causing the negative relationship between nesting temperatures and nest survival is unclear. This pattern reflects variation between nests while active rather than variation between warm and cold years; therefore, the decline in nest survival likely arose from changes in nest predator activity rather than from changes in abundance. Ambient temperature does not seem to affect nest depredation from small mammals; however, depredation rates from avian predators increase when temperatures are warmer (Cox et al. 2013). Warming temperatures may modify parental activity around nests, potentially making nests easier to detect by predators, though previous studies have suggested that provisioning rates decrease in warmer conditions (Rauter et al. 2000, Wiley & Ridley 2016, Barras et al. 2021). Regardless of the mechanistic cause, climate warming at both range positions likely contributed to the long-term decline in productivity at the high-elevation plots.

Despite declining over time and being directly influenced by climate, local changes in productivity were not related to local BTBW population declines. The very productive high elevations may provide recruits to lower elevations in a form of source-sink dynamics (González-Megías et al. 2005), such that declining productivity at the high elevations led to declining recruitment and breeding density at the low elevations. While birds have been documented recruiting from higher to lower elevations at the trailing edge, this is not a major driver of low-elevation population dynamics (Chapter 3). Furthermore, the temporal and climatic effects on productivity did not differ between range positions, as would be expected if productivity is the mechanism behind population declines at the trailing edge. Declining productivity at the high elevations likely influenced trailing edge BTBW declines, though changes in productivity seem unlikely to be the primary drivers of the declines (Chapter 3).

Unlike the other two breeding-ground effects, the temporal trend in nestling mass varied by range position but not by elevation. Nestling mass is a good predictor of post-fledging and first-year survival (Ringsby et al. 1998, Monros et al. 2002, Dybala et al. 2013); therefore, the substantial decline in nestling mass at the trailing edge likely led to declining recruitment to the area. Furthermore, declining nestling mass may have led to increased permanent emigration of adults away from areas with poor breeding conditions (Doligez et al. 2002). Despite the strong temporal trend, no climate model adequately explained the decline in nestling mass. I may not have incorporated the correct climate variable that directly affects nestling mass. For example, I was only able to incorporate climate variables predicted to the elevations of the study plots, but nestling mass is affected by microclimate conditions within the nest (Dawson et al. 2005, Andreasson et al. 2018). Furthermore, nestling mass may be more strongly affected by extreme climate events rather than averages (Cunningham et al. 2013, de Zwaan et al. 2020). Another possibility is that the effects of climate change on BTBW nestling mass were indirect. Nestling mass is affected by many factors, including predation pressure and food abundance (Van Balen 1973, Sillett et al. 2004, de Zwaan et al. 2018). I found both food abundance and predation pressure to be directly affected by climate; therefore, climate change may be leading to increases in predation pressure and declines in late-season food, which are then driving the decline in nestling mass. Regardless of the reason why I did not find a direct link with climate, the precipitous decline in nestling mass likely contributed to the BTBW population declines at the trailing edge.

Conclusions

The results of this chapter suggest that climate change is affecting trailing edge populations through multiple mechanistic pathways. One of the primary pathways seems to be through declining late-season food abundance at the low and mid elevations. Declining food resources at these elevations did not affect local productivity but may have contributed to the steep decline in nestling mass. Declines in late-season food and nestling mass likely led to reduced first-year survival for young fledged at these plots. These declines may have been exacerbated by increased depredation and declining productivity at the high elevations. The long-term declines in all breeding-ground effects suggest that the number of young birds recruiting at the trailing edge declined over the course of the study. I hypothesize that those young birds recruiting to the trailing edge may have still settled in the higher-quality habitats at the high elevations, but increasingly avoided the warmest, driest, and increasingly poorest-quality habitats at the lower elevations.

Declining breeding conditions at the lower elevations also may have driven permanent emigration of adult BTBW to better-quality habitats at higher elevations. Permanent emigration is difficult to study in small and highly mobile birds, but evidence suggests that first-time breeders in poor-quality habitats frequently shift to higher-quality breeding habitats in subsequent years (Holmes et al. 1996). Furthermore, adult emigration from poor-quality habitats is a major driver of local population declines at the trailing edge (Chapter 2). Declining nestling mass and late-season food at the low elevations may have led, not just to declining recruitment, but also to increasing adult emigration.

While changes in productivity, nestling mass, and late-season food abundance are all likely to have affected trailing edge populations, only food abundance was negatively affected by climate and showed the same elevational pattern of population declines as BTBW at the trailing edge. Changes in food abundance seem to be the most important mechanism driving the declines, likely through interacting effects on nestling mass and other demographic metrics. Food abundance often limits population dynamics (White 1978, Martin 1987, Newton 1998) and is frequently cited as a mechanistic effect of climate change (van de Pol et al. 2010, Cahill et al. 2013, Desforges et al. 2021). Changes in food distribution or availability may be a widespread mechanism through which climate change affects populations. Incorporating predicted changes in food availability into models predicting species' responses to climate change would likely improve predictive accuracy (Schweiger et al. 2011, Adams-Hosking et al. 2012, Pacifici et al. 2015).

Population declines in trailing edge BTBW are strongly correlated with conditions on the breeding grounds, but this does not imply that conditions during the non-breeding season are unimportant. Threats experienced on the non-breeding grounds can be major drivers of population dynamics during the breeding season (Robbins et al. 1989, Norris et al. 2004, Rappole et al. 2003), and both breeding and non-breeding conditions likely interact to drive population dynamics (Sherry & Holmes 1995, Sillett et al. 2000, Runge & Marra 2005). Future research should refine estimates of migratory connectivity at both range positions to determine if habitat loss during the non-breeding season could be driving breeding dynamics.

My results also do not imply that climate change has not affected BTBW population at the range core. While I was unable to determine if the declines in breeding-ground effects at the range core were caused by climate change or changes in habitat, both nest survival and food biomass were sensitive to changes in climate. Furthermore, apparent survival at the low-elevation plot at the range core has declined in relation to warming temperatures, which is predicted to lead to population declines at this plot over the next decade (Chapter 2). Further climate change will likely affect BTBW populations across their entire range.

My results show that climate change affected BTBW populations through both top-down effects of nest predators and bottom-up effects of caterpillars. To understand the mechanisms behind BTBW population declines, we need to understand how climate change is affecting communities at the trailing edge (Gilman et al. 2010, Walther 2010). Climate change affected trailing edge BTBW populations through declining caterpillar biomass at the low elevations; however, we do not know how the composition of the Lepidoptera community has changed over time, or the exact mechanism through which climate change is driving late-season declines. Understanding the causes of lepidopteran declines is of the utmost importance, as the results of this chapter are consistent with many other studies showing an alarming decline of invertebrate communities across the globe (e.g., Dirzo et al. 2014, Hallmann et al. 2017, Wagner 2020). Similarly, we have little information on the identity of nest predators at the trailing edge, or how this community may have been altered by climate change. I suggest that researchers investigating the proximate mechanisms of climate change should not study specific species in isolation, but instead should endeavor to understand how climate change affects composition and interactions within the entire community.

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Table 4.1. Model selection results for determining the factors affecting nest daily survival rates (DSR) of black-throated blue warblers from across the breeding range. Nest DSR was allowed to vary by all possible combinations of range position (trailing edge or range core), linear effect of year, and elevation (low, mid, or high). All models included a fixed effect of female density. See text for more details.

Model	k	AICc	ΔAICc	w
Year * Elevation	7	7564.0	0	0.86
Year * Range Position * Elevation	13	7567.7	3.7	0.14
Range Position * Elevation	7	7586.2	22.2	<0.001
Elevation	4	7588.4	24.4	<0.001
Year	3	7617.9	53.9	<0.001
Year * Range Position	5	7618.3	54.4	<0.001
Range Position	3	7629.2	65.2	<0.001
Null	2	7630.3	66.3	<0.001

Table 4.2. Model selection results for ordinal regression determining the factors affecting probability of female black-throated blue warblers successfully fledging 0, 1, or 2 clutches in a season. Probability of successful clutches was allowed to vary by all possible combinations of range position (trailing edge or range core), linear effect of year, and elevation (low, mid, or high). All models included a fixed effect of female density. See text for more details.

Model	k	AICc	ΔAICc	w
Year * Elevation	8	2447.2	0	0.968
Year * Range Position * Elevation	14	2454.8	7.6	0.022
Elevation	5	2456.6	9.4	0.009
Range Position * Elevation	8	2460.3	13.2	0.001
Year * Range Position	6	2490.1	42.9	<0.001
Range Position	4	2499.4	52.2	<0.001
Year	4	2500.7	53.5	<0.001
Null	3	2507.3	60.1	<0.001

Table 4.3. Model selection results for determining the effects of climate variables on nest daily survival rates of black-throated blue warblers from across the breeding range. Nest DSR was allowed to vary by combinations of elevation (low, mid, or high), range position (trailing edge or range core), early-breeding thermal sums (EBTS), annual precipitation (AP), average daily thermal sums during the nesting period (ATSN), and average daily precipitation during the nesting period (APN). All models included a fixed effect of female density. See text for more details.

Model	k	AICc	ΔAICc	w
Elevation * ATSN	7	5899.5	0	0.95
Elevation * Range Position * ATSN	13	5905.6	6.1	0.05
Elevation * Range Position * APN	13	5918.0	18.5	<0.001
Elevation * Year	7	5918.6	19.1	<0.001
ATSN	3	5922.5	23.0	<0.001
Range Position * ATSN	5	5924.4	24.9	<0.001
Elevation * APN	7	5938.4	38.9	<0.001
Elevation * EBTS	7	5938.7	39.2	<0.001
Elevation * AP	7	5940.2	40.7	<0.001
Elevation * Range Position * EBTS	13	5940.4	40.9	<0.001
Elevation * Range Position * AP	13	5948.7	49.2	<0.001
Range Position * APN	5	5948.8	49.3	<0.001
Range Position * EBTS	5	5955.2	55.7	<0.001
EBTS	3	5957.7	58.2	<0.001
Null	2	5957.9	58.4	<0.001
APN	3	5959.0	59.5	<0.001
AP	3	5959.6	60.1	<0.001
Range Position * AP	5	5961.4	61.9	<0.001

Table 4.4. Model selection results for explaining variation in day 6 black-throated blue warbler nestling mass from across the breeding range. Nestling mass was allowed to vary by all possible combinations of range position (trailing edge or range core), linear effect of year, and elevation (low, mid, or high). All models included a fixed effect of female density and a random effect of brood ID. See text for more details.

Model	k	AICc	ΔAICc	w
Range Position * Year	7	-4849.0	0	0.922
Range Position	5	-4844.1	4.9	0.078
Range Position * Elevation	9	-4814.6	34.4	<0.001
Year	5	-4810.0	39.1	<0.001
Null	4	-4796.7	52.4	<0.001
Elevation * Year	9	-4791.2	57.9	<0.001
Range Position * Elevation * Year	15	-4787.1	61.9	<0.001
Elevation	6	-4780.0	69.0	<0.001

Table 4.5: WAIC model selection results for determining the effect of year, elevation (low, med, high), and sampling period (1-5 at the trailing edge, 1-4 at the range core) on caterpillar biomass at the trailing edge and range core of the black-throated blue warbler breeding range. Models were run separately at each range position. See text for more details.

Range position	Model	WAIC	ΔWAIC	w
Trailing edge	Year * Elevation * Sampling Period	10705.1	0	1
Trailing edge	Year * Sampling Period	10773.8	68.7	<0.001
Trailing edge	Elevation * Sampling Period	10846.4	141.3	<0.001
Trailing edge	Sampling Period	10877.1	172.0	<0.001
Trailing edge	Year * Elevation	10993.7	288.7	<0.001
Trailing edge	Year	11042.7	337.7	<0.001
Trailing edge	Elevation	11122.5	417.4	<0.001
Trailing edge	Null	11188.8	483.8	<0.001
Range core	Year * Elevation * Sampling Period	13816.4	0	1
Range core	Elevation * Sampling Period	13828.4	12.0	<0.001
Range core	Sampling Period	13937.5	121.1	<0.001
Range core	Year * Sampling Period	13939.5	123.1	<0.001
Range core	Year * Elevation	14232.2	415.8	<0.001
Range core	Elevation	14289.4	473.0	<0.001
Range core	Year	14302.0	485.6	<0.001
Range core	Null	14335.2	518.8	<0.001

Table 4.6: WAIC model selection results for determining the effect of climate variables on caterpillar biomass at the trailing edge and range core of the black-throated blue warbler breeding range. Models were run separately for the early and late breeding seasons at each range position. All models except for the null model included an interactive effect of elevation. Caterpillar biomass was allowed to vary by early-breeding thermal sums (EBTS), annual precipitation (AP), spring precipitation (SpP), growing-season thermal sums in the previous year (TSGrow), sum of daily maximum spring temperatures (MSpT), or average daily mean January temperature (AJT). See text for more details.

Range position	Season	Model	WAIC	ΔWAIC	w
Trailing edge	Early	AJT	2896.0	0	0.75
Trailing edge	Early	TSGrow	2898.2	2.2	0.25
Trailing edge	Early	MSpT	2921.7	25.7	<0.001
Trailing edge	Early	SpP	2929.9	33.9	<0.001
Trailing edge	Early	Year	2935.4	39.4	<0.001
Trailing edge	Early	AP	2948.8	52.8	<0.001
Trailing edge	Early	EBTS	2951.4	55.4	<0.001
Trailing edge	Early	Null	3027.8	131.8	<0.001
Trailing edge	Late	TSGrow	7962.5	0	1
Trailing edge	Late	MSpT	8004.2	41.7	<0.001
Trailing edge	Late	Year	8036.5	73.9	<0.001
Trailing edge	Late	SpP	8064.4	101.9	<0.001
Trailing edge	Late	EBTS	8067.2	104.6	<0.001
Trailing edge	Late	AJT	8067.5	105.0	<0.001
Trailing edge	Late	AP	8067.9	105.4	<0.001
Trailing edge	Late	Null	8133.4	170.9	<0.001
Range core	Early	Year	5750.7	0	1
Range core	Early	MSpT	5783.6	32.9	<0.001
Range core	Early	AJT	5784.8	34.1	<0.001
Range core	Early	TSGrow	5786.4	35.7	<0.001
Range core	Early	EBTS	5792.6	41.9	<0.001
Range core	Early	AP	5798.6	47.9	<0.001
Range core	Early	SpP	5804.6	53.9	<0.001
Range core	Early	Null	5855.1	104.4	<0.001
Range core	Late	TSGrow	8156.3	0.0	1
Range core	Late	MSpT	8170.7	14.4	<0.001

Range core	Late	AJT	8181.7	25.5	<0.001
Range core	Late	Year	8185.3	29.1	<0.001
Range core	Late	AP	8191.7	35.4	<0.001
Range core	Late	SpP	8205.4	49.1	<0.001
Range core	Late	EBTS	8210.3	54.0	<0.001
Range core	Late	Null	8314.7	158.4	<0.001

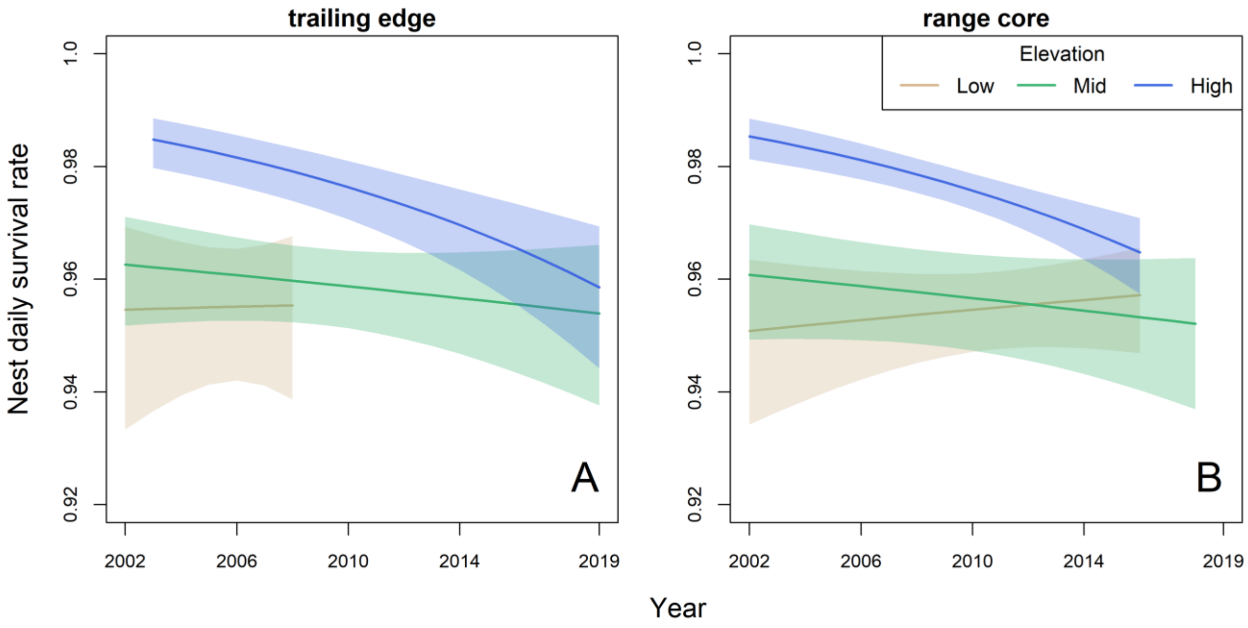

Figure 4.1. Model-averaged estimates of daily survival rates for black-throated blue warbler nests at the trailing edge (A) and range core (B) over the course of the study. Trend estimates are shown for three different elevation study plots (low, mid, high) at each range position. Mean estimates and 95% confidence intervals are shown. At the trailing edge, the high-elevation plot was not sampled before 2003 while the low-elevation plot was not sampled after 2008. The low and high elevation plots were not sampled after 2016 at the range core.

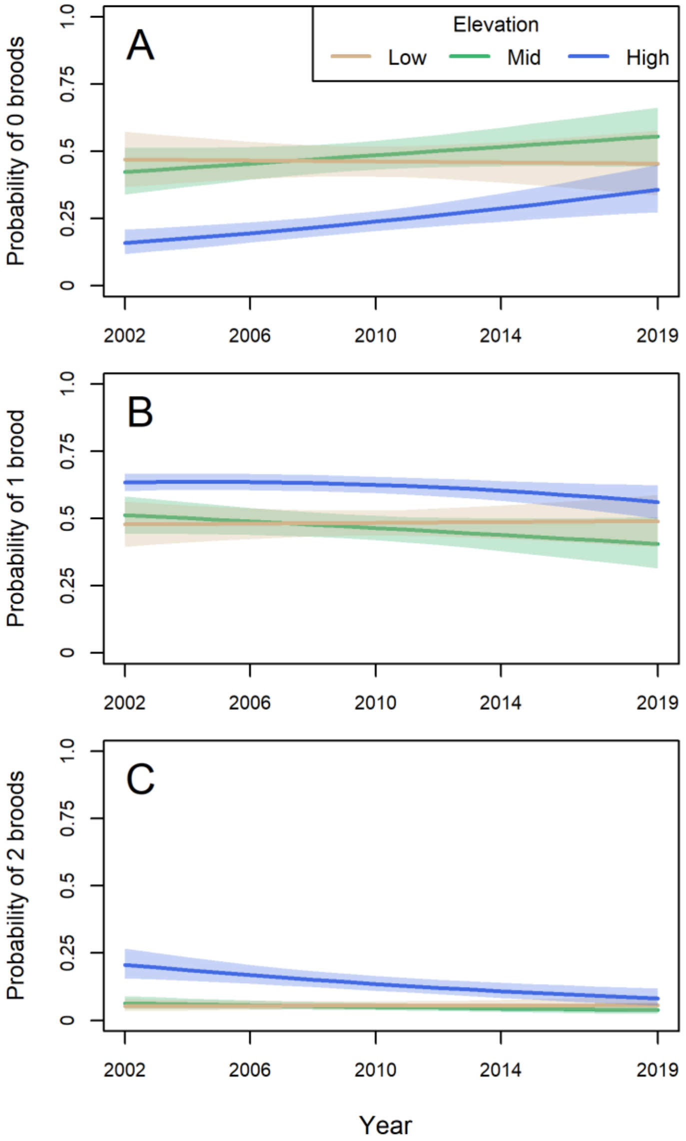

Figure 4.2. Estimated probability of female black-throated blue warblers successfully raising 0 (A), 1 (B), or 2 (C) broods in a breeding season. Trend estimates are shown for three different elevation study plots (low, mid, high) over the course of the study period. Mean estimates and 95% confidence intervals are shown. Model selection indicated that effects were similar between birds breeding at the trailing edge and the range core.

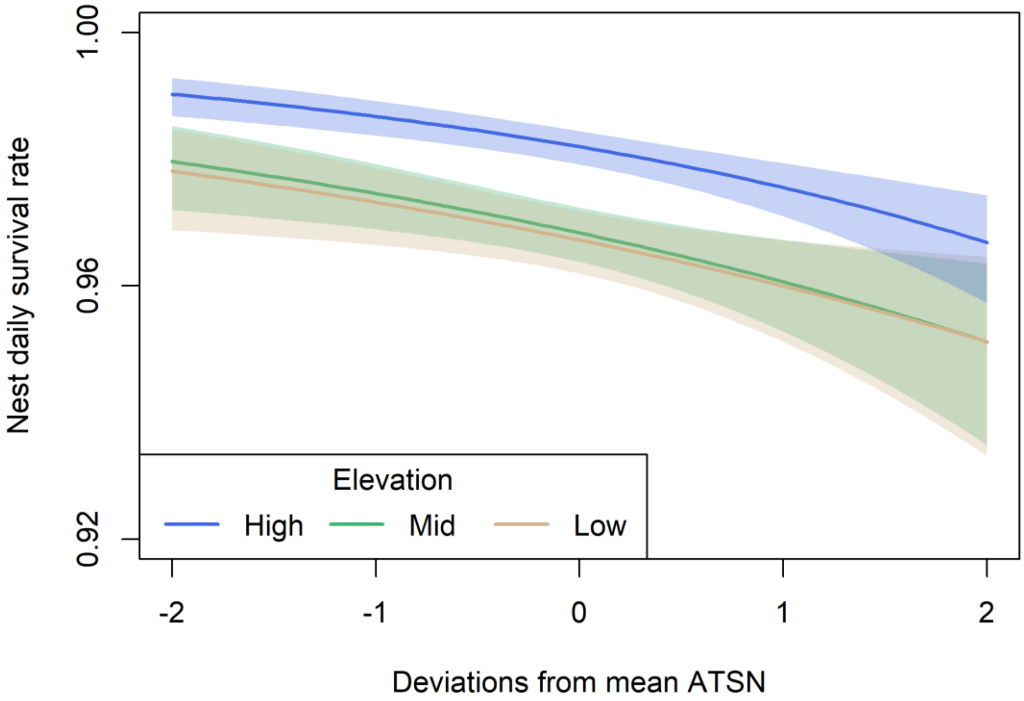

Figure 4.3. Estimated daily survival rate of black-throated blue warbler nests in relation to increasing mean daily thermal sums during the nesting period (ATSN). Trend estimates are shown for low, mid, and high elevation study plots. To compare across elevations, ATSN is shown as the deviations from the mean ATSN at each elevation. Mean estimates and 95% confidence intervals are shown. Model selection indicated that effects were similar between birds breeding at the trailing edge and the range core.

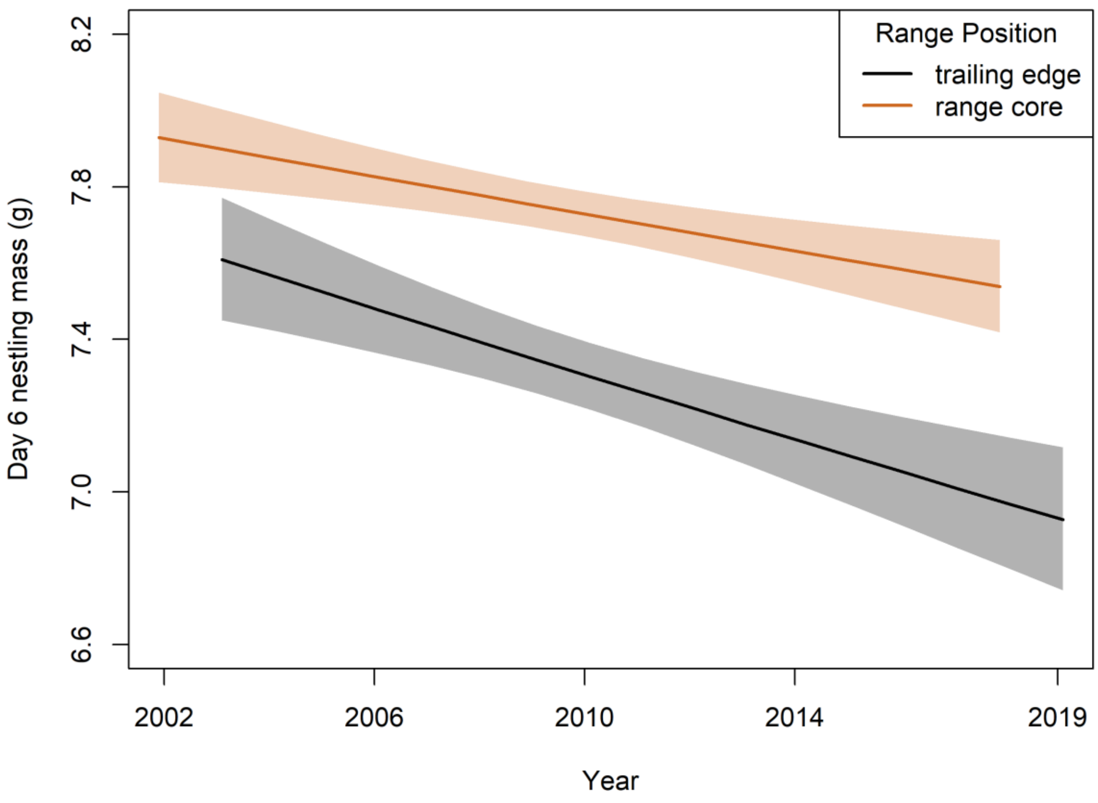

Figure 4.4. Change in average mass of black-throated blue warbler nestlings over the course of the study period at the trailing edge and the range core. Nestling mass was measured 6 days after hatching. Estimated means and 95% confidence intervals are shown. Nestling mass was not recorded at the trailing edge until 2003. Model selection indicated that effects were similar across elevations at each range position.

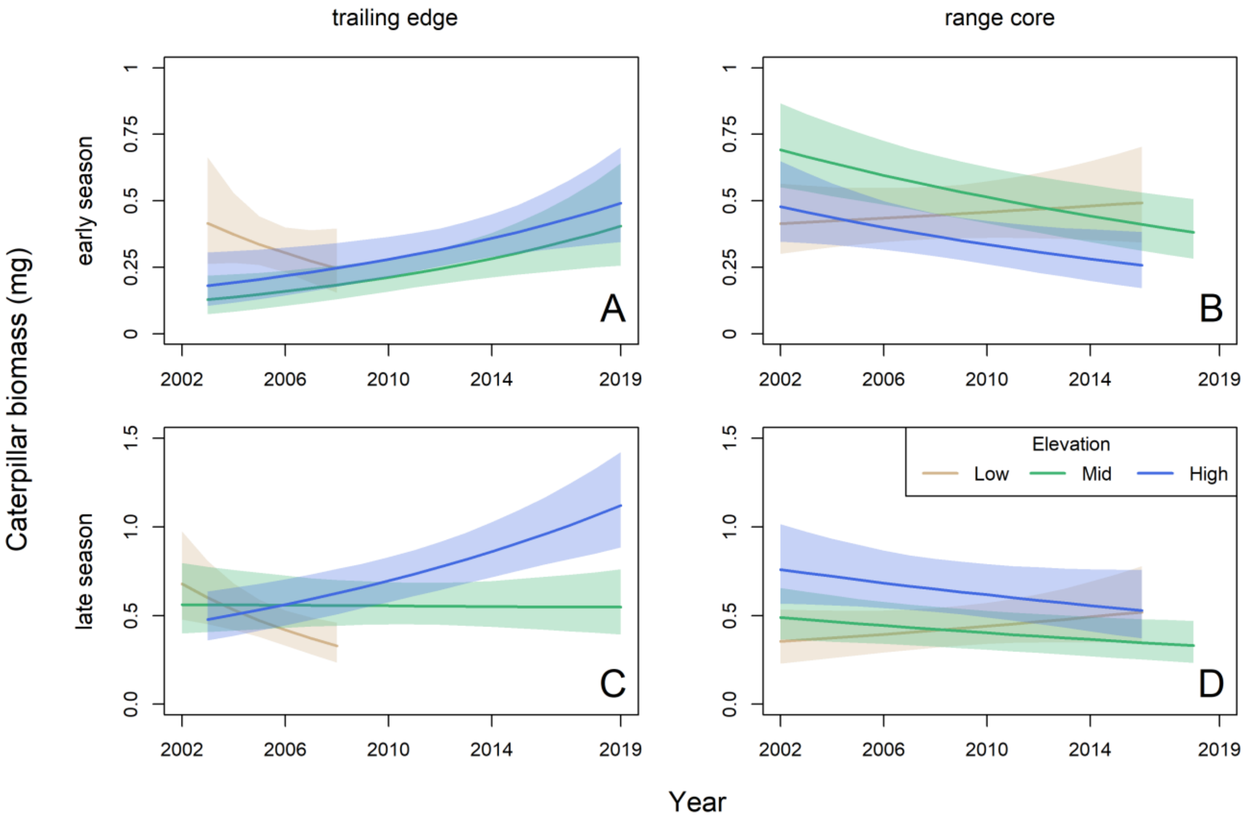

Figure 4.5. Model estimates of change in total caterpillar biomass over the course of the study period at the trailing edge (A, C) and the range core (B, D) of the geographic range of the black-throated blue warbler. At each range position, biomass was estimated at three different elevation plots (low, mid, and high) for both the early (A, B) and late (C, D) breeding seasons. Estimated medians and 95% credible intervals are shown.

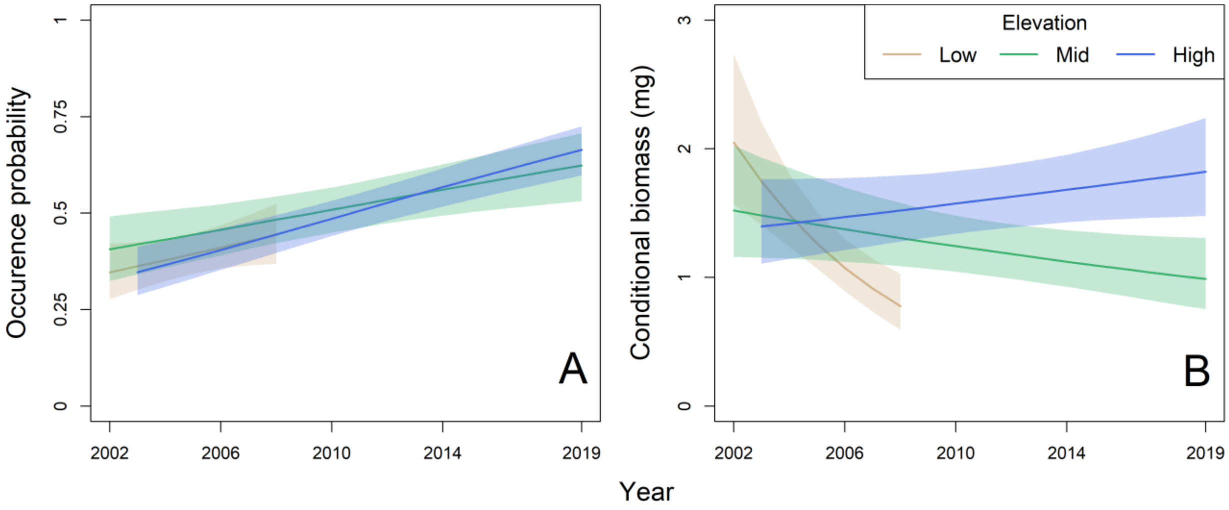

Figure 4.6. Model estimates of change in late-season caterpillar probability of occurrence (A) and conditional biomass of caterpillars when present (B) at the trailing edge of the geographic range of black-throated blue warblers. Estimated medians and 95% credible intervals are shown for caterpillar occurrence and conditional biomass at three different elevation study plots (low, mid, and high).

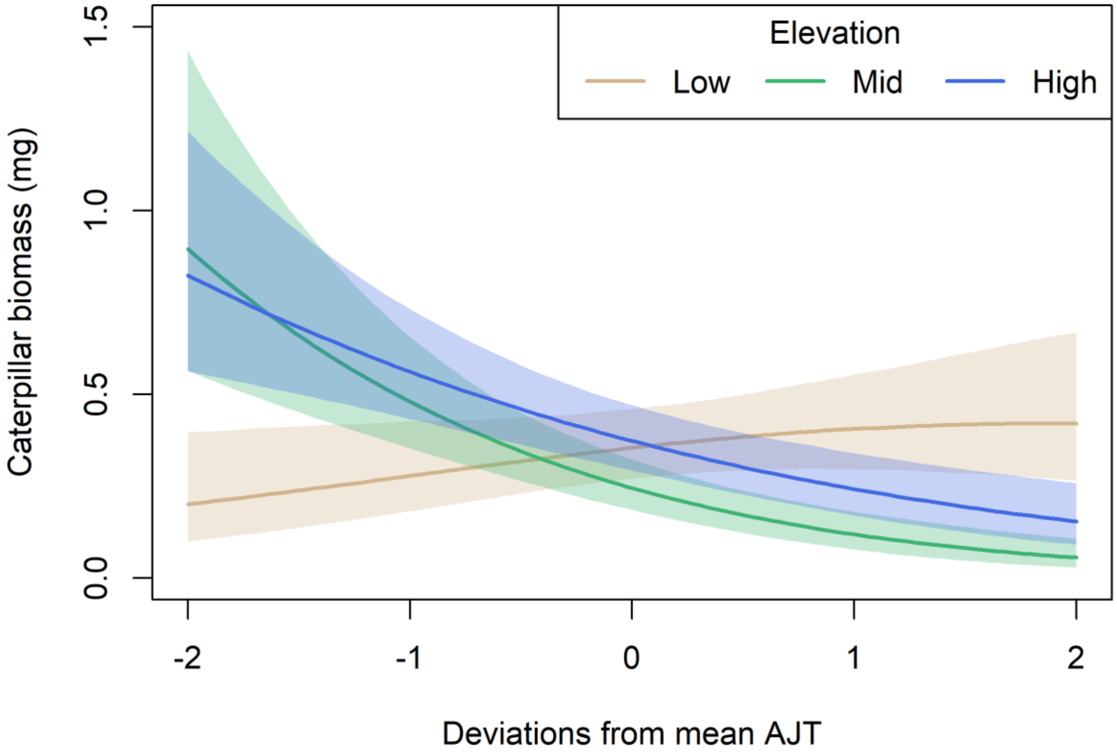

Figure 4.7. Estimated total early-season caterpillar biomass in relation to the average of the daily mean January temperatures (AJT) from the previous winter at the trailing edge of the geographic range of black-throated blue warblers. Estimates are shown for three different elevation study plots (low, mid, high). To compare across elevations, AJT is shown as the deviations from the mean AJT at each study plot. Median estimates and 95% credible intervals are shown.

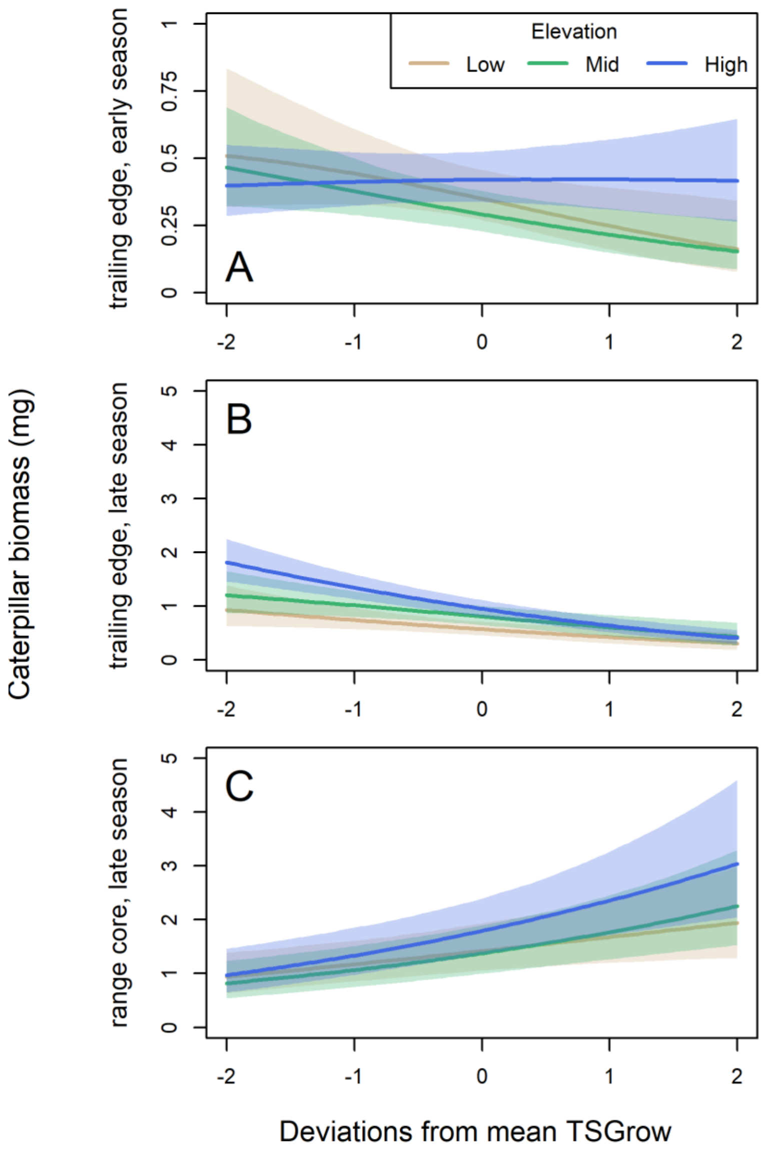

Figure 4.8. Estimated total caterpillar biomass in relation to the thermal sums of the previous growing season (TSGrow) at the trailing edge (A, B) and range core (C) of the geographic range of black-throated blue warblers. Estimates are shown for the relationship between TSGrow and total caterpillar biomass in the early (A) and late (B, C) breeding season. Estimates are shown at three different elevation study plots (low, mid, higher). To compare across elevations and range positions, TSGrow is shown as the deviations from the mean TSGrow at each study plot. Median estimates and 95% credible intervals are shown.

CHAPTER 5

HABITAT LOSS DURING THE NON-BREEDING SEASON AS A POSSIBLE EXACERBATOR OF BREEDING-GROUND POPULATION DECLINES IN THE BLACK-THROATED BLUE WARBLER (SETOPHAGA CAERULESCENS)[1]

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[1] Lewis, W.L., R.J. Cooper, M.T. Hallworth, A.R. Brunner, and T.S. Sillett. To be submitted to *Journal of Field Ornithology*.

Abstract

Determining the causes of population declines in migratory species requires knowledge of the threats faced throughout the entire annual cycle. Populations of many long-distance migratory species are declining at the trailing edge of the breeding range in the Southern Appalachians, but the causes of these declines are not well understood. I sought to determine if conditions on the overwintering grounds could explain breeding-ground population declines for one such trailing edge species, the black-throated blue warbler (*Setophaga caerulescens*). I used light-level geolocators to track the fall migratory routes and overwintering distributions of adult warblers breeding at the trailing edge (n=5), where populations are declining, and core (n=8) of the range, where populations are stable. Migratory connectivity was moderately strong, with range-core birds overwintering broadly across the Caribbean and trailing edge birds overwintering in a restricted area on Hispaniola. The restricted overwintering range subjected trailing edge birds to significantly higher levels of deforestation over the past 2 decades than range core birds. My results show that forest loss in Hispaniola may be interacting with climate change on the breeding grounds to drive population declines in the Southern Appalachians.

Introduction

Almost 3 billion birds breeding in North America have been lost over the past 50 years (Rosenberg et al. 2019). Declines vary by habitat type and have been broadly observed across many taxonomic groups, but the strongest declines have frequently been documented in long-distance migrants (Robbins et al. 1989, Ballard et al. 2003, Rosenberg et al. 2019). The pattern of decline for most species is generally not constant across the entire range; instead, populations are declining in some regions but increasing or stable in others (Sauer et al. 2017). Understanding the causes of these declines is complicated by the fact that migratory birds are subjected to a wide range of conditions and threats from the breeding grounds, non-breeding grounds, and along migratory routes (Rappole & McDonald 1994, Sherry & Holmes 1995, Faaborg et al. 2010, Sergio et al. 2019). Conditions on the overwintering grounds and during migration can affect breeding-season demographic rates and population dynamics (Robbins et al. 1989, Marra et al. 1998, Norris et al. 2004, Newton 2006, Sanderson et al. 2006, Ilán et al. 2014, Hewson et al. 2016), and conditions experienced throughout the annual cycle likely interact to drive population dynamics (Sherry & Holmes 1995, Sillett et al. 2000, Runge & Marra 2005). Threats experienced during the non-breeding season are most likely to cause regional population declines on the breeding grounds if migratory connectivity is strong, such that individuals from declining populations use broadly different non-breeding areas or migratory pathways compared to individuals from stable or increasing populations (Finch et al. 2017, Kramer et al. 2018). Assessing migratory connectivity and potential threats during the non-breeding season is critically important for understanding the causes of breeding declines in migratory birds (Webster et al. 2002, Webster & Marra 2005).

Migratory connectivity of larger bird species has frequently been studied using GPS or satellite tags, but many species are too small to carry these units (McKinnon & Love 2018). Genetic markers, stable isotopes, and band recoveries have been used to assess migratory connectivity in small bird species (e.g., Rubenstein et al. 2002, Van Wilgenburg & Hobson 2011, Ruegg et al. 2014), though these methods require intensive sampling and provide very coarse-scale connectivity estimates. Technological miniaturization of archival light-level geolocators has recently allowed scientists to track the migratory journeys of birds as small as 9g (Kramer et al. 2018, Delancey et al. 2020). Geolocators possess a clock and a data logger which records ambient light levels every few minutes; light data are recorded and stored throughout the entire annual cycle, which can then be retrieved and analyzed once the bird returns to its deployment location (Bridge et al. 2011). The archived light data can then be used to infer the daily longitude and latitude of the unit during the previous year. Though accuracy is much lower than with satellite and GPS tags (~200km, McKinnon & Love 2018), geolocators currently provide the best method for assessing migratory connectivity of small birds.

Many species of migratory birds which breed predominantly in Canada and the northern United States are declining in abundance at the trailing edge of their ranges in the southern Appalachian Mountains, despite remaining relatively stable or increasing within the core of the breeding range (Sauer et al. 2017). Trailing edge species in the Southern Appalachians are restricted to high-elevation forests, where conditions are cooler, wetter, and more similar to conditions further north within the core of the breeding range (Merker & Chandler 2021, Chapter 2). Trailing edge population declines in the Southern Appalachians are associated with abandonment of low-elevation breeding habitats and upslope range shifts (Stodola et al. 2013, Merker 2017, Chapter 2). This strong elevational pattern suggests that trailing edge population declines are largely driven by climate change on the breeding grounds (Chapter 2); however, breeding declines could be exacerbated by threats encountered on the non-breeding grounds. Currently, little is known about the degree of migratory connectivity for most of these trailing edge species. Furthermore, little is known about the degree to which threats on the non-breeding grounds may interact with climate change on the breeding grounds to drive population declines in the Southern Appalachians.

Geolocators were deployed on black-throated blue warblers (*Setophaga caerulescens*, hereafter BTBW) to test the hypothesis that habitat loss on the non-breeding grounds is exacerbating trailing edge population declines in the Southern Appalachians. BTBW are small

(9-10g), sexually dimorphic songbirds which breed predominantly in the northern United States and Canada, with a trailing edge distribution in the Southern Appalachians (Holmes et al.2017). Birds primarily overwinter in the Caribbean. Since 2002, BTBW breeding demography has been extensively studied at both the trailing edge in the Southern Appalachians and at the range core in New England. Populations have been declining at low elevations at the trailing edge but have remained relatively stable within the range core (Sauer et al. 2017, Chapter 2). BTBW migratory connectivity should be strong if habitat loss on the non-breeding grounds is exacerbating trailing edge declines in the Southern Appalachians. Specifically, BTBW from the trailing edge should use different migratory pathways or overwinter in broadly different parts of the Caribbean from range core birds. Furthermore, overwintering areas utilized by trailing edge birds should have experienced a greater degree of habitat loss compared to areas utilized by range core birds.

Methods

Geolocators were deployed on adult BTBW at two range positions: the trailing edge of the range within the Nantahala National Forest in the Appalachian Mountains of North Carolina (35.1°N, 83.4°W), and at the range core at the Hubbard Brook Experimental Forest in New Hampshire (43°56′N, 71°45′W). Geolocators were deployed on males at both range positions, though some were also deployed on females at the range core in 2017-2018. Territorial males were captured with mist nets using conspecific playback, while females were captured passively or by flushing off of nests. Captured birds were banded with a USGS aluminum leg band and unique combination of 3 colored leg bands. Birds were fitted with a 0.36g Intigeo P30Z11-7-DIP geolocator (Migrate Technology, Cambridge, UK) using a leg-loop harness made of elastic beading cord (Naef-Daenzer 2007). The combined mass of the geolocator and harness was <5% of warbler body mass. I deployed 36 geolocators at the trailing edge between 2018-2019, and 83 were deployed at the range core in 2015, 2017, and 2018. Geolocators were recovered in the subsequent year by searching areas near deployment locations and netting returning birds. This method assumes that migratory routes and overwinter areas are broadly similar for all members of a population. Dominance hierarchies may cause fine-scale segregation between age and sex classes on the overwintering grounds (Holmes et al. 1989, Wunderle 1995), but there is no evidence of broad-scale separation that would be beyond the error radius inherent to geolocation (~200km).

All analyses were performed in program R v. 4.0.4 (R Core Team 2020). I used the "threshold" method for estimating geographic positions. This method determines the time of twilight events (i.e., sunrise, sunset) based on when light readings cross a pre-specified light/dark threshold; the timing of successive twilight events can then be used to infer twice-daily estimates of longitude and latitude (Lisovski et al. 2020). Twilights were assigned with the TwGeos package (Lisovski et al. 2015, Lisovski et al. 2020) using a light threshold of 1 and a minimum time between sunset and sunrise of 8 hours. Light data from a few birds showed extreme and variable shading on the breeding grounds, which occurs when light is blocked from reaching the geolocator (e.g., the bird is in thick vegetation or at the bottom of a mountain valley). In these cases, I used a light threshold of 1.5. Twilights were manually edited if 1) they were at least 30 minutes different from the corresponding twilight events on the previous and subsequent days, and 2) they did not occur during periods when the bird was likely to have been migrating. Calibration was performed from light readings during times when birds were known to be at the deployment location (e.g., before August 1st). I extended the calibration period for 1 unit until August 31st because it was not deployed until early August and the bird did not leave the deployment area until September. Calibration infers error associated with light recordings by calculating a reference zenith angle (position of the sun relative to the vertical plane at twilight) for the period when the bird was known to be stationary. Some birds exhibited different zenith angles between the breeding and non-breeding grounds, likely due to differences in weather, topography, or habitat between areas (Lisovski et al. 2012, Hallworth 2015). In these instances, I calculated a separate zenith angle for the non-breeding season using the GeoLight package (Lisovski & Hahn 2012, Lisovski et al. 2020).

I used program SGAT to estimate geographic positions and associated error from the light data (Wortherspoon et al. 2013). SGAT incorporates raw estimates of geographic position from the threshold analysis, a behavioral model describing likely flight speeds, and a spatial model restricting stationary periods to land. I defined the behavioral model with separate flight speeds for stationary and migratory periods (Hallworth et al. 2021). Similar to Tonra et al. (2019), I generated a spatial mask using BTBW occurrence data from the Spatio-Temporal Exploratory Model (STEM) from eBird (Fink et al. 2020). The spatial mask reduces the likelihood of positions falling outside the normal range of BTBW. I ran models 3 times with Markov Chain Monte Carlo (MCMC) simulations, using 3 chains of 3000 iterations. Each subsequent model was initialized with the median estimates of longitude and latitude from the previous run (Lisovski et al. 2020). Stationary periods were determined from location estimates generated from the MCMC posterior distribution, using the MigSchedule function from the LLmig package (https://github.com/MTHallworth/LLmig, Tonra et al. 2019). I estimated the migratory distance travelled by each bird by summing the great circle distance (shortest distance between points on a sphere) between the 50% longitude and latitude estimates for successive stationary periods during migration. The assumptions of parametric statistical tests could not be met, so I assessed differences in migratory route length between range positions with a Mann-Whitney U test.

I calculated the degree of migratory connectivity between breeding and overwintering locations using the MigConnectivity package (Cohen et al. 2018) with 1000 bootstrap runs. The strength of migratory connectivity is estimated as the distance between birds in one season which were in close proximity in a different season. Estimates range from -1 (weak connectivity) to 1 (strong connectivity). MigConnectivity incorporates relative abundance of the study species between deployment regions, which I calculated with the eBird STEM. BTBW breeding abundance was extracted for each Bird Conservation Region, subset down to the state in which each deployment region was located (North Carolina Appalachian Mountains and New Hampshire Northern Hardwood Forest).

BTBW are primarily associated with forested habitat throughout the annual cycle (Holmes et al. 2017); therefore, forest loss in the Caribbean likely represents non-breeding habitat loss. Forest cover loss from 2000-2019 was summarized for each country in the Caribbean using the Global Forest Change dataset (v. 1.7, Hansen et al. 2013) in Google Earth Engine (Gorelick et al. 2017). Forest cover loss was converted to percentage forest cover loss by dividing by the area of the country. Percent forest cover loss was weighted by the country-specific probability of overwinter occurrence (December 1 – March 1) from the MCMC posterior distribution, generating a value of percent habitat loss experienced by each bird during the overwintering period. I used a Mann-Whitney U-test to determine if birds breeding at the trailing edge experienced greater decline in forest cover on the overwintering grounds compared to birds breeding at the range core.

Results

Geolocators were recovered from 5 birds at the trailing edge and 8 birds at the range core. Only 1 unit was recovered from a female. An additional 4 birds (2 from each range position) returned without their geolocators; omitting these birds, recovery rates were 15% at the trailing edge and 10% at the range core. Return rates varied by year, from 7-20% at the trailing edge and from 4-20% at the range core. Tracking data were collected from all 13 geolocators; however, fall migratory routes could not be determined for 3 range core birds due to extreme shading resulting in obviously incorrect stopover assignment (e.g., in South America).

BTBW breeding at the two range positions showed a general longitudinal divide in overwintering areas. Range core birds overwintered broadly across the Caribbean, from Cuba to the Dominican Republic, but probability of occurrence peaked in central Cuba (Figure 5.1 A). Of the 8 range core birds, 3 overwintered in central to eastern Cuba, 2 overwintered in either Jamaica or southern Cuba, and 3 overwintered in Hispaniola. The lone female for which I had data overwintered in southern Cuba or Jamaica. The overwintering country could not be determined for 2 Hispaniolan birds, but the third bird appeared to overwinter in the Dominican Republic. In contrast to the longitudinal spread of range core birds, all 5 trailing edge birds overwintered in Hispaniola, largely in the Dominican Republic (Figure 5.1 B). No returning birds overwintered in Puerto Rico or western Cuba. BTBW showed a general east/west divide during the non-breeding season, so I used 2 overwintering areas (Cuba and Jamaica vs. Hispaniola) for the migratory connectivity analysis. The combination of a restricted overwintering range for trailing edge birds and diffuse range for range core birds resulted in moderately strong migratory connectivity (MC mean = 0.42, se = 0.26).

Fall migratory routes also differed between range positions. Trailing edge BTBW largely migrated south through Florida and Cuba before turning east to Hispaniola (Figure 5.2B). In contrast, many range core birds followed the coast southwest until reaching the Carolinas, after which they flew directly across the ocean to overwintering areas in Cuba or Jamaica (Figure 5.2A). This direct flight from the Carolinas to Cuba could have saved birds up to 300km of flight distance compared to the overland route through Florida. Migratory routes were generally shorter at the trailing edge (mean = 2545km, SD = 271km) than at the range core (mean = 2991km, SD= 434 km), but this difference was not significant (W = 3, p = 0.056). The stopover locations in Fig. 1 should be interpreted with caution. Most BTBW migrated during the fall equinox when latitude cannot be reliably estimated; however, the differential migration routes between the range positions is not an artifact of location uncertainty. Longitude estimates are unaffected by the equinox, and only one range core bird definitively reached the longitude of Florida during fall migration.

Caribbean countries varied in their degree of forest cover loss since 2000. Proportional forest cover loss was greatest in the Dominican Republic (7.2%), followed by Jamaica (4.6%), Cuba (3.7%), and Haiti (2.8%). Due to their restricted overwintering range in the Dominican Republic, trailing edge BTBW were exposed to significantly greater habitat loss on the non-breeding grounds than were range core birds (W = 36, p = 0.009).

Discussion

BTBW exhibited moderately strong migratory connectivity between breeding and overwintering areas, with trailing edge birds overwintering on Hispaniola and range core birds overwintering primarily in Cuba. Though breeding populations were not completely isolated on the overwintering grounds, BTBW exhibited stronger migratory connectivity than has been observed in many other species (Finch et al. 2017, Cohen et al. 2019, Tonra et al. 2019, Hallworth et al. 2021, but see Hallworth et al. 2015, Kramer et al. 2018). The greater degree of migratory connectivity in BTBW could possibly be an artifact of the low sample size of returning birds (McKinnon & Love 2018); however, previous research using stable isotopes has also found longitudinal separation on the overwintering grounds between southern and northern breeding BTBW (Rubenstein et al. 2002). The geolocator tracks confirm the findings of Rubenstein et al. (2002), but they also show that the size of overwintering ranges differ between breeding populations. Range core birds overwintered broadly across the Caribbean, from central Cuba to eastern Hispaniola, but trailing edge birds concentrated into Hispaniola. These results show that trailing edge BTBW not only overwinter in somewhat different areas from range core birds, but also have a greatly restricted overwintering range.

The restricted overwintering range of trailing edge BTBW suggests that they are particularly vulnerable to habitat loss or hurricane activity on Hispaniola. This restricted range in the Dominican Republic is likely caused, at least partially, by the near-complete loss of primary forest in Haiti (Hedges et al. 2018), thereby forcing birds that overwinter on Hispaniola into the more intact forests of the Dominican Republic. Despite retaining more forest cover than its neighbor, the Dominican Republic has experienced much greater forest cover loss than other Caribbean countries over the past few decades (Lloyd & León 2019). This widespread deforestation on Hispaniola likely subjected trailing edge BTBW to significantly greater overwintering habitat loss than range core birds. Though 3/8 of range core birds also overwintered in Hispaniola, and thus should have been exposed to the same negative effects of deforestation, most overwintered further west in Cuba. Conservation efforts have led to substantial recovery of forested land in Cuba (Goulart et al. 2018); therefore, the diffuse overwintering range of range core BTBW may have buffered against any population-level effects of deforestation in the eastern Caribbean. Broad-scale habitat loss on Hispaniola is likely to have been disproportionately detrimental to the range-restricted trailing edge population (Simberloff 1995, Gilroy et al. 2016, Staude et al. 2020), potentially exacerbating breeding-ground declines (Robbins et al. 1989, Sherry & Holmes 1996, Sanderson et al. 2006).

Fall migratory routes also differed between the breeding populations. Changing conditions along the migratory routes may have exacerbated the trailing edge declines (Baker et al. 2004, Hewson et al. 2016); however, several lines of evidence suggest that this may be unlikely. First, migration is the most energetically expensive and hazardous phase of the annual cycle, and the majority of annual mortality occurs during migration (Sillett & Holmes 2002, Klaassen et al. 2013, Paxton et al. 2017, Sergio et al. 2019). Longer migratory routes may therefore be associated with higher mortality, but routes tended to be longer for range core birds. Second, trailing edge birds predominantly migrated over land, while many range core birds made long transoceanic flights. Geolocator tracking has revealed that Connecticut warblers (*Oporornis agilis*, McKinnon et al. 2017, Hallworth et al. 2021) and, to a greater extent, blackpoll warblers (*Setophaga striata*, DeLucca et al. 2015) undertake similar trans-Atlantic flights during migration. Most birds likely can complete these long flights without incident, though prolonged overwater crossings may lead to high mortality if birds are physiologically unprepared or encounter inclement weather en route (Newton 2007, Ward et al. 2018). Finally, most trailing edge birds made a stopover in Cuba, which is the primary overwintering area for range core birds. Any threats facing trailing edge birds stopping in Cuba likely would have had a greater effect on the range core birds overwintering there. The longer migratory route and prolonged trans-Atlantic flight may explain why apparent survival is lower at the range core (Chapter 2), but conditions along the migratory routes may not have had much effect on trailing edge population declines.

Tracked BTBW likely overwintered in Cuba, Jamaica, and Hispaniola, though I did not detect any birds overwintering in Puerto Rico. Stable isotopes suggest that Puerto Rican BTBW are likely to breed in the Appalachians (Rubenstein et al. 2002). I found no evidence of this with the geolocator tracks, though Puerto Rican birds may breed further north of the trailing edge study site (e.g., West Virginia or Pennsylvania). I may not have detected any birds migrating to Puerto Rico for 2 reasons: 1) birds from the study populations did not overwinter there; or 2) birds did overwinter in Puerto Rico, but no birds returned to the breeding grounds due to high non-breeding mortality (Rushing et al. 2021). Trailing edge birds therefore may have overwintered in Puerto Rico, but declining conditions on the island led to reduced survival and return rates to the breeding grounds. Forest cover has tripled in Puerto Rico since the 1970s (Yuan et al. 2017), but changes in habitat quality or other threats could have affected overwintering BTBW. Deploying geolocators on the overwintering grounds, especially in Puerto Rico, would be beneficial for refining estimates of BTBW migratory connectivity.

Recovery rates of geolocator-tagged BTBW were low, but in the same general range as most other studies deploying geolocators on small birds (Salewski et al. 2013, DeLuca et al. 2015, Delancey et al. 2020, Hallworth et al. 2021, but see Peterson et al. 2015). While this study was not designed to evaluate the fitness effects of geolocators, the low return rates may indicate that geolocators had a negative effect on BTBW apparent survival. Studies have reported conflicting results on the fitness consequences of geolocators (e.g., Arlt et al. 2013, Peterson et al. 2015, Raybuck et al. 2017), but a recent metanalysis found only minor effects of geolocators on apparent survival (Brlík et al. 2020). Several BTBW dispersed >100m between years, and one bird was recaptured 750m from its deployment location. Geolocator deployment may have directly led to emigration, e.g., the extra weight left birds at a competitive disadvantage, though adult emigration is not uncommon in BTBW (Holmes et al. 1996, Chapter 2). Long-distance breeding dispersal has also been observed for geolocator-tagged cerulean warblers (*Setophaga cerulea*, Raybuck et al. 2017); therefore, geolocator return rates are likely to underestimate true survival.

The results of this chapter should not be interpreted as evidence that trailing edge declines in the Southern Appalachians are solely driven by overwintering habitat loss. If deforestation on Hispaniola is driving breeding declines, then population declines should be observed across all breeding elevations in the Southern Appalachians. Instead, populations have remained stable at the highest elevations but declined at the lowest, warmest elevations in response to warming temperatures (Chapter 2). Furthermore, many trailing edge species are declining on the breeding grounds in the Southern Appalachians despite overwintering in broadly different areas. For example, populations of BTBW, Canada warblers (*Cardellina canadensis*), and Veeries (*Catharus fuscescens*) are declining at low elevations in the Southern Appalachians; however, these species predominantly overwinter in the Caribbean, Andes Mountains, and Brazil, respectively (Merker 2017, Chapter 2). For overwintering habitat loss to be driving breeding declines in all of these species, each would have to exhibit strong migratory connectivity with trailing-edge populations overwintering in areas with high rates of forest loss or other threats. The results of this chapter instead show that habitat loss on the overwintering grounds could exacerbate climate-induced population declines at the trailing edge. My results suggest that more intensive study is needed on the overwintering grounds, particularly examining how conditions on the overwintering grounds may interact with breeding-ground climate change to drive population declines.

In conclusion, BTBW geolocator tracks revealed that non-breeding habitat loss may exacerbate trailing edge population declines: 1) populations exhibit moderately strong migratory connectivity between breeding and wintering areas; and 2) the trailing edge population overwintered in a restricted area which has experienced substantial forest loss. Deforestation rates have been accelerating in the Dominican Republic (Lloyd & León 2019), which is likely to disproportionately affect trailing edge BTBW. Hispaniola also provides important overwintering habitat for other species, such as the Bicknell's thrush (*Catharus bicknelli*, McFarland et al. 2013); therefore, protecting forested land on Hispaniola should be a top conservation priority. Promoting sustainable agricultural practices, such as shade-grown coffee, may also provide suitable habitat for a variety of forest-dwelling species, including BTBW (Wunderle & Latta 1996, Wunderle 1999). Sustainable agricultural practices generally support lower biodiversity than primary forest and should be considered as lower priority than conservation of native forest (Rappole et al. 2003, Chandler et al. 2013). Though breeding declines in the Southern Appalachians appear largely driven by climate change, deforestation in the Caribbean may be exacerbating these declines. Further work from elsewhere in the breeding and non-breeding range is needed to refine estimates of migratory connectivity in BTBW to determine the relative influence of threats experienced throughout the annual cycle on trailing edge population declines.

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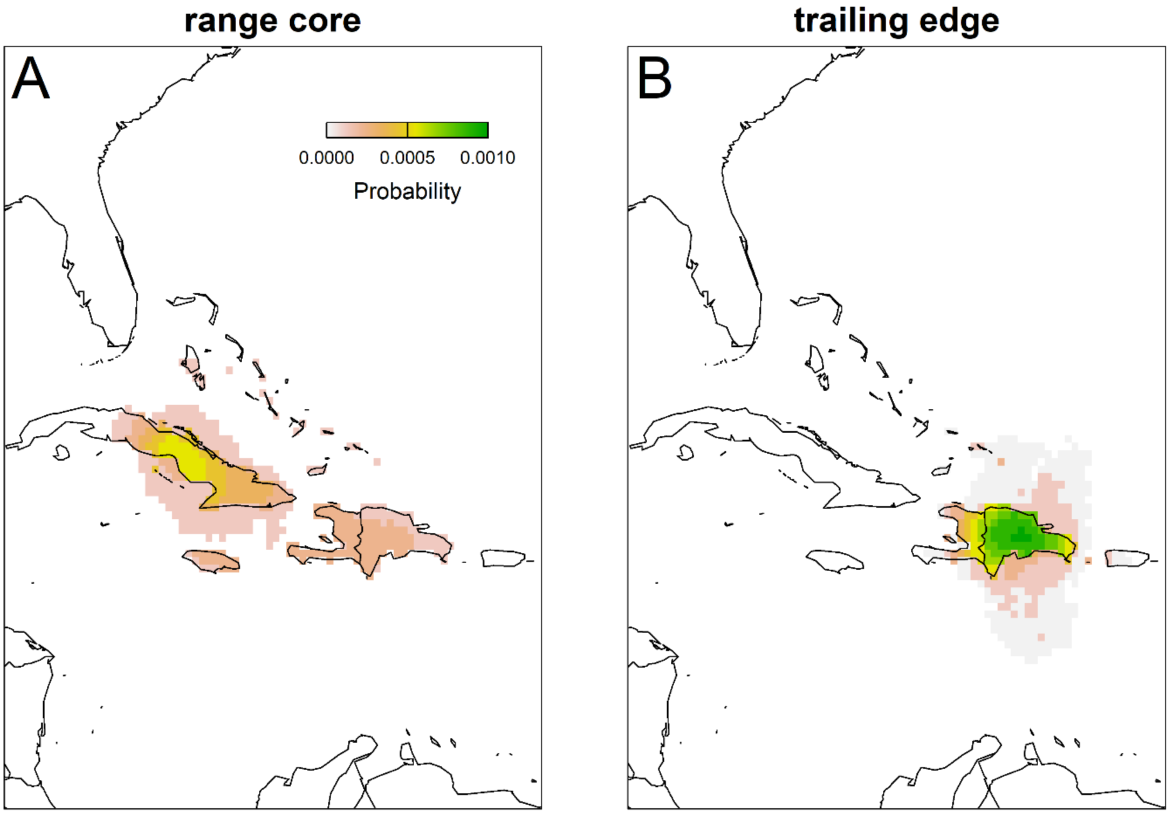

Figure 5.1. Overwintering distribution (December 1 – March 1) determined via geolocation for black-throated blue warblers breeding at the range core (A, n=8) and trailing edge (B, n= 5). Heat maps show 95% credible intervals for winter probability of occurrence (green = highest probability). Range core birds overwintered broadly across the Caribbean, but probability of occurrence was centered in Cuba. Trailing edge birds overwintered in the Dominican Republic.

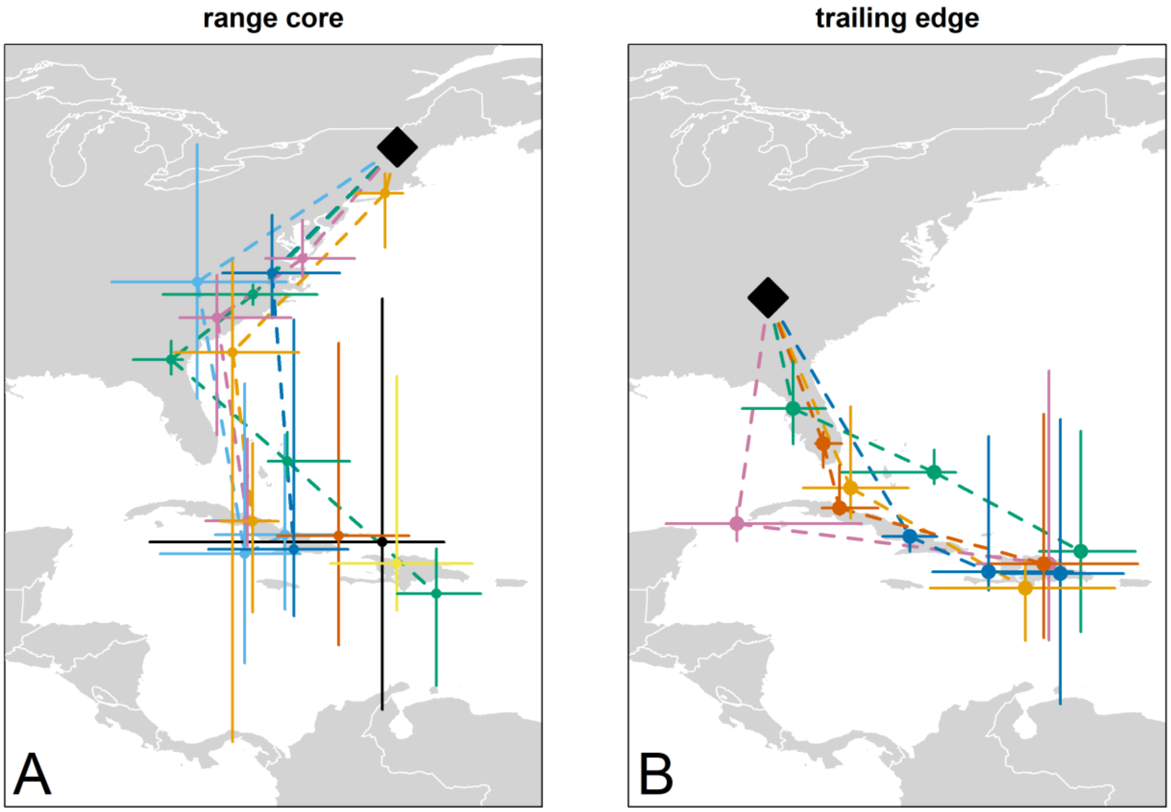

Figure 5.2. Fall migratory routes determined via geolocation for range core (A, n=8) and trailing edge (B, n= 5) black-throated blue warblers. Deployment locations are shown with black diamonds. Median longitude and latitude are shown for stationary periods for each bird, as well as 95% credible intervals. Different colors represent migratory tracks for different individuals. Migratory tracks could not be determined for 3 range core birds, though estimated overwinter locations are shown. The light blue track from the range core (subfigure A) was from a female; all other tracks were from males. Successive stopover locations are connected with a dotted line, but this does not represent the actual flight path that the bird took.

CHAPTER 6

CONCLUSIONS

This concluding chapter begins with a summary and synthesis of the findings from chapters 2-5. I then describe my recommendations for the future of the long-term black-throated blue warbler monitoring project. Finally, I discuss the management and conservation implications of my findings.

Summary and synthesis

Like many other species with predominantly northern ranges, warming temperatures have caused declines in black-throated blue warbler populations at the trailing edge of the range in the southern Appalachian Mountains. Declines were first observed at the lowest, warmest elevation breeding plot and later expanded up the mountain. This elevational pattern is consistent with climate change pushing the low-elevation range limit steadily upslope. Temperatures in the southeastern United States are predicted to rise by 2-4°C by 2100 (Melilo et al. 2014), which may push the low-elevation range limit further and further upslope until reaching the tops of the mountains (Şekercioğlu et al. 2008). Apparent survival also declined with warming temperatures at the lowest, warmest elevation study plot at the range core, which is predicted to drive population declines over the next decade. This result shows that even populations within the core of the range may not remain stable over the long term in the face of ongoing climate change.

BTBW declines were consistent with climate change predictions, but the exact mechanisms through which climate change is driving population declines are complex and not due to a single obvious cause. Declining productivity at the high-elevation plot likely exacerbated the declines, but does not seem to be the primary mechanism through which climate change is affecting trailing edge populations. Instead, changes in late-season food biomass appeared to have the strongest effect on trailing edge population declines. Late-season food abundance meets both requirements to be considered a mechanism underlying trailing edge population declines (McLean et al. 2016): 1) it has declined at the lower elevations at the trailing edge in response to climate change, and 2) it is positively correlated with population dynamics. Declining late-season food biomass may have affected population declines through multiple pathways, such as by negatively affecting nestling mass, post-fledging survival, and emigration and immigration decisions. One limitation of this study is that these were the only potential mechanisms for which I had long-term data. Climate change likely also affected BTBW populations through other mechanistic pathways, such as direct physiological stress or spread of pathogens (S. Merker unpub. data). The results of my dissertation suggest that climate change is not having just one effect on BTBW populations; instead, climate change is causing trailing edge population declines through multiple interacting mechanistic pathways.

I found that local population trajectories, demographic rates, and drivers of population dynamics varied at fine scales. Some population declines may have been driven by declining recruitment, though adult emigration away from poor-quality habitats also is likely to be a major demographic driver of declines. Declining food, productivity, and nestling quality at the trailing edge likely led to reduced recruitment to the region (Ringsby et al. 1998, Sillett et al. 2000, Townsend et al. 2016). Young birds that recruited to the trailing edge may have preferentially settled in the highest quality habitats available to them rather than in the declining-quality habitats at low elevations. Declining food abundance and nestling quality at the low elevations also may have caused adults to permanently emigrate from these areas (Holmes et al. 1996, Doligez et al. 2002, Cline et al. 2013). Little is known about where birds settle after leaving the study plots, but local emigration likely reflects regional redistribution rather than long-distance dispersal (Camus & Lima 2002, Rushing et al. 2017). Furthermore, BTBW engaging in breeding dispersal typically shift from low-quality to high-quality habitats (Holmes et al. 1996, Rodenhouse et al. 2003). These results suggest that low-elevation declines may be associated with regional movements of individuals, but more data is needed to test this hypothesis. As climate change pushes the factors setting the low-elevation range limit upslope, birds may persist at or below the elevational limit due to site fidelity or site-dependence forcing subordinate birds into marginal habitat. Continued warming could push these birds further and further from their ecological tolerance (Cahill et al. 2014, Coristine & Kerr 2015), leading to local extirpation and upslope range shifts over the long term.

While climate change on the breeding grounds seems to be a strong driver of trailing edge population declines, the moderately strong migratory connectivity in BTBW shows that non-breeding habitat loss may have exacerbated the trailing edge declines. Breeding and non-breeding causes of declines are not mutually exclusive, and threats encountered over the entire annual cycle likely contributed to the trailing edge declines (Sillett et al. 2000, Webster & Marra 2005). For example, habitat loss on Hispaniola may have led to reduced adult and juvenile overwinter survival; this, in turn, would allow birds returning to the Southern Appalachians to preemptively settle at higher elevations and avoid declining breeding conditions at the lower elevations. Deforestation rates have become increasingly rapid in the Dominican Republic (Lloyd & León 2019) and hurricane activity is predicted to increase with climate change (Knutson & Tuleya 2004); therefore, overwintering habitat loss could increasingly limit BTBW populations in the future.

Recommendations for the BTBW Project

Continued monitoring is needed to document BTBW population declines, as ongoing climate change may cause extirpation in currently declining areas and future declines in areas which are currently stable. Populations should be monitored through the entire period of decline until they are confirmed to be extirpated. Continued monitoring will likely help elucidate the mechanisms behind population declines, but the exact mechanisms remain unclear even after almost 20 years of monitoring. This suggests that monitoring efforts should be enhanced, or at least modified, to collect other types of data.

Of particular note, the results of this dissertation suggest that recruitment to the trailing edge may have declined while adults may have increasingly emigrated from poorer-quality habitats; however, little is known about the dispersal patterns of BTBW. With enough effort, broadcast point counts could be performed in a wide area around the study plots in an attempt to relocate banded birds. Dispersal data could then be used to separate emigration from true survival, as in Schaub & Royle (2014), or to estimate first-year survival. Obtaining a better understanding of dispersal behavior is needed to test the hypothesis that low-elevation population declines at the trailing edge are driven by birds increasingly recruiting and immigrating to the higher-quality habitats at the higher elevations.

BTBW populations were also exposed to both top-down and bottom-up trophic effects on the breeding grounds; therefore, understanding the mechanisms underlying population declines requires studying the community-level effects of climate change. We need a better understanding of the specific makeup of the caterpillar and nest predator communities and how these communities are affected by climate change. A first step is to determine the major nest predators at each study plot, which could be achieved by wiring video cameras to 12V sealed lead acid batteries for prolonged nest filming. Targeted surveys could then be used to assess predator abundance, such as track plates for small mammals (Emmering & Schmidt 2011) or point counts for avian predators (Sillett et al. 2004). We also do not know if caterpillar declines are due to changes in the lepidopteran community or due to changes in caterpillar size and spatial distribution. To better understand the makeup of the lepidopteran community, at least a subset of caterpillars should be identified to species. Establishing species-specific relationships between caterpillars and host plants, and then relating these to long-term changes in vegetation on the study plots, may help elucidate the mechanisms behind caterpillar declines.

Food frequently limits avian populations (Martin 1987, Rodenhouse & Holmes 1992, Newton 1998), so declining low-elevation food abundance likely had a major effect on BTBW populations. If this is the case, however, how are warm-adapted species, such as the hooded warbler (*Setophaga citrina*, hereafter HOWA), able to tolerate declines in food abundance at low elevations? Warming temperatures may shift competitive interactions (Heegard & Vandvick 2004, Stenseth et al. 2015) such that HOWA outcompete BTBW for the limited caterpillars at low elevations. Birds can also switch to alternate prey items, such as spiders and beetles, when caterpillar abundance is low (Naef-Daenzer et al. 2000, Maley 2011). HOWA may be more capable of switching to alternate prey than are BTBW. These hypotheses could be tested by comparing prey items provisioned to nestlings by BTBW and HOWA in areas where they co-occur. Surveys should also document all potential prey species to assess alternate food sources when caterpillar abundance is low. Assessing the abundance of alternate prey items is also important at the range core, as prey-switching is a potential explanation for why BTBW populations have remained stable despite declining caterpillar biomass.

The results of my dissertation also show that local population dynamics can vary at fine scales, even from study plots separated by 1km. Inferences from a small number of study plots may therefore lead to biased estimates of region-wide population processes. Furthermore, it can be difficult to separate the effects of temperature, precipitation, food, and habitat under the current study design, as they are all confounded with elevation. Climate could be recorded at individual study plots and within nests, to assess potential influences of microclimate on hatch rates and nestling growth (Dawson et al. 2005, S. Merker unpub. data); however, the ideal method to address these issues would be to collect data at multiple study plots spanning a range of habitat conditions at different elevations. The value of paired study plots which differ in habitat quality is evident from Chapter 2, where I show that population declines at the mid elevation at the trailing edge are caused by adult emigration from poor-quality habitat rather than from changes in true survival. An expanded series of study plots has already been established at the trailing edge (R. Chandler unpub. data), though my results show the need for continued demographic monitoring at all study locations rather than just at the long-term plots.

Finally, the relative influence of breeding and non-breeding factors limiting BTBW populations requires further study. More detailed information on the distribution and habitat use of overwintering BTBW in the Caribbean would help assess this problem. If winter habitat is limiting trailing edge populations, then rates of crowding and non-territorial floaters may be higher in the Dominican Republic compared to in Cuba (Sherry & Holmes 1996). Additionally, birds overwintering in the Dominican Republic may exhibit negative carry-over effects such as lower mass on departure for spring migration (Harrison et al. 2011). Capture-mark-recapture data from the overwintering grounds would permit building a full-annual-cycle population model similar to Rushing et al. (2017), allowing estimation of overwinter effects on population growth.

The population models from Chapters 2 and 3 could also be used to directly assess the effect of overwintering habitat loss on breeding population dynamics. Yearly estimates of change in landscape composition and configuration could be calculated for the core overwintering areas of each breeding population, which could then be used to model trend effects on recruitment and apparent survival. Directly estimating the effect of non-breeding conditions on breeding populations requires accurate estimates of migratory connectivity. Deploying geolocators on the overwintering grounds, especially in Puerto Rico, would greatly refine estimates of migratory connectivity and allow for stronger inferences about the effects of overwinter habitat on breeding populations.

Adding all these additional projects to the existing monitoring framework is, of course, prohibitively costly. This problem may be solved by scaling-down to representative sampling instead of intensive sampling. For example, rather than intensively searching for and monitoring every nest, the long-term data and simulations could be used to determine the minimum sampling effort necessary to estimate productivity. A similar method could be used to determine how many leaves need to be sampled to estimate period-specific food abundance at each study plot. The same approach could be taken for any new sampling protocol, though pilot studies would likely be needed to determine the minimum effort for representation (e.g., how many caterpillars need to be identified to species to estimate community composition or how many nests need to be filmed to assess differences between species in provisioned food). Effort could also be reallocated by sampling a reduced area on each study plot or by checking nests every 3 days rather than every 2. If the goal of the BTBW monitoring project is to determine the mechanisms underlying population declines, then research efforts should focus on collecting representative community data at multiple study plots rather than intensive BTBW demographic data at only a few plots.

Conservation Implications

What can be done to conserve trailing edge BTBW? If population declines are driven by overwintering habitat loss, then forest preservation in the Dominican Republic may help to stabilize populations. Though lower priority than forest conservation, sustainable forms of agriculture, such as shade-grown or integrated open-canopy coffee, may offer a balance between economic needs and providing habitat for a variety of forest-dwelling species (Perfecto et al. 1996, Wunderle & Latta 1996, Chandler et al. 2013). Actions that could be taken if declines are driven by climate change are less clear, other than a global effort to reduce greenhouse gas emissions. Climate change is affecting trailing edge populations through multiple mechanistic pathways, so even if action could be taken to mediate one mechanism (e.g., removing nest predators) BTBW populations would likely still decline via other mechanisms. In the face of ongoing climate change, BTBW may eventually disappear from the trailing edge study area regardless of conservation efforts (Gilbert et al. 2019). Fortunately, birds are highly mobile and have the potential to disperse north as southern breeding areas become unsuitable. In some areas with taller mountains, such as the Great Smoky Mountains, BTBW may be able to expand their range upslope into previously unsuitable habitat. These high-elevation areas may provide temporary refuge for some birds but are unlikely to persist over the long-term.

The best course of action in the face of ongoing climate change may be to maintain habitats at high elevations along the length of the Appalachian Mountains. High-elevation habitats at the southern edge of the range may not be viable over the long-term, but can serve as progressive stepping-stones or corridors of dispersal for birds gradually retreating from the low-latitude and low-elevation limits of the range (Littlefield et al. 2017). Trailing edge BTBW are generally associated with the distribution of their preferred nesting substrate, *Rhododendron maximum*, especially in cool and wet ravines (Holmes et al. 2017, R. Chandler unpub. data). Preserving these habitats along the length of the Appalachians may help BTBW retreat from climate change. This may conserve nesting substrate for BTBW, but we do not know how the distribution and abundance of nest predators, caterpillars, or competitors will change in the future. Strictly conserving areas of high-quality nesting habitat for BTBW may also do little to protect species not strongly associated with *Rhododendron*. Given these uncertainties, a better alternative may be to conserve a diverse forest ecosystem at high elevations along the length of the Appalachians to facilitate dispersal for a wide range of species retreating from climate change (Noss 2001, Heller & Zavaleta 2009, Mori et al. 2013).

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APPENDIX A

SAMPLE JAGS CODE FOR FITTING THE BAYESIAN HIERARCHICAL POPULATION MODEL

APPENDIX A. Sample JAGS code for fitting the Bayesian hierarchical population model. Code for temporal trends on per-capita and recruitment are shown; for climate models (t-7)/4 would be substituted with climate variable. All climate variables were standardized prior to running models. The model for the trailing-low study plot was modified slightly so that η in 2017 and 2018 was multiplied by a measure of detection probability with an informative prior to account for imperfect detection during surveys in those years. See text for more details.

```
model {

  ## Priors
  psi ~ dunif(0, 1)                     # Pr(being in population at start of study)
  gamma0 ~ dnorm(0, 1)                        # Intercept for recruitment
  gamma1 ~ dnorm(0, 0.1)                # Temporal/climate trend for recruitment
  phi0sy ~ dnorm(0, 0.4)                      # Intercept for apparent survival term (SY)
  phi0asy ~ dnorm(0, 0.4)               # Intercept for apparent survival term (ASY)
  phi1 ~ dnorm(0, 0.1)                  # Temporal/climate trend for apparent survival
  tau ~ dunif(0, 1)                     # Age ratio in year 1
  pcap0  ~ dnorm(0, 0.4)                      # Intercept for capture probability
  pcap1  ~ dnorm(0, 0.1)                      # Temporal trend for capture probability
  eta0  ~ dnorm(0, 0.4)                 # Pr(detecting a banded bird breeding on the study
plot)
  kappa ~ dunif(0, 1)                   # Pr(determining age on capture)



  ## Derived parameters
  for(t in firstYear:lastYear) {
    N[t] <- sum(z[,t])                  # Annual abundance
    NSY[t] <- sum(state[,t]==1)
    D[t] <- N[t]/Area                   # Density
    ED[t] <- sum(EN[,t])/Area
    Q[t] <- NSY[t]/max(N[t],1)                # Age ratio (proportion SY)
    markedAlive[t] <- marked[1:M,t] %*% z[1:M,t]
    U[t] <- N[t]-markedAlive[t]               # Alive, unmarked,
    u[t] ~ dbin(eta[t], U[t])
    logit(pcap[t]) <- pcap0 + pcap1*(t-7)/4
    logit(eta[t]) <- eta0
    ## Observation states:
    ## 1: Not detected
    ## 2: Detected as SY
    ## 3: Detected as ASY
```

```
  ## 4: Detected as AHY
  pi.y[1,1,t] <- 1-pcap[t]
  pi.y[1,2,t] <- pcap[t]*kappa
  pi.y[1,3,t] <- 0
  pi.y[1,4,t] <- pcap[t]*(1-kappa)
  pi.y[2,1,t] <- 1-pcap[t]
  pi.y[2,2,t] <- 0
  pi.y[2,3,t] <- pcap[t]*kappa
  pi.y[2,4,t] <- pcap[t]*(1-kappa)
  pi.y[3,1,t] <- 1
  pi.y[3,2,t] <- 0
  pi.y[3,3,t] <- 0
  pi.y[3,4,t] <- 0
}

EN[1,firstYear] <- M*psi*(1-tau)              # Expected number of SYs
EN[2,firstYear] <- M*psi*tau                            # Expected number of ASYs
for(t in 1:(firstYear-1)) {
  pi.b[t] <- 0                                # Must do this for any year before firstYear
}
pi.b[firstYear] <- sum(EN[,firstYear])/M
for(t in (firstYear+1):lastYear) {
  ## Projection matrix
  log(gamma[t-1]) <- gamma0 + gamma1 * (t-7)/4
  logit(phiSY[t-1]) <- phi0sy + phi1*(t-7)/4
  logit(phiASY[t-1]) <- phi0asy + phi1*(t-7)/4
  phi[t-1] <- phiSY[t-1]*Q[t-1] + phiASY[t-1]*(1-Q[t-1])
  W[1,1:2,t-1] <- c(gamma[t-1], gamma[t-1])
  W[2,1:2,t-1] <- c(phiSY[t-1], phiASY[t-1])
  ## Compute dominant eigenvalue (Elam, the asymtotic growth rate)
  part1[t-1] <- W[1,1,t-1]+W[2,2,t-1]
  part2[t-1] <- W[1,1,t-1]*W[2,2,t-1]-W[1,2,t-1]*W[2,1,t-1]
  Elam[t-1] <- part1[t-1]/2 + sqrt(part1[t-1]*part1[t-1]/4 - part2[t-1])
  EN[1:2,t] <- W[,,t-1] %*% EN[,t-1]                # Expected number of SYs and ASYs
  ER[t] <- EN[1,t]
  pi.b[t] <- ER[t]/M
  R[t] <- sum(recruited[1:M,t])                     # nRecruits each year
  S[t] <- sum(survived[1:M,t])                      # nSurvivors
  lambda[t] <- N[t]/N[t-1]
}
ENsuper <- sum(EN[,firstYear])+sum(ER[(firstYear+1):lastYear])
omega <- ENsuper/M
pi.b[lastYear+1] <- 1-omega

## Ecological states:
## 1: Alive SY
```

```
  ## 2: Alive ASY
  ## 3: Dead (Unborn and dead)
  for (i in 1:M) {
    b[i] ~ dcat(pi.b[])
    z[i,firstYear] <- ifelse(equals(b[i],firstYear), 1, 0)
    age[i,firstYear] ~ dcat(c(1-tau, tau))
    state[i,firstYear] <- z[i,firstYear]*age[i,firstYear] +
                          (1-z[i,firstYear])*3
    for (t in (firstYear+1):lastYear) {
      z0[i,t] ~ dbern(z[i,t-1]*W[2,age[i,t-1],t-1])
      z[i,t] <- ifelse(b[i]==t, 1, z0[i,t])
      age[i,t] <- ifelse(b[i]==t, 1, 2)
      state[i,t] <- z[i,t]*age[i,t] + (1-z[i,t])*3
      recruited[i, t] <- equals(state[i,t], 1)
      survived[i, t] <- equals(state[i,t], 2)
      alive[i,t] <- (state[i,t]==1) || (state[i,t]==2)
    }
    ## Capture data.
    ## Birds are never recaptured, only resighted after first capture
    for(t in firstYear:firstcap[i]) {
      ycap[i,t] ~ dcat(pi.y[state[i,t],1:4,t])
    }
    ## Resight data
    ## Birds can be individually identified by sight if
    ##   they are marked in the year they are captured and afterward.
    ##   Can only be resighted if breeding on study plots.
    for(t in firstcap[i]:lastYear) {
      ydet[i,t] ~ dbern(z[i,t]*eta[t])
    }
    everAlive[i] <- max(z[i,firstYear:lastYear])
  }
  Nsuper <- sum(everAlive[1:M])
}
```

APPENDIX B

PARAMETER ESTIMATES FROM THE BAYESIAN HIERARCHICAL POPULATION MODELS

APPENDIX B. Parameter estimates from the Bayesian hierarchical population models. Models were run separately for each of the six study plots allowing recruitment and apparent survival to vary by time (T), annual precipitation (AP), or early-breeding thermal sums (EBTS). The median, lower ,and upper 95% credible intervals are shown for per-capita recruitment rate (γ), apparent survival (ϕ), ratio of ASYs (τ), probability of classifying the bird into a specific age class upon capture (k), capture probability ($p^{(c)}$), and probability of being detected while breeding on plot ($p^{(\eta)}$). Subscripts denote the intercept (0) or a temporal or climate trend effect (t, w). See text for more details.

Range	Elevation	Model	Parameter	Mean	SD	Lower CI	Median	Upper CI
Trailing	Low	T	γ_0	-1.27	0.27	-1.88	-1.24	-0.84
Trailing	Low	T	γ_w	-0.13	0.36	-0.94	-0.09	0.44
Trailing	Low	T	ϕ_0(SY)	1.5	1	-0.2	1.41	3.7
Trailing	Low	T	ϕ_0(ASY)	-1.69	0.86	-3.51	-1.63	-0.21
Trailing	Low	T	ϕ_w	-1.24	1.04	-3.44	-1.16	0.55
Trailing	Low	T	τ	0.34	0.19	0.06	0.31	0.75
Trailing	Low	T	k	0.94	0.05	0.8	0.96	1
Trailing	Low	T	$p^{(c)}_0$	0.41	0.62	-0.79	0.4	1.63
Trailing	Low	T	$p^{(c)}_t$	1.33	0.65	0.09	1.32	2.63
Trailing	Low	T	$p^{(\eta)}_0$	0.72	0.42	-0.07	0.71	1.57
Trailing	Mid	T	γ_0	-0.68	0.1	-0.9	-0.68	-0.49
Trailing	Mid	T	γ_w	0.09	0.08	-0.06	0.09	0.25
Trailing	Mid	T	ϕ_0(SY)	0.27	0.39	-0.43	0.24	1.11
Trailing	Mid	T	ϕ_0(ASY)	-0.72	0.3	-1.32	-0.71	-0.15
Trailing	Mid	T	ϕ_w	-0.39	0.21	-0.84	-0.38	-0.004
Trailing	Mid	T	τ	0.46	0.22	0.07	0.46	0.88
Trailing	Mid	T	k	0.97	0.02	0.91	0.97	1
Trailing	Mid	T	$p^{(c)}_0$	-0.38	0.2	-0.77	-0.38	0.01
Trailing	Mid	T	$p^{(c)}_t$	0.57	0.16	0.27	0.57	0.89
Trailing	Mid	T	$p^{(\eta)}_0$	1.59	0.33	0.99	1.58	2.29
Trailing	High	T	γ_0	-0.9	0.1	-1.1	-0.9	-0.72
Trailing	High	T	γ_w	0.05	0.07	-0.08	0.05	0.18

Trailing	High	T	ϕ_0(SY)	1.1	0.35	0.46	1.09	1.82
Trailing	High	T	ϕ_0(ASY)	-0.13	0.21	-0.54	-0.12	0.28
Trailing	High	T	ϕ_w	-0.1	0.13	-0.36	-0.1	0.16
Trailing	High	T	τ	0.76	0.19	0.31	0.81	0.99
Trailing	High	T	k	0.95	0.02	0.9	0.95	0.98
Trailing	High	T	$p^{(c)}_0$	-0.39	0.17	-0.72	-0.39	-0.07
Trailing	High	T	$p^{(c)}_t$	0.49	0.12	0.25	0.49	0.73
Trailing	High	T	$p^{(\eta)}_0$	1.15	0.18	0.81	1.15	1.51
Core	Low	T	γ_0	-0.4	0.06	-0.52	-0.4	-0.28
Core	Low	T	γ_w	0.02	0.07	-0.13	0.02	0.17
Core	Low	T	ϕ_0(SY)	-0.12	0.2	-0.51	-0.12	0.29
Core	Low	T	ϕ_0(ASY)	-0.87	0.25	-1.38	-0.86	-0.38
Core	Low	T	ϕ_w	-0.38	0.17	-0.72	-0.38	-0.06
Core	Low	T	τ	0.25	0.19	0.01	0.21	0.7
Core	Low	T	k	0.91	0.02	0.87	0.92	0.95
Core	Low	T	$p^{(c)}_0$	0.52	0.15	0.23	0.52	0.82
Core	Low	T	$p^{(c)}_t$	0.15	0.14	-0.13	0.15	0.44
Core	Low	T	$p^{(\eta)}_0$	1.46	0.19	1.09	1.45	1.84
Core	Mid	T	γ_0	-0.56	0.04	-0.63	-0.56	-0.49
Core	Mid	T	γ_w	-0.05	0.05	-0.14	-0.05	0.03
Core	Mid	T	ϕ_0(SY)	0.17	0.13	-0.08	0.16	0.42
Core	Mid	T	ϕ_0(ASY)	-0.57	0.13	-0.82	-0.57	-0.32
Core	Mid	T	ϕ_w	0.06	0.09	-0.12	0.06	0.23
Core	Mid	T	τ	0.42	0.09	0.25	0.41	0.61
Core	Mid	T	k	0.94	0.01	0.92	0.94	0.96
Core	Mid	T	$p^{(c)}_0$	0.91	0.1	0.72	0.91	1.11
Core	Mid	T	$p^{(c)}_t$	0.1	0.1	-0.09	0.1	0.29
Core	Mid	T	$p^{(\eta)}_0$	1.43	0.11	1.21	1.43	1.66
Core	High	T	γ_0	-0.69	0.06	-0.81	-0.69	-0.58
Core	High	T	γ_w	0.1	0.07	-0.03	0.1	0.23
Core	High	T	ϕ_0(SY)	0.41	0.18	0.07	0.4	0.77
Core	High	T	ϕ_0(ASY)	-0.32	0.15	-0.62	-0.32	-0.03
Core	High	T	ϕ_w	-0.25	0.12	-0.48	-0.25	-0.01
Core	High	T	τ	0.43	0.1	0.25	0.43	0.62
Core	High	T	k	0.93	0.02	0.9	0.94	0.96
Core	High	T	$p^{(c)}_0$	0.58	0.12	0.34	0.58	0.83

Core	High	T	$p^{(c)}_t$	-0.14	0.12	-0.37	-0.14	0.08
Core	High	T	$p^{(\eta)}_0$	1.49	0.15	1.2	1.49	1.8
Trailing	Low	EBTS	γ_0	-1.38	0.28	-2	-1.36	-0.93
Trailing	Low	EBTS	γ_w	-0.51	0.36	-1.25	-0.5	0.17
Trailing	Low	EBTS	ϕ_0(SY)	1.48	1.02	-0.2	1.38	3.76
Trailing	Low	EBTS	ϕ_0(ASY)	-0.82	0.62	-2.06	-0.82	0.38
Trailing	Low	EBTS	ϕ_w	0.16	0.63	-1.04	0.15	1.47
Trailing	Low	EBTS	τ	0.36	0.19	0.06	0.34	0.76
Trailing	Low	EBTS	k	0.94	0.05	0.8	0.96	1
Trailing	Low	EBTS	$p^{(c)}_0$	0.37	0.61	-0.81	0.37	1.57
Trailing	Low	EBTS	$p^{(c)}_t$	1.32	0.64	0.08	1.31	2.6
Trailing	Low	EBTS	$p^{(\eta)}_0$	0.69	0.43	-0.1	0.67	1.58
Trailing	Mid	EBTS	γ_0	-0.59	0.07	-0.74	-0.59	-0.45
Trailing	Mid	EBTS	γ_w	0.06	0.15	-0.22	0.06	0.35
Trailing	Mid	EBTS	ϕ_0(SY)	-0.11	0.29	-0.66	-0.12	0.49
Trailing	Mid	EBTS	ϕ_0(ASY)	-0.87	0.3	-1.47	-0.86	-0.29
Trailing	Mid	EBTS	ϕ_w	-0.08	0.21	-0.5	-0.08	0.33
Trailing	Mid	EBTS	τ	0.47	0.22	0.09	0.47	0.89
Trailing	Mid	EBTS	k	0.97	0.02	0.91	0.97	1
Trailing	Mid	EBTS	$p^{(c)}_0$	-0.37	0.2	-0.77	-0.37	0.02
Trailing	Mid	EBTS	$p^{(c)}_t$	0.58	0.16	0.27	0.58	0.9
Trailing	Mid	EBTS	$p^{(\eta)}_0$	1.61	0.33	1.01	1.6	2.3
Trailing	High	EBTS	γ_0	-0.85	0.07	-0.98	-0.84	-0.72
Trailing	High	EBTS	γ_w	-4E-04	0.12	-0.24	0.0004	0.24
Trailing	High	EBTS	ϕ_0(SY)	1.02	0.32	0.46	0.99	1.7
Trailing	High	EBTS	ϕ_0(ASY)	-0.22	0.18	-0.56	-0.22	0.13
Trailing	High	EBTS	ϕ_w	0.03	0.17	-0.3	0.02	0.37
Trailing	High	EBTS	τ	0.78	0.18	0.32	0.82	0.99
Trailing	High	EBTS	k	0.95	0.02	0.9	0.95	0.98
Trailing	High	EBTS	$p^{(c)}_0$	-0.4	0.17	-0.73	-0.4	-0.07
Trailing	High	EBTS	$p^{(c)}_t$	0.49	0.12	0.25	0.49	0.73
Trailing	High	EBTS	$p^{(\eta)}_0$	1.13	0.18	0.79	1.13	1.49
Core	Low	EBTS	γ_0	-0.35	0.05	-0.45	-0.35	-0.25
Core	Low	EBTS	γ_w	-0.14	0.09	-0.32	-0.14	0.03
Core	Low	EBTS	ϕ_0(SY)	-0.26	0.19	-0.62	-0.26	0.11

Core	Low	EBTS	ϕ_0(ASY)	-0.92	0.26	-1.44	-0.91	-0.43
Core	Low	EBTS	ϕ_w	-0.19	0.16	-0.51	-0.19	0.12
Core	Low	EBTS	τ	0.29	0.23	0.01	0.23	0.87
Core	Low	EBTS	k	0.91	0.02	0.87	0.92	0.95
Core	Low	EBTS	$p^{(c)}_0$	0.52	0.15	0.23	0.52	0.82
Core	Low	EBTS	$p^{(c)}_t$	0.16	0.15	-0.12	0.16	0.45
Core	Low	EBTS	$p^{(\eta)}_0$	1.45	0.19	1.09	1.44	1.83
Core	Mid	EBTS	γ_0	-0.58	0.03	-0.64	-0.58	-0.52
Core	Mid	EBTS	γ_w	-0.01	0.06	-0.13	-0.01	0.1
Core	Mid	EBTS	ϕ_0(SY)	0.18	0.12	-0.04	0.18	0.42
Core	Mid	EBTS	ϕ_0(ASY)	-0.56	0.12	-0.81	-0.56	-0.32
Core	Mid	EBTS	ϕ_w	-0.01	0.08	-0.18	-0.01	0.15
Core	Mid	EBTS	τ	0.41	0.09	0.24	0.41	0.59
Core	Mid	EBTS	k	0.94	0.01	0.92	0.94	0.96
Core	Mid	EBTS	$p^{(c)}_0$	0.91	0.1	0.72	0.91	1.11
Core	Mid	EBTS	$p^{(c)}_t$	0.1	0.1	-0.09	0.1	0.29
Core	Mid	EBTS	$p^{(\eta)}_0$	1.43	0.11	1.22	1.43	1.66
Core	High	EBTS	γ_0	-0.66	0.05	-0.76	-0.66	-0.56
Core	High	EBTS	γ_w	0.13	0.08	-0.04	0.13	0.29
Core	High	EBTS	ϕ_0(SY)	0.35	0.17	0.02	0.34	0.7
Core	High	EBTS	ϕ_0(ASY)	-0.39	0.16	-0.7	-0.38	-0.09
Core	High	EBTS	ϕ_w	-0.13	0.12	-0.37	-0.13	0.11
Core	High	EBTS	τ	0.44	0.1	0.25	0.44	0.63
Core	High	EBTS	k	0.93	0.02	0.9	0.94	0.96
Core	High	EBTS	$p^{(c)}_0$	0.57	0.12	0.33	0.57	0.81
Core	High	EBTS	$p^{(c)}_t$	-0.14	0.12	-0.37	-0.14	0.09
Core	High	EBTS	$p^{(\eta)}_0$	1.48	0.15	1.19	1.48	1.78
Trailing	Low	AP	γ_0	-1.25	0.2	-1.68	-1.24	-0.89
Trailing	Low	AP	γ_w	-0.05	0.38	-0.77	-0.07	0.73
Trailing	Low	AP	ϕ_0(SY)	2.1	1.13	0.15	2.02	4.5
Trailing	Low	AP	ϕ_0(ASY)	-1.09	0.56	-2.27	-1.06	-0.06
Trailing	Low	AP	ϕ_w	0.54	0.82	-1.12	0.54	2.12
Trailing	Low	AP	τ	0.33	0.18	0.05	0.31	0.72
Trailing	Low	AP	k	0.94	0.06	0.79	0.96	1
Trailing	Low	AP	$p^{(c)}_0$	0.42	0.61	-0.77	0.41	1.63
Trailing	Low	AP	$p^{(c)}_t$	1.35	0.65	0.11	1.34	2.64

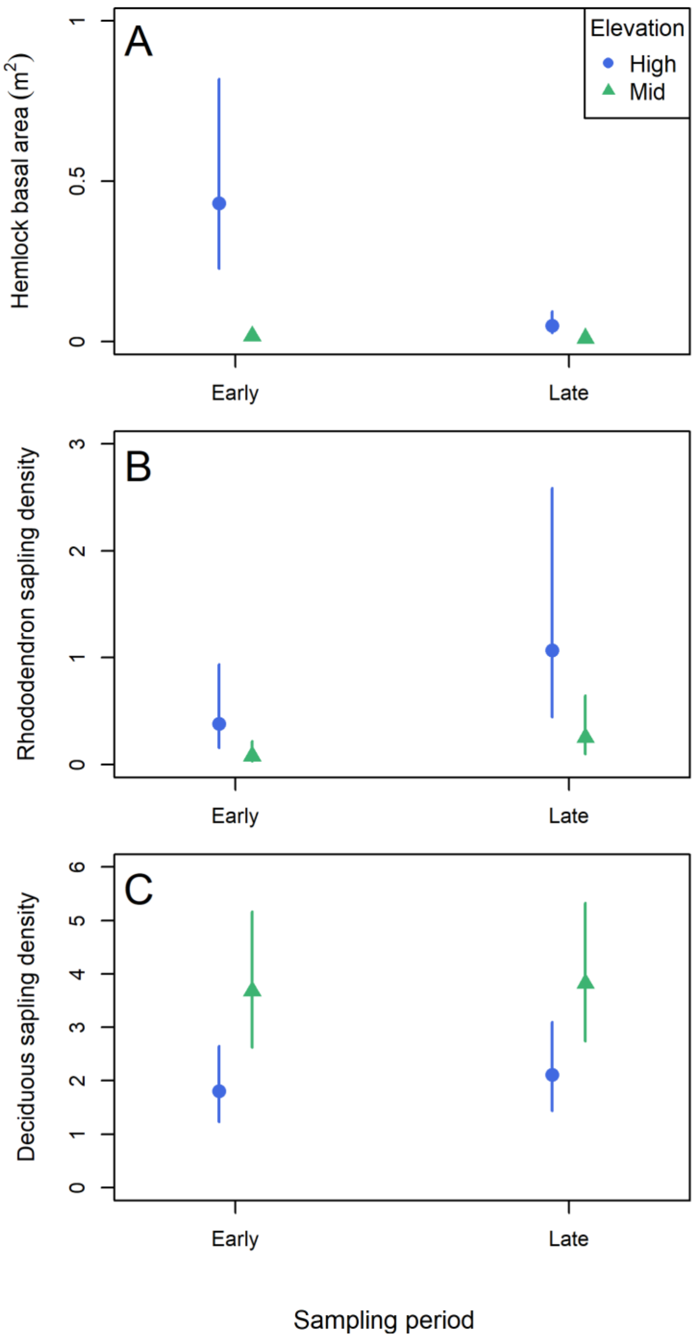
Trailing	Low	AP	$p^{(\eta)}_0$	0.7	0.41	-0.08	0.68	1.55
Trailing	Mid	AP	γ_0	-0.59	0.08	-0.74	-0.59	-0.44
Trailing	Mid	AP	γ_w	0.13	0.14	-0.15	0.14	0.41
Trailing	Mid	AP	ϕ_0(SY)	-0.1	0.3	-0.67	-0.11	0.51
Trailing	Mid	AP	ϕ_0(ASY)	-0.86	0.31	-1.48	-0.86	-0.25
Trailing	Mid	AP	ϕ_w	-0.14	0.21	-0.56	-0.14	0.27
Trailing	Mid	AP	τ	0.5	0.22	0.08	0.5	0.9
Trailing	Mid	AP	k	0.97	0.02	0.91	0.97	1
Trailing	Mid	AP	$p^{(c)}_0$	-0.38	0.2	-0.77	-0.38	0.02
Trailing	Mid	AP	$p^{(c)}_t$	0.58	0.16	0.27	0.57	0.9
Trailing	Mid	AP	$p^{(\eta)}_0$	1.6	0.34	0.99	1.59	2.31
Trailing	High	AP	γ_0	-0.84	0.07	-0.97	-0.83	-0.71
Trailing	High	AP	γ_w	0.15	0.11	-0.06	0.15	0.36
Trailing	High	AP	ϕ_0(SY)	0.98	0.33	0.41	0.96	1.69
Trailing	High	AP	ϕ_0(ASY)	-0.23	0.18	-0.59	-0.23	0.11
Trailing	High	AP	ϕ_w	-0.09	0.16	-0.4	-0.09	0.22
Trailing	High	AP	τ	0.81	0.15	0.42	0.85	0.99
Trailing	High	AP	k	0.95	0.02	0.9	0.95	0.98
Trailing	High	AP	$p^{(c)}_0$	-0.4	0.17	-0.73	-0.4	-0.08
Trailing	High	AP	$p^{(c)}_t$	0.49	0.12	0.26	0.49	0.73
Trailing	High	AP	$p^{(\eta)}_0$	1.14	0.18	0.79	1.14	1.49
Core	Low	AP	γ_0	-0.33	0.05	-0.43	-0.33	-0.24
Core	Low	AP	γ_w	-0.12	0.1	-0.32	-0.12	0.08
Core	Low	AP	ϕ_0(SY)	-0.28	0.18	-0.65	-0.28	0.08
Core	Low	AP	ϕ_0(ASY)	-0.96	0.26	-1.48	-0.96	-0.47
Core	Low	AP	ϕ_w	-0.32	0.16	-0.65	-0.32	-0.01
Core	Low	AP	τ	0.26	0.22	0.01	0.2	0.75
Core	Low	AP	k	0.91	0.02	0.87	0.92	0.95
Core	Low	AP	$p^{(c)}_0$	0.52	0.15	0.22	0.52	0.82
Core	Low	AP	$p^{(c)}_t$	0.17	0.15	-0.12	0.17	0.46
Core	Low	AP	$p^{(\eta)}_0$	1.45	0.19	1.09	1.45	1.85
Core	Mid	AP	γ_0	-0.59	0.03	-0.66	-0.59	-0.52
Core	Mid	AP	γ_w	0.07	0.06	-0.06	0.07	0.19
Core	Mid	AP	ϕ_0(SY)	0.18	0.12	-0.04	0.18	0.42
Core	Mid	AP	ϕ_0(ASY)	-0.57	0.12	-0.82	-0.57	-0.33

Core	Mid	AP	ϕ_w	0.03	0.09	-0.15	0.03	0.21
Core	Mid	AP	τ	0.41	0.09	0.24	0.41	0.59
Core	Mid	AP	k	0.94	0.01	0.92	0.94	0.96
Core	Mid	AP	$p^{(c)}_0$	0.91	0.1	0.72	0.91	1.11
Core	Mid	AP	$p^{(c)}_t$	0.1	0.1	-0.09	0.1	0.29
Core	Mid	AP	$p^{(\eta)}_0$	1.43	0.11	1.21	1.43	1.66
Core	High	AP	γ_0	-0.66	0.05	-0.77	-0.65	-0.56
Core	High	AP	γ_w	0.11	0.09	-0.06	0.11	0.29
Core	High	AP	ϕ_0(SY)	0.33	0.18	0.004	0.33	0.69
Core	High	AP	ϕ_0(ASY)	-0.36	0.15	-0.66	-0.36	-0.06
Core	High	AP	ϕ_w	-0.04	0.12	-0.28	-0.04	0.2
Core	High	AP	τ	0.44	0.1	0.25	0.43	0.64
Core	High	AP	k	0.93	0.02	0.9	0.94	0.96
Core	High	AP	$p^{(c)}_0$	0.57	0.12	0.34	0.57	0.82
Core	High	AP	$p^{(c)}_t$	-0.14	0.12	-0.37	-0.14	0.09
Core	High	AP	$p^{(\eta)}_0$	1.48	0.16	1.18	1.48	1.79

APPENDIX C

CHANGE IN VEGETATION BETWEEN 2002 AND 2020 AT THE TRAILING EDGE

APPENDIX C. Change in vegetation composition between 2002/2003 (early) and 2019/2020 (late) at the trailing edge of the black-throated blue warbler range (Appalachian Mountains of North Carolina). Change in hemlock basal area (A), stem density of sapling *Rhododendron maximum* (the preferred warbler nesting substrate at the trailing edge) (B), and stem density of deciduous saplings (C) is shown for the mid-elevation (green triangles) and high-elevation (blue circles) study plots. Vegetation was surveyed in both sampling periods at 36 locations at the mid-elevation plot and 32 locations at the high-elevation plot. Diameter at breast height (DBH) was measured for each tree (DBH>9.9cm) within 11.3m of location center. DBH was converted to basal area. Sapling density was measured by counting every stem (>1.4m tall and 10>DBH>2.5cm) within 3m of location center. Average values of vegetation measures for each study plot and sampling period were estimated with a linear mixed-effects model, incorporating location ID as a random effect. Mean estimates and 95% confidence intervals are shown.


A
B
C
Hemlock basal area (m^2)
Rhododendron sapling density
Deciduous sapling density
0
0.5
1
0
1
2
3
0
1
2
3
4
5
6
Elevation
● High
▲ Mid
Early
Late
Early
Late
Early
Late
Sampling period