DEMOGRAPHIC DRIVERS OF BLACK-THROATED BLUE WARBLER POPULATION DYNAMICS AT THE TRAILING EDGE AND CORE OF THE SPECIES' RANGE

by

RYAN WORLEY CHITWOOD

(Under the Direction of Richard B. Chandler and Robert J. Cooper)

ABSTRACT

Species' ranges are shifting poleward and to higher elevations in response to climate change. Very few studies have determined how demography links environmental change to range shifts. To investigate the demographic drivers of range shifts, I examined spatial and temporal variation in population density and demography of black-throated blue warblers (*Setophaga caerulescens*) near the core and trailing edge of the species' range. Population density declined at the trailing edge, but remained stable in the core of the range, which supported the hypothesis that this species' range is shifting. Survival rates were higher, but recruitment rates were lower at the trailing edge, suggesting that low recruitment may explain trailing-edge population declines. Future work should seek to understand how climate influences recruitment at trailing-edge range margins via shifts in reproduction, juvenile survival, or dispersal.

INDEX WORDS: Bayesian population models, Black-throated blue warbler, Climate change, Demography, Population dynamics, Range shifts

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DEDICATION

I dedicate this thesis to my grandfather, Otto Worley Chitwood, for showing me that true joy in life is attained through working hard and loving others well.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Studying patterns in species' distributions a major focus of ecology for over a century, but ecologists' understanding of the mechanisms driving patterns and changes in species' distributions is lacking (Hoffmann and Blows 1994, Brown et al. 1996, Sexton et al. 2009, Baselga et al. 2012). Rapid climate change is shifting many species' ranges towards the poles and to higher elevations (Parmesan and Yohe 2003, Root et al. 2003). Climate-driven range shifts may result in reduced genetic diversity if populations are not able to track their climate optima through adaptation or dispersal (Thomas et al. 2004). Hence, forecasting climate-driven range shifts and understanding their drivers are among the highest priorities in ecological research (Clark et al. 2001).

Regarding the factors limiting species distributions, the niche concept was first used to describe the relationship between a species or community and its environment (Darwin 1859, Grinnell and Swarth 1913, Elton 1927). The conceptualization of the niche as a characteristic of the environment was later challenged by G. Evelyn Hutchinson, who proposed that the niche was a function of the species (Hutchinson 1957). In this view, the niche is described by demographic responses (reproduction, mortality, and movement) mapped over environmental conditions (Holt 2009). Since then, few empirical studies have studied spatial variation in population dynamics and demography at more than one location in a species' range (Schurr et al. 2012).

The common approach for studying range dynamics is to use static models that correlate species occurrence directly with environmental variables (Guisan and Thuiller 2005). When using these models to forecast range shifts, the key assumption is that observed species-environment relationships accurately describe favorable conditions for that species (Yackulic et al. 2015). This ideal species-environment relationship corresponds to Hutchinson's fundamental niche, defined as the "a state of the environment which would permit the species to exist indefinitely" (Hutchinson 1957). Instead, data from observational studies arise from a species' realized niche, which includes influences on demography from other factors such as competition and demographic stochasticity. As a result, complex dynamics can be observed at the range level where species can occur outside areas with favorable conditions, or remain absent from areas with favorable conditions (Schurr et al. 2012). For example, source-sink dynamics can result in populations being maintained in unfavorable environments (Pulliam 1988). Alternatively, dispersal limitation can restrict species from colonizing favorable areas (Guisan and Thuiller 2005). In addition, time-delayed local extinction can result in species occupying currently unfavorable environments (Thuiller et al. 2008). Because the realized niche can differ from the fundamental niche, it is impossible to thoroughly understand the factors limiting geographical ranges using static models and simple correlations between abundance and environmental variables (Yackulic et al. 2015). Long-term demographic studies of marked individuals can provide much better information about the processes contributing to range shifts (Normand et al. 2014).

Several factors have contributed to the lack of research regarding demographic drivers of range shifts. Foremost, demographic data are not widely available for most species and most locations because these data often require intensive field work to collect. Studies that have investigated how environmental characteristics and demography interact to limit ranges often lack information on one or more demographic process or do not capture sufficient variation in demography across a species' range. Because observed range dynamics result from reproduction, mortality, and movement, documenting spatial and temporal variation in only one demographic parameter cannot provide reliable inference about range shifts (Gaston 2009).

In cases where studies do capture multiple demographic processes, they may lack sufficient variation in environmental conditions to test hypotheses relevant to large-scale range shifts. Many studies have used elevation gradients in small geographic areas to study range shifts across a variety of climatic conditions, but the expectation that species should move upslope in response to warming climate has recently been called into question (Colwell et al. 2008, Campos-Cerqueira et al. 2017). Recent evidence shows that some species may be shifting downslope in response to climate change under a variety of mechanisms including changes in precipitation regimes and vegetation composition (Lenoir et al. 2010). Therefore, studies attempting to capture climatic variation in demographic rates should incorporate both latitudinal and elevational variation to test for differential responses to warming climate.

Most of the studies investigating climate-driven range shifts at the local scale have focused on leading edge expansion (Hampe and Petit 2005), but determining how ranges are limited at their trailing edge is also a high priority for research because trailing-edge populations are the most vulnerable to extinction (Franco et al. 2006, Chen et al. 2011). Additionally, recent evidence indicates that many trailing-edge populations are evolutionarily older and harbor high genetic diversity, and the loss of these populations will likely have negative consequences for biodiversity and adaptive potential (Eckert et al. 2008, Parisod and Joost 2010, Cahill et al. 2014).

Recent developments in hierarchical population models have paved the way for studying the demographic drivers of large-scale phenomena such as range shifts. These models provide a framework for modeling state processes (e.g. abundance) and transitions (e.g. survival and recruitment) while accounting for uncertainty arising from sampling and observation error (Royle and Dorazio 2008, Kéry and Schaub 2011). Hierarchical models are flexible enough to describe structured population dynamics and can even accommodate time-varying individual traits in addition to sources of variation arising from spatial structure and density dependence (Royle 2008, Royle et al. 2013).

To uncover the demographic drivers of range shifts, I studied spatial variation in the population dynamics and demography of black-throated blue warblers (*Setophaga caerulescens*) over a fifteen-year period. This study took place at two sites: a trailing-edge site in North Carolina and a range-core site in New Hampshire. Within both sites, three plots were arranged across an elevation gradient that correlated strongly with a black-throated blue warbler habitat quality (i.e. highest quality habitat at high elevations) (Fig. 1) (Stodola et al. 2009, Kaiser et al. 2015). These six plots are referred to as trailing-low, trailing-mid, trailing-high, core-low, core-mid, and core-high. To determine the extent to which survival and recruitment contributed to a potential black-throated blue warbler range shift, I fit a stage-structured population model to draw inferences about spatial variation in black-throated blue warbler demography.

This thesis consists of an introductory chapter, a data chapter, and a concluding chapter. Chapter two begins with a more detailed introduction to climate-driven range shifts, particularly current knowledge on climate impacts on migratory bird populations. I introduce the major competing hypotheses evaluated by this study and review evidence supporting these hypotheses from previous studies. Then, I review relevant background information regarding the ecology of black-throated blue warblers and major findings from the two study sites from which this thesis originates. I describe the field methods, data that were collected, and the population model that was developed. Then, I report observed spatio-temporal patterns in black-throated blue warblers population density across the climate gradient. I discuss the major findings from the population model and connect the resulting information on population processes to the greater observed pattern of range shifts. The concluding chapter reviews the principle findings from chapter two. I place major findings from this thesis in the greater context of climate-driven range shifts. Then, I propose a research agenda for further development of this thesis. Finally, I outline research needs for developing a greater mechanistic understanding of climate-driven range shifts.

CHAPTER 2

DEMOGRAPHIC DRIVERS OF BLACK-THROATED BLUE WARBLER POPULATION DYNAMICS AT THE TRAILING EDGE AND CORE OF THE SPECIES' RANGE [1]

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

Abstract

Species' ranges are shifting poleward and to higher elevations in response to climate change. Very few studies have determined how demography links environmental change to range shifts, which has limited the ability to forecast the biotic impacts of climate change. To investigate the demographic drivers of range shifts, I examined spatial and temporal patterns in black-throated blue warbler (*Setophaga caerulescens*) density at the core and trailing edge of the species' range to evaluate the initial hypothesis that this species' range is shifting. Then I used capture-recapture data from these two sites to evaluate the alternative hypotheses that the apparent range shift in this species is driven by climate change effects on recruitment, a primarily breeding ground factor, or that the range shift is driven by changes in survival, a primarily non-breeding factor. Population density declined at the trailing edge, but remained stable in the core of the range, supporting the hypothesis that the black-throated blue warblers range is shifting. Survival rates were higher but recruitment rates were lower at the trailing edge, supporting the hypothesis that low recruitment is driving trailing-edge population declines. Future work should seek to understand how climate influences recruitment at trailing-edge range margins via changes in either reproduction, juvenile survival, or dispersal because recruitment appears to drive population dynamics for this species.

Introduction

Climate change is shifting the ranges of numerous species toward higher elevations and latitudes (Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011). The effects of climate-driven range shifts on biodiversity remain uncertain, but predicted outcomes vary from loss of genetic diversity to extinction of peripheral populations (Thomas et al. 2004, Parmesan 2006). Understanding the factors contributing to range shifts requires information about the factors limiting species distributions (Darwin 1859, Dobzhansky 1950, MacArthur 1972), yet ecologists often lack the demographic data needed to investigate the mechanisms behind climate-driven range shifts.

The common approach for studying species ranges and predicting range dynamics is using static species distribution models (SDMs) to correlate species occurrence or abundance data with environmental data (Guisan and Thuiller 2005). The major problem with this approach is that it ignores the demographic processes that link environmental characteristics to species occurrence or abundance on the landscape (Normand et al. 2014). Range shifts cannot occur unless there is spatial variation in survival, recruitment, and/or movement rates (Gaston 2009). Therefore, ecological studies should focus on examining these processes rather than direct species-environment relationships (Schurr et al. 2012, Yackulic et al. 2015).

One of the main factors that has inhibited study of the demographic drivers of range shifts has been the lack of long-term studies of marked populations in multiple parts of species' ranges. Large-scale species occurrence data are often available from long-term monitoring efforts (NatureServe 2008, Sauer et al. 2017), but demographic data from marked populations are much less common, often restricted to few locations or short time periods. This has led to a call for increased effort and coordination in the collection of demographic data (Schurr et al. 2012). However, it is unfeasible to collect demographic data at every location within most species' range.

Although most studies of climate-driven range shifts have focused on leading-edge expansion, populations at the trailing edge of shifting ranges are being forced to adapt or disperse to avoid extinction. Mounting evidence shows that many trailing-edge populations harbor high genetic diversity, so the loss of these populations will likely reduce biodiversity and adaptive potential at the species level (Hampe and Petit 2005, Eckert et al. 2008, Parisod and Joost 2010).

Therefore, reliably forecasting trailing-edge population response to climate change is a high priority (Cahill et al. 2014).

Most studies addressing the demographic drivers of range shifts have focused on long-lived plants with limited dispersal ability (Cahill et al. 2014), but taxa with shorter generation time and greater dispersal ability have the potential to respond more rapidly to range shifts. Therefore, migratory songbirds are an appropriate candidate group for studying climate driven range shifts over a relatively short time periods. Because long-distance migratory birds may need to adjust their annual cycles to track global change, they have already been a major focus of climate change research (Both et al. 2006, Knudsen et al. 2011). Additionally, USGS Breeding Bird Survey (Sauer et al. 2017), which can be used to track spatial and temporal patterns in avian abundance, provide evidence that many migratory songbirds that breed throughout northeastern North America and southward into the southern Appalachian Mountains are declining at their southern range border and increasing at their northern range border. This pattern strongly suggests that range shifts are occurring in this group of species (Matthews et al. 2004, McDonald et al. 2012), but no studies have investigated the demographic drivers of this pattern, nor have they linked demography to local population dynamics to determine whether range shifts are occurring at smaller scales.

Recent developments in hierarchical population models have paved the way for studying the demographic drivers of large-scale phenomena such as range shifts. These models provide a framework for modeling state processes (e.g. abundance) and transitions (e.g. survival and recruitment) while accounting for uncertainty arising from sampling and observation error (Royle and Dorazio 2008, Kéry and Schaub 2011). Hierarchical models are flexible enough to describe structured population dynamics and can even accommodate time-varying individual traits in addition to sources of variation arising from spatial structure and density dependence (Royle 2008, Royle et al. 2013).

For species' ranges that are shifting in response to climate change, temporal changes in demography should result in declining trailing-edge populations while populations at the core of the range remain stable (Chen et al. 2011, Cahill et al. 2014). To evaluate this hypothesis, I compared population dynamics and demography of trailing-edge populations of black-throated blue warblers (*Setophaga caerulescens*) in North Carolina to those near the range core in New Hampshire over a fifteen-year period. A cross-site comparison between trailing edge and core site was used to capitalize on existing demographic data from two long-term studies. First, I examined the prediction that if the black-throated blue warbler rang is shifting, trailing-edge populations in North Carolina should be declining while core populations in New Hampshire are stable or increasing. Breeding Bird Survey trend estimates provide preliminary evidence of a black-throated blue warbler range shift (Fig. 2), but finer scale data are needed to support this claim. To evaluate this prediction, I used pre-breeding survey data of male warbler abundance to examine trends in population density at both study sites. Next, I examined two alternative predictions regarding the demographic drivers of a black-throated blue warbler range shift. Core population stability and trailing-edge population decline is primarily driven by difference in recruitment or difference in survival. If recruitment limits trailing-edge populations but maintains core populations, climate change may be implicated in changes on the breeding grounds (Ghalambor and Martin 2001, Greenberg and Marra 2005, Sillett and Holmes 2005). Alternatively, if survival limits trailing-edge populations but maintains core populations, changes during the migratory and wintering periods are the likely cause of population change (Rappole 1995, Sillett and Holmes 2002, Greenberg and Marra 2005). To examine these alternate predictions, I fit a stage-structured population model using mark-resight data from the same study area. This stage-structured model allowed for inference on the factors contributing to spatial and temporal variation in survival and recruitment rates, including the influences of age and sex structure as well as density dependence.

Methods

Study sites

Data were collected between May and August of 2002 to 2016 at two main study sites. The trailing-edge study site was located near the Coweeta Hydrologic Laboratory (Otto, NC, USA) within the Nantahala National Forest. The core study site was located at the Hubbard Brook Experimental Forest (Woodstock, NH, USA) within the White Mountain National Forest. Both study sites are contiguous northern hardwood forest with very little fragmentation in the surrounding area (Bormann and Likens 1979, Day et al. 1988, Bormann and Likens 2012). *Rhododendron maximum, Kalmia latifolia,* and *Vaccinium erythrocarpum* are the predominant understory species at the trailing-edge site (Day and Monk 1974), and aside from various tree saplings, *Viburnum alnifolium* and *Acer pensylvanicum* are the main understory species at the core site (Holmes 2011). Within both sites, three large plots were arranged across an elevation gradient has been linked to black-throated blue warbler habitat quality (i.e. highest quality habitat at high elevations) (Stodola et al. 2009, Kaiser et al. 2015). These six plots are referred to as trailing-low, trailing-mid, trailing-high, core-low, core-mid, and core-high (Fig. 1, Table 1).

Study species

The black-throated blue warbler (*Setophaga caerulescens*) is a Neotropical migratory songbird that breeds in mature, northern hardwood forests of eastern North America (Holmes et al. 2005). Most of the black-throated blue warbler range is in the northeastern United States and southeastern Canada, but its range extends southward along the southern Appalachian Mountains.

The trailing edge of the range is in northern Georgia and western North Carolina. The primary diet of black-throated blue warblers consists of arthropods, mainly caterpillars (Lepidoptera larvae), which they glean from foliage. Adult black-throated blue warblers are sexually dimorphic such that an individual’s sex can be determined without need for physical capture. Upon physical capture, an individual’s age can be classified into one of three stages: juveniles (those born in the same year of capture; not sexually mature), yearlings (those born in the previous year; first breeding season), and adults (born two or more years ago; experienced breeder). For this study, I used only pre-breeding data; that is, no juveniles were included in the survey data or mark-resight data because the primary aim was to create a pre-breeding model.

On average, black-throated blue warbler males arrive on the breeding grounds and establish territories in mid spring (Holmes et al. 2005). Phenology varies considerably between the two study sites with arrivals beginning in late April at the trailing-edge site and mid to late May at the core site (Nagy and Holmes 2005b, Stodola et al. 2009). Pairing occurs shortly after females arrive followed by clutch initiation, the timing of which depends largely on local conditions (Holmes et al. 2005). Nests are placed within the shrub layer, usually within 1 to 1.5 m off the ground (Holmes et al. 2005). *S. caerulescens* is a facultative double-brooder. If a first brood fledges, a second (and rarely a third) brood will be attempted, given favorable food availability (Nagy and Holmes 2005b). Because food availability appears to constrain the probability of double brooding, changes in late season food availability can have strong impacts of annual fecundity (Nagy and Holmes 2005a). Current evidence suggests that double brooding is less common at the trailing-edge than at the core of the black-throated blue warbler range (Stodola et al. 2009).

After yearlings breed for the first time, they retain high breeding site fidelity in subsequent years. Current evidence shows that the majority of breeding dispersal distances were between 0 and 300 meters, with younger and female birds dispersing greater distances on average (Cline et al. 2013). However, relatively little is known about dispersal events from the natal summer to the first breeding attempt. Studies tracking marked individuals in other species indicate that natal dispersal distances are greater than breeding dispersal (Weatherhead and Forbes 1994, Villard et al. 1999, Vitz and Rodewald 2010), but the only evidence of long-distance natal dispersal was derived from stable isotope data (Studds et al. 2008).

Spatial variation in population density trends

To describe spatial and temporal variation in population density, annual male abundance data were recorded by surveying each plot at least every other day and recording all male *S. caerulescens* locations using handheld GPS units. Individual locations were compiled into core territories, and individuals were included in the dataset if at least 50% of the individual's territory was within the plot boundary. I summarized breeding male density across the climate gradient by counting the number of territorial males on each plot and dividing by that plot's total area in hectares. These survey data differ from estimates of male population size in that they include both marked and unmarked males. Computational problems prevented us from accommodating unmarked birds, detected during resighting surveys, in the population model. Because plots within the trailing-edge site were smaller than those at the core site (Table 1), I also examined density trends with expanded trailing-edge plot boundaries. The expanded boundaries at trailing-edge plots reached beyond the extent of mark-resight data collections, but were sampled for male density using the same methods for pre-breeding abundance data. For all abundance data, I used to simple linear regression to plot a trend line of density for each plot.

Spatial variation in demography

To estimate spatial and temporal variation in demography, individuals within the plot boundaries were captured, marked, and resighted. Using playback and a decoy, males were captured in mist nets and 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. During the marking procedure, individual-level covariates were recorded including age (one of two stages: yearlings or adults), sex, and location. Throughout the study, each male's territory was visited every other day from early May to early August, and their presence or absence was recorded to allow for estimation of detection probability. Re-sight locations were recorded with handheld GPS units to map territories. Researchers followed marked males to find their social mates and their nest locations. Females were captured by flushing them off their nests into mist nets midway through their incubation. Females were marked using the same procedure described for males.

I modified the Bayesian state-space version of the Jolly-Seber model (Jolly 1965, Seber 1965, Kéry and Schaub 2011) to estimate age- and sex-specific demographic rates. The Jolly-Seber model is an open population model that uses individual capture histories to estimate apparent survival (ϕ) and recruitment rates (γ). The capture-recapture data are linked to the state process (survival and recruitment) through an observation process (detection/non-detection). I used the restricted occupancy parameterization of this model with data augmentation (Royle et al. 2007, Kéry and Schaub 2011). Data augmentation is a method that enables statistical estimation of individual-level parameters when the true number of individuals is unknown (Royle et al. 2007). I augmented the data set equal to three times the number of observed birds to ensure a sufficient level of augmentation.

One of the major assumptions of the traditional Jolly-Seber model is that all animals in the study population are equally catchable. Because males and females were captured via different methods (playback-decoy vs. capture-at-nest) and because their reported dispersal distances differ (Cline et al. 2013), I relaxed this assumption and modeled sex specific detection probability. Additionally, because this study aimed to determine differences in demography across a climate gradient, I modeled each plot independently. This independence assumption is justified in that no dispersal events between plots were included in this analysis.

Age and sex information were provided to the model as data for the captured individuals. The age and sex of uncaptured individuals were modeled as Bernoulli random variables with probability ρ for sex and τ for age. For both apparent survival (ϕ) and recruitment rates (γ), I included a temporal trend effect to determine whether each rate has changed consistently over time. The apparent survival rate ($\phi_{i,t}$) was estimated as a logit-linear sub-model with an intercept (β_0), sex effect (β_1), age effect (β_2), and trend effect (β_3):

$$logit(\phi_{i,t}) = \beta_0 + \beta_1 \mathrm{sex}_i + \beta_2 \mathrm{age}_i + \beta_3 t$$

The per capita recruitment rate (γ_t) was estimated as a log-linear sub-model with an intercept (β_0), a negative effect of conspecific female density (β_1), and a trend effect (β_2):

$$log(\gamma_t) = \beta_0 - \beta_1 \mathrm{NF}_t + \beta_2 t$$

To separate the recruitment process from breeding dispersal, I modeled recruitment strictly as the entry of yearling breeders into the population. The assumption that breeding dispersal should have smaller impacts on population size than recruitment of new breeders is supported by relatively small breeding dispersal distances reported in other studies (Cline et al. 2013). Each model was fit using Markov chain Monte Carlo techniques in the JAGS program (Plummer 2003) called through the R package ‘rjags’ in R version 3.4.1 (Plummer 2013, R-Core-Team 2017). I implemented

12,000 iterations, and visually inspected of the MCMC output to assess model convergence (see Appendix A for JAGS code).

To consider the joint effects of survival and recruitment, two metrics of population dynamics were calculated from model estimates of survival and recruitment. To examine how age- and sex- specific differences interact with recruitment rates, the annual asymptotic population growth rate was calculated using eigenanalysis for females only (Caswell 2001). To determine how survival and recruitment interact to influence entry of new individuals into the population, annual turnover rates were calculated by the following equation:

$$turnover_t = \frac{\gamma_t}{\phi_t + \gamma_t}$$

where survival is averaged over age and sex (Hanski 1999).

Results

Spatial and temporal variation in population density

Density of territorial males was higher at the trailing-edge relative to the core site (Fig. 3). Within both sites, male density increased with elevation. Male density at all three plots at the core site remained stable or increased during the entire period. In contrast, male density decreased at all three plots at the trailing-edge site. Trend lines in density support this result as their slopes were all positive for the core site and all negative for the trailing-edge site. The negative trends in trailing-edge density were even more pronounced when examining density beyond the mark-resight plot areas (Fig. 4)

The greatest declines occurred at the low-elevation plot within the trailing-edge site. In 2008, there were just three males breeding on the entire 24-hectare mark-resight plot causing the research team to suspend study of that plot. In early July 2017, the trailing-low site was resurveyed using conspecific playback during the late-breeding season when breeding activity should be easily detectable. No black-throated blue warblers were encountered during these surveys, suggesting that the population went locally extinct.

Detection probability

At both sites, estimates of the sex-specific detection probability were similar with male detection greater than female (Table 2). Additionally, detection probability tracked elevation with the highest detection at high elevation.

Spatial and temporal variation in age and sex structure

Age and sex structure was also examined to describe how demographic rates influence population structure. The estimated ratio of females to males did not differ greatly among all sites, and was close to 1:1 (Table 2). However, the mean estimated ratio of adults to yearlings was greater than 1:1 at the trailing-edge site and less than 1:1 at the core site (Table 2). Within the trailing-edge site, the age ratio tracked elevation with the highest ratio of adults to yearlings occurring at the high-elevation plot. Within the core site, age ratios did differ greatly, but again the highest ratio of adults to yearlings occurred at the high-elevation plot, followed by the low-elevation plot, and then the mid-elevation plot.

Temporal variation in sex-specific age ratios was also considered using age- and sex-specific abundance estimates (Fig. 8). Again, I found that, on average, trailing-edge populations had a higher ratio of adults to yearlings, but patterns differed depending on which age and sex were being considered. For example, the ratio of adult to yearling males was always 1:1 or higher at the trailing-low plot, but was always 1:1 or lower at the core-low plot. Additionally, adult-to-yearling ratio appeared to decline over time at the trailing-mid plot while it increased at the core-mid plot.

Spatial and temporal variation in survival

Overall, survival rates were higher at the trailing-edge site than at the core site (Table 2, Fig. 5). At every plot except the high-elevation core plot, mean estimates of yearling survival rate were greater than adult survival rates (Fig. 5). The difference between yearling and adult survival rates was greater for plots within the trailing-edge site. There were no significant differences in survival rates between the sexes (Table 2, Fig. 5). At both sites, survival did not strongly track elevation (Fig. 5). However, the pattern between the two sites was similar with survival highest at high elevation, followed by low elevation, and finally mid elevation (Fig. 5). The trend effect on survival was weak for most sites. Survival at the trailing-mid plot trended negatively over time, whereas survival at the core-mid plot increased slightly over time (Fig. 7). The mean trend effects for the other four plots were all slightly negative, but with credible intervals overlapping zero.

Spatial and temporal variation in recruitment

Per-capita recruitment rates were higher at the core site than at the trailing-edge site (Table 2, Fig. 7). Within both sites, recruitment increased with elevation (Fig. 7). Together, the recruitment intercept (on the log scale) follows the latitude-elevation gradient in a near-linear pattern (Table 2). The negative density-dependence effect on recruitment was much higher at low elevation than mid and high elevation for both sites (Fig. 6). These effects were similar at each level of elevation with very little difference between the two sites. The trend effects on recruitment were weak at the trailing-low, trailing-mid, core-mid, and core-high plots (Fig. 7). At both the trailing-high and core-low plots, the trend effect on recruitment was strongly positive. When considered jointly, there was much more overlap in the region of survival and recruitment in for trailing-edge plots than core plots.

Spatial and temporal variation in population growth rate and turnover

Resulting trends in population rates were uncertain overall, with many credible intervals overlapping one, which corresponds to population stability (Fig. 9). At the trailing-low plot, four out of seven annual estimates of λ were below one, indicating population declines in those years. The other five plots all had multi-year periods of consecutive population growth. Growth periods for trailing-edge plots were all in the first half of the study period, but growth periods for the core plots were interspersed throughout. Turnover rates were always greater than 50% for core plots. Trailing-edge plots all had lower turnover rates, with the lowest overall turnover rates occurring at the trailing-low plot. Overall, fluctuations in population growth rate and turnover most closely align with fluctuations in recruitment (Figs. 7, 9, and 10).

Discussion

By pairing abundance and mark-resight data, I was able to examine the individual-level demographic processes result in emergent population patterns for black-throated blue warblers at long-term study plots at the trailing-edge and core of the species' range. Although I found higher population densities at the trailing edge of this species' range, the trailing edge population was generally in decline, whereas the core population was slightly increasing. This finding supports the initial hypothesis that the black-throated blue warbler range is shifting (Hampe and Petit 2005). The finding that trailing-edge population densities are higher than core population densities conflicts with the abundant-center hypothesis (Brown 1984), which has recently been questioned for its over simplification of complex patterns of variable abundance (Dallas et al. 2017). Trailing-edge survey results show that the greatest declines in black-throated blue warbler density occurred at the trailing-low plot, but declines were noted at all three trailing-edge plots. These results suggest that instead of trailing-edge populations shifting upward in elevation in response to climate change, trailing-edge populations may be declining throughout the trailing edge. Trailing-edge low-elevation subpopulations may experience the highest extinction risk because their population densities are already relatively low. Core census results did not provide evidence of elevational range shift either. Male black-throated blue warbler density on all core plots either remained stable or increased slightly following the expectation that core populations are not experiencing negative effects of climate change (Parmesan et al. 1999).

Regarding the demographic drivers of range shifts, I found that survival is higher and recruitment is lower for trailing-edge populations than for core populations. Broadly, this finding supports the hypothesis that that low recruitment is driving the black-throated blue warbler's range shift, which suggests that climate change is altering recruitment on the breeding grounds. On the other hand, the finding of higher survival at the trailing edge versus the core does not support the hypothesis that trailing-edge declines are caused by changes during the migratory and wintering periods.

The observed differences in recruitment and survival between the two sites follow the pattern in demographic tradeoffs across latitude in other bird species (Ghalambor and Martin 2001). The expected tradeoff is that increased predation risk to young towards the equator should result in higher adult survival and lower fecundity. While predation risk was not a component of this study, high survival and low recruitment at the trailing edge do align with this tradeoff hypothesis. However, this hypothesis alone cannot explain the observed trailing-edge population declines. Low recruitment in trailing-edge black-throated blue warbler populations could be offset by higher survival, which would result in populations at equilibrium. In contrast, I found that recruitment was more variable over time at the trailing edge but survival remained constant. Meanwhile, core populations experienced high enough recruitment to offset low survival, which made these populations stable over time. If climate change is altering recruitment patterns in this species, which is primarily a breeding ground process, trailing-edge populations with low recruitment should face the highest extinction risk.

Differences in survival rates between the two sites could also be explained by the increased mortality risk imposed by longer migration distance for core populations. For black-throated blue warblers, mortality appears to be concentrated during the migratory periods of the annual cycle (Sillett and Holmes 2002), but carryover effects from breeding and wintering periods may also affect survival rates (Holmes 2007). Because I observed higher survival rates at the trailing-edge and that they were constant over time, it is unlikely that changes during the migratory or wintering periods are driving trailing-edge black-throated blue warbler population declines.

By calculating female population growth and turnover rates, I was able to consider the joint impacts of survival and recruitment on population dynamics. Population growth rates were variable over time, with few emergent patterns apart from more consecutive years of growth at core plots. Estimates of female population growth rate did not correspond the stability and decline observed using the male density survey data. One explanation for this is that population growth rate calculations were based on female-only estimates, whereas density survey data were for males only. This choice was made because female abundance should be a better indicator of reproductive activity than male abundance, but estimates of detection probability were lower for females, which could contribute to the high uncertainty of population growth rate estimates. Furthermore, computational problems prohibited including unmarked animals into estimate of population size and growth rate in the population model. If our model were able to include this information, estimates of population growth rate should more closely correspond to fluctuations in population density observed from survey data. In contrast to the few clear patterns in population growth rate, turnover rates were higher overall at core plots. Higher overall turnover at core plots may mean that core populations are more resilient to stochastic changes in fecundity or survival. That is, if core populations turn over at higher rates, random low productivity or low survival at the local scale may be compensated for by overall shuffling of new individuals into the population. Finally, temporal fluctuations in both population growth rate and turnover rate were highly correlated with fluctuations in recruitment. This suggests that recruitment is the dominant driver of population dynamics for both sites. This finding aligns with previous information for this species which showed that density-dependent fecundity, which a major component of recruitment, was most important driver of population growth rates (Holmes et al. 2005). Recruitment of yearlings is a complex demographic process that is comprised by several sub-processes, including density-dependent fecundity. To be recruited into the population, an individual must be born in the previous year, survive through the nestling, post-fledging, fall migration, over-wintering, and spring migration periods, and finally settle into the area. Changes in any one of these processes could play a significant role in fluctuation in recruitment, but the best supported explanations for black-throated blue warblers is the interaction between food availability and facultative double-brooding (Nagy and Holmes 2005b). Further efforts to tease apart the complex dynamics in recruitment should focus on these interactions.

Because turnover rates were lower at the trailing edge, differences in age structure between the trailing edge and core of the black-throated blue warbler range should arise. The higher observed ratio of adults to yearlings at the trailing edge reflects the higher survival and recruitment rates at this part of the range. When considering that trailing-edge adult survival rates were lower than yearling survival rates and that these populations were more adult-biased, realized survival rates for trailing-edge populations should be lower than if age structure were more uniform. This age-structured dynamic in survival could be further exacerbated by already low densities at low elevation and overall low recruitment at the trailing edge of the black-throated blue warbler’s range.

Furthermore, spatial variability in the strength of density dependent recruitment further indicates the vulnerability of trailing-edge populations to climate change (Keith et al. 2008). Negative density dependence can play a critical role in regulation population size, and there is strong evidence of this phenomenon in black-throated blue warbler populations (Rodenhouse et al. 2003). The finding that density-dependent compensation is higher at the range core means that declines at the trailing edge may not be compensated for by increased recruitment in subsequent years. Specifically, density-dependence in early life stages has been found to decrease population viability versus density dependence acting evenly across life stages (Keith et al. 2008).

The fact that all trailing-edge plots declined suggests that there should be some negative trend in either survival or recruitment. However, no overwhelming patterns in survival or recruitment trends were found. Instead, it appears that complex interactions between age structure and demographic rates produced the declines I observed in trailing-edge black-throated blue warbler populations. The strongest trend in a demographic rate that I observed was a positive trend in recruitment at the trailing-high plot. This suggests that increases in recruitment are better explained by the trend than they are by conspecific density. If this trend continues, high elevation subpopulations may be maintained while lower elevations continue to decline. Trailing-edge black-throated blue warblers may become further isolated to high elevation mountaintop islands (Bellard et al. 2012). Eventually, populations may reach an upper limit where there is no longer any available habitat, and dispersal ability may limit this species’ ability to track climate change.

An alternate explanation for the mismatch between trailing edge declines and no corresponding trends in demographic rates is that changes movement rates are driving trailing-edge populations declines. The stage-structured population model presented here did not directly model dispersal; however, the model did capture some of the variation in dispersal by modeling recruitment of only yearlings because black-throated blue warbler adult breeding dispersal rates are much lower than yearling dispersal rates (Cline et al. 2013). There is currently no evidence that black-throated blue warbler breeding dispersal distances are great enough to result in declines that I observed (Cline et al. 2013). Additionally, other researchers using passive mist-netting at multiple sites in the area have not noted significant long-distance breeding dispersal in black-throated blue warblers (Chandler, unpublished data).

For black-throated blue warblers, these results demonstrate that trailing-edge declines and core stability result from interactions between age structure and differential survival/recruitment. This finding emphasizes the importance of considering how individual demographic processes link climatic variation to the emergent global pattern of range shifts. If ecologists are to accurately predict species' response to climate change, they must consider the role that demography plays in linking environmental variation to species occurrence and abundance.

CHAPTER 3

CONCLUSIONS

Major findings of this thesis include support for the prediction that trailing-edge populations are declining while core populations are stable or increasing under climate-driven range shifts. I found that, for black-throated blue warblers, recruitment appears to be the major driver of populations dynamics overall, and that recruitment is lowest at low elevations at the trailing edge of the species' range. Also, survival is higher at the trailing-edge than at the core of the range, but declines with age. I found no evidence of a negative trend in survival or recruitment that would implicate either survival or recruitment as the driver of trailing-edge population declines. Instead, I found that the combination of older age structure, low adult survival rates, low recruitment of yearlings explains how trailing-edge populations are declining.

The focus of this work was to investigate the demographic drivers of range shifts by examining trends and population dynamics and relate them to demography. I used the black-throated blue warbler as a model species because the ample work on its population dynamics that had already been done and because it is one of many migratory songbirds whose ranges appear to be shifting (McDonald et al. 2012, Sauer et al. 2017). I chose to focus on comparing trailing-edge population dynamics to those at the core this species' range because trailing-edge populations are predicted to face the highest risk of extinction under climate change, and because the range core populations are predicted to be remain stable under climate change.

Further extensions of this work should include more sites, particularly a leading-edge site to determine how leading-edge demography compares to trailing edge demography. Additionally, the latitude-elevation study design used here captured significant climatic variation, but I did not include climate as direct variable in the model. Climate can have many different effects on vital rates at multiple spatial scales, so future efforts to correlate climate and demography should take this into account. One major source of uncertainty not accounted for in the stage-structured population model shown here was known variation in capture effort within the population and resulting in known abundance of unmarked individuals within study plots. This study could have benefited from a mark-resight type model, but I was unable to fit such a model in the JAGS software. Using a mark-resight approach would make model estimates of population size and growth rate correspond directly with the census data included in this thesis. Additionally, making the model spatially explicit would allow for modeling dispersal directly, effectively addressing every adult demographic rate. Finally, there is great need to scale up climate-demography relationships to draw inference climate effects on species at the range level. One approach highly suitable to this aim is spatially-explicit integrated population models (Chandler and Clark 2014). Using this approach researchers can link capture-recapture data to large-scale monitoring data to model how a species' distribution evolves as a result of variation in survival, recruitment, and dispersal.

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TABLES AND FIGURES

Table 1. Description of black-throated blue warbler census/capture-recapture plots across an elevation gradient at the trailing-edge (Otto, North Carolina) and core (Woodstock, New Hampshire) of the species' range.

Region	***Plot***	***Average Elev. (m)***	***Area (ha)***	***Sampling Period***
Trailing Edge	Low Elevation	1050	23	2002-2007
	Mid Elevation	1200	18	2002-2016
	High Elevation	1350	15	2003-2016
Core	Low Elevation	300	98	2002-2015
	Mid Elevation	550	24	2002-2015
	High Elevation	800	56	2002-2015

Table 2. Estimates of parameter means and 95% credible intervals from Bayesian stage-structured Jolly-Seber model of black-throated blue warbler trailing-edge and core populations fit in JAGS. The effects on recruitment and survival are described in sub model equations. Inclusion probability represents the proportion of augmented pseudo-individuals included in the dataset.

	Trailing Low	***Trailing Mid***	***Trailing High***	***Core Low***	***Core Mid***	***Core High***
Recruitment intercept	1.11 (-0.13, 2.29)	1.24 (0.5, 1.91)	1.41 (0.89, 1.94)	1.72 (1.32, 2.11)	1.8 (0.93, 2.72)	2.01 (1.26, 2.76)
Density effect on recruitment	7.81 (3.73, 9.91)	2.37 (0.74, 4.07)	2.1 (1.4, 2.88)	7.29 (5.05, 9.53)	2.74 (1.32, 4.3)	3.54 (2.28, 4.8)
Trend effect on recruitment	0.11 (-0.18, 0.4)	0.01 (-0.05, 0.06)	0.08 (0.02, 0.15)	0.07 (0.03, 0.12)	0 (-0.04, 0.06)	0.01 (-0.02, 0.04)
Male detection probability	0.72 (0.56, 0.85)	0.73 (0.63, 0.82)	0.78 (0.72, 0.84)	0.68 (0.61, 0.75)	0.76 (0.67, 0.84)	0.8 (0.75, 0.85)
Female detection probability	0.52 (0.35, 0.7)	0.61 (0.5, 0.71)	0.65 (0.58, 0.72)	0.6 (0.52, 0.68)	0.61 (0.52, 0.7)	0.7 (0.65, 0.75)
Survival intercept	1.52 (-0.19, 3.48)	0.39 (-0.33, 1.16)	1.4 (0.73, 2.12)	-0.8 (-1.33, -0.26)	-1.18 (-1.85, -0.54)	-0.04 (-0.44, 0.36)
Female effect on survival	-0.62 (-1.91, 0.69)	0.11 (-0.48, 0.7)	-0.01 (-0.48, 0.47)	0.22 (-0.19, 0.62)	-0.23 (-0.73, 0.29)	-0.01 (-0.31, 0.3)
ASY effect on survival	-1.46 (-2.96, -0.07)	-0.45 (-1.03, 0.12)	-1.08 (-1.58, -0.58)	-0.06 (-0.5, 0.37)	-0.22 (-0.76, 0.3)	0.09 (-0.21, 0.39)
Trend effect on survival	0 (-0.39, 0.39)	-0.08 (-0.15, 0)	-0.06 (-0.13, 0.01)	-0.03 (-0.09, 0.02)	0.1 (0.04, 0.17)	-0.03 (-0.07, 0.02)
Inclusion probability	0.17 (0.09, 0.26)	0.05 (0.03, 0.08)	0.05 (0.03, 0.07)	0.02 (0.01, 0.03)	0.05 (0.03, 0.08)	0.04 (0.03, 0.05)
Female to male ratio	-0.01 (-0.72, 0.68)	-0.16 (-0.55, 0.23)	0.07 (-0.22, 0.37)	-0.2 (-0.45, 0.04)	0.29 (-0.03, 0.61)	0.03 (-0.17, 0.23)
Adult to yearling ratio	0.41 (-0.88, 1.77)	1.49 (-0.06, 3.41)	1.73 (0.57, 3.17)	-0.55 (-1.65, 0.44)	-0.84 (-1.89, 0.1)	-0.2 (-0.83, 0.43)

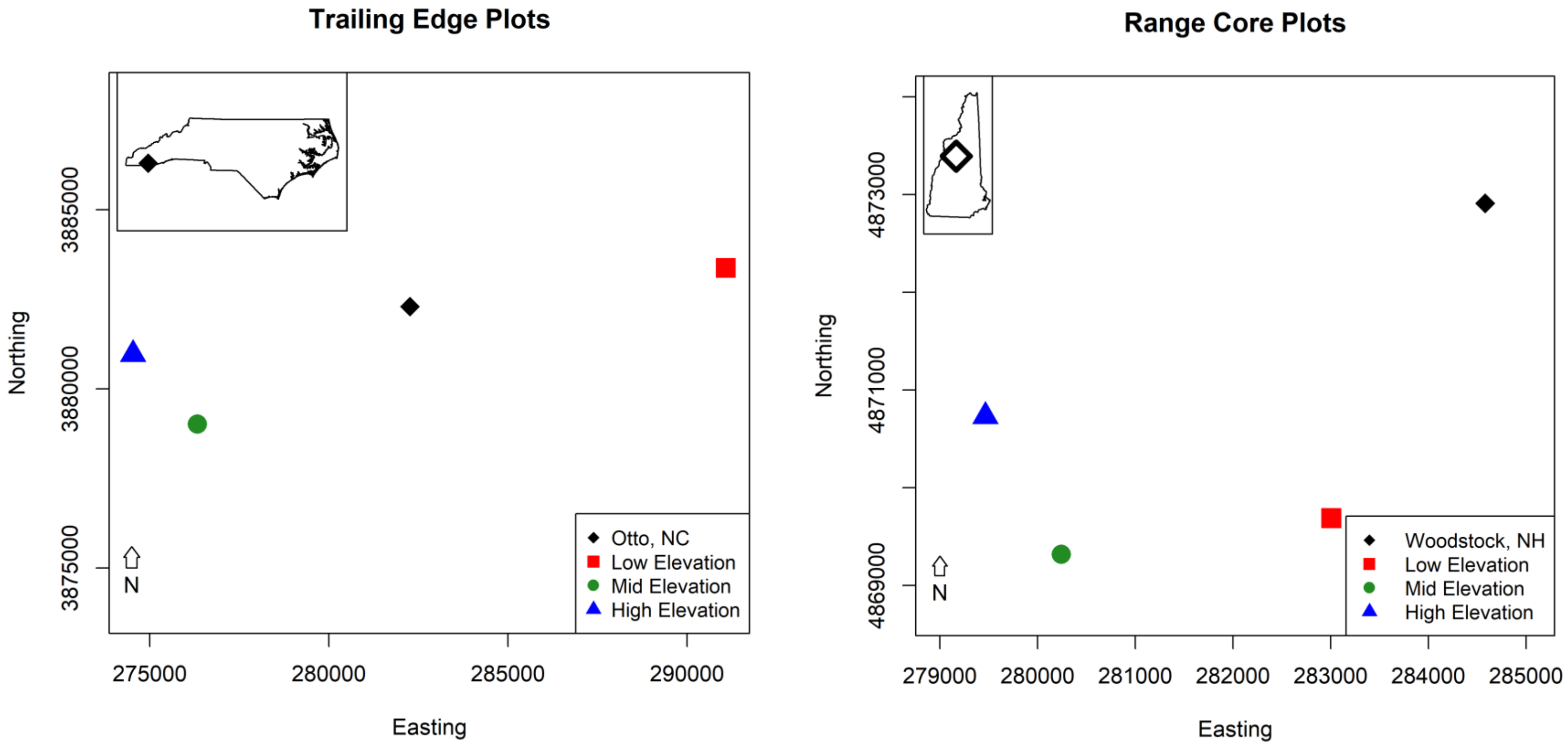


Fig. 1. Specific locations of each plot across an elevation gradient within the trailing edge site (left) and core site (right). Nearby town centers are represented by black diamonds.

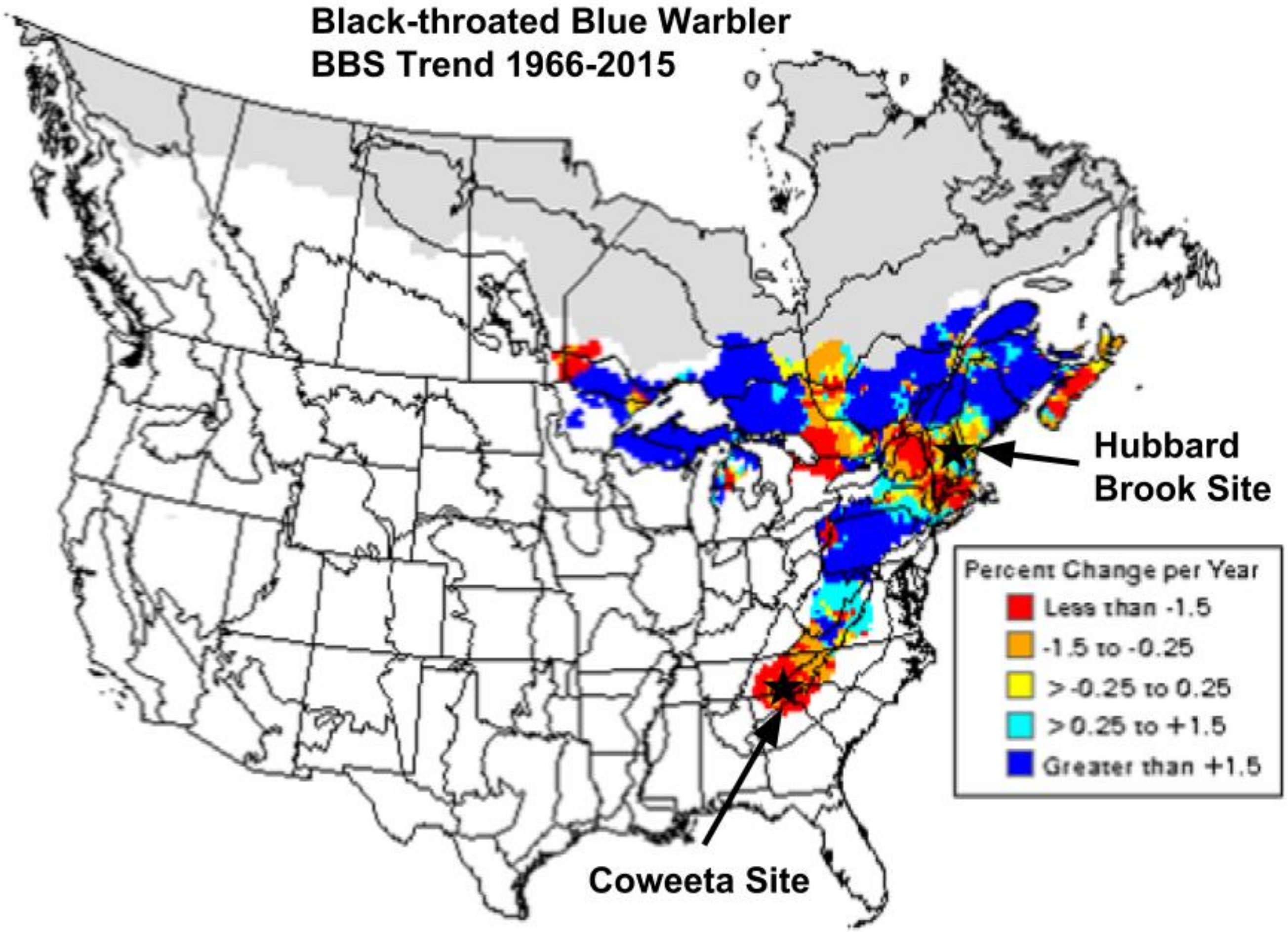


Fig. 2. Breeding Bird Survey trend map for black-throated blue warbler (*Setophaga caerulescens*) from 1966 to 2015. Black stars show relative location of the trailing edge site (Coweeta) and core site (Hubbard Brook) within the species' range.

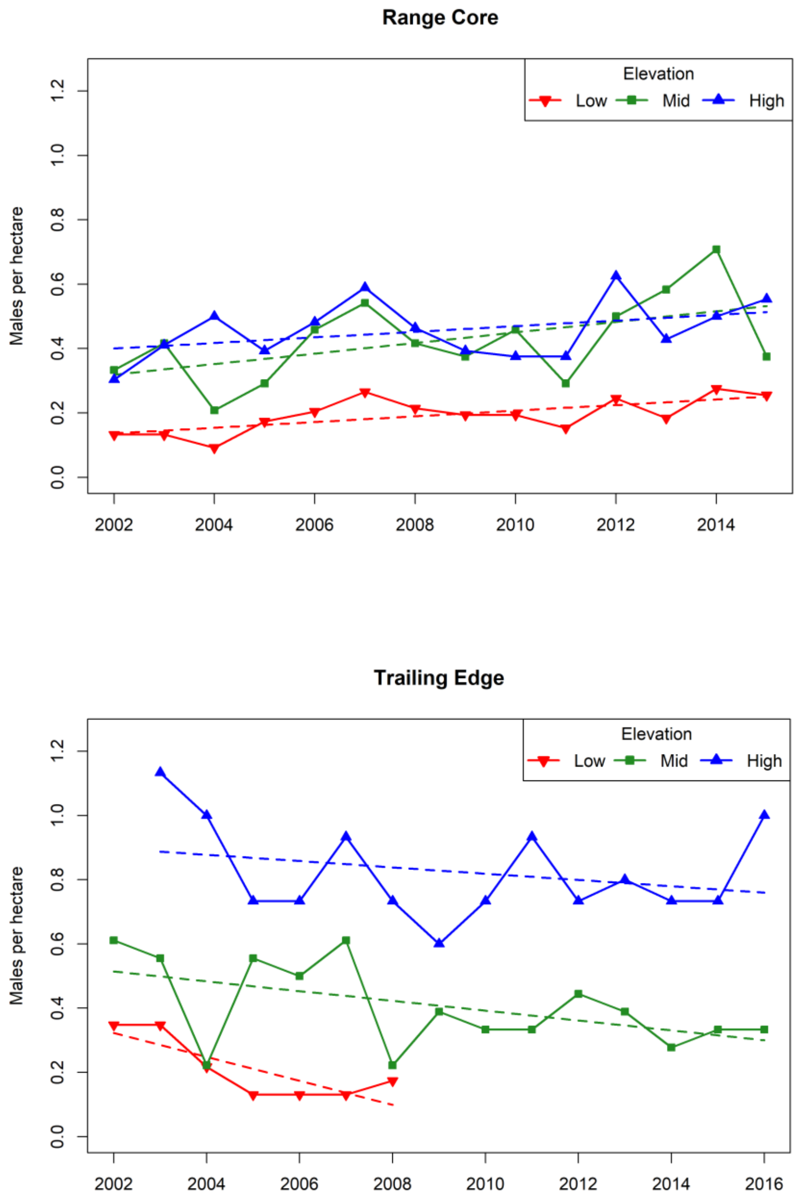


Fig. 3. Annual variation in black-throated blue warbler male population density at the trailing edge (bottom panel) and core (top panel) of the species' range. Each line represents plots arranged across an elevation gradient: low elevation (red), mid elevation (green), and high elevation (blue). Male density was calculated using pre-breeding census data. Trend lines are shown in dotted lines and were calculated using simple linear regression. Each plot represented here corresponds to the same area in the capture-recapture portion of this study.

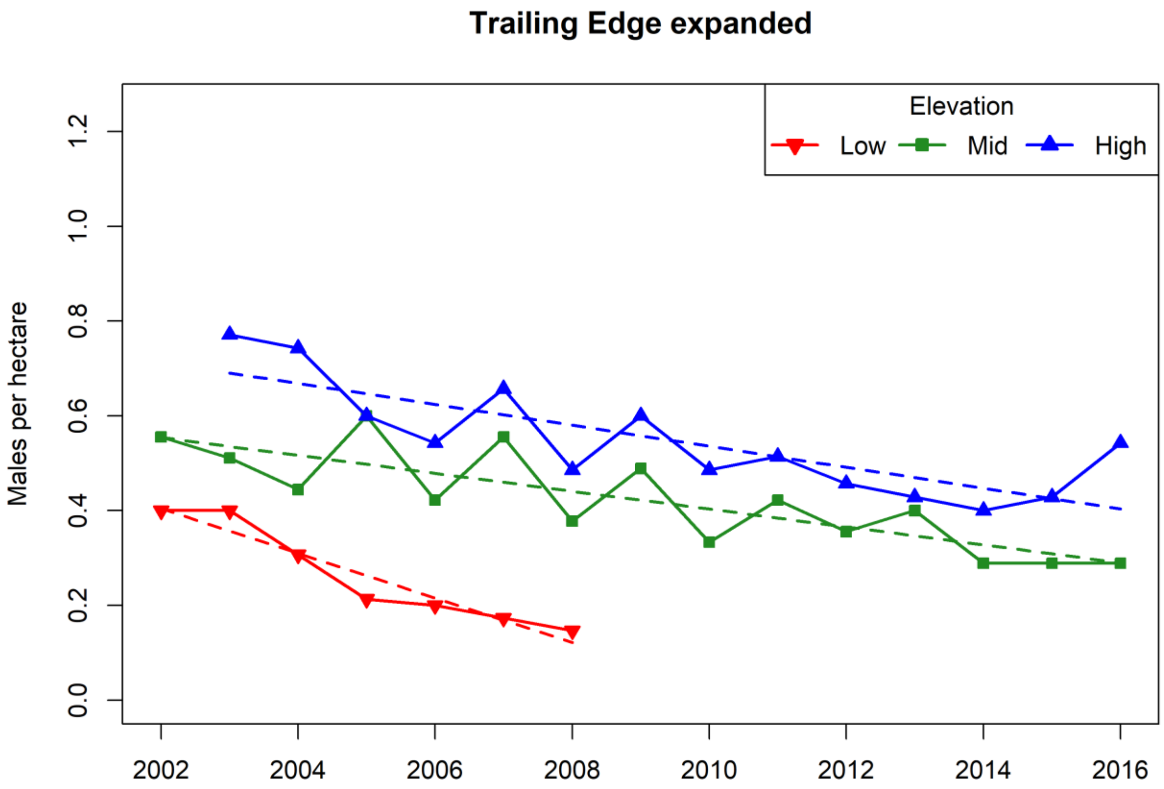


Fig. 4. Annual variation in black-throated blue warbler male population density at the trailing edge of the species' range. Each line represents plots arranged across an elevation gradient: low elevation (red), mid elevation (green), and high elevation (blue). Male density was calculated using pre-breeding census data. Trend lines are shown in dotted lines and were calculated using simple linear regression. These data encompass a larger plot area than considered capture-recapture area shown in Fig. 3.

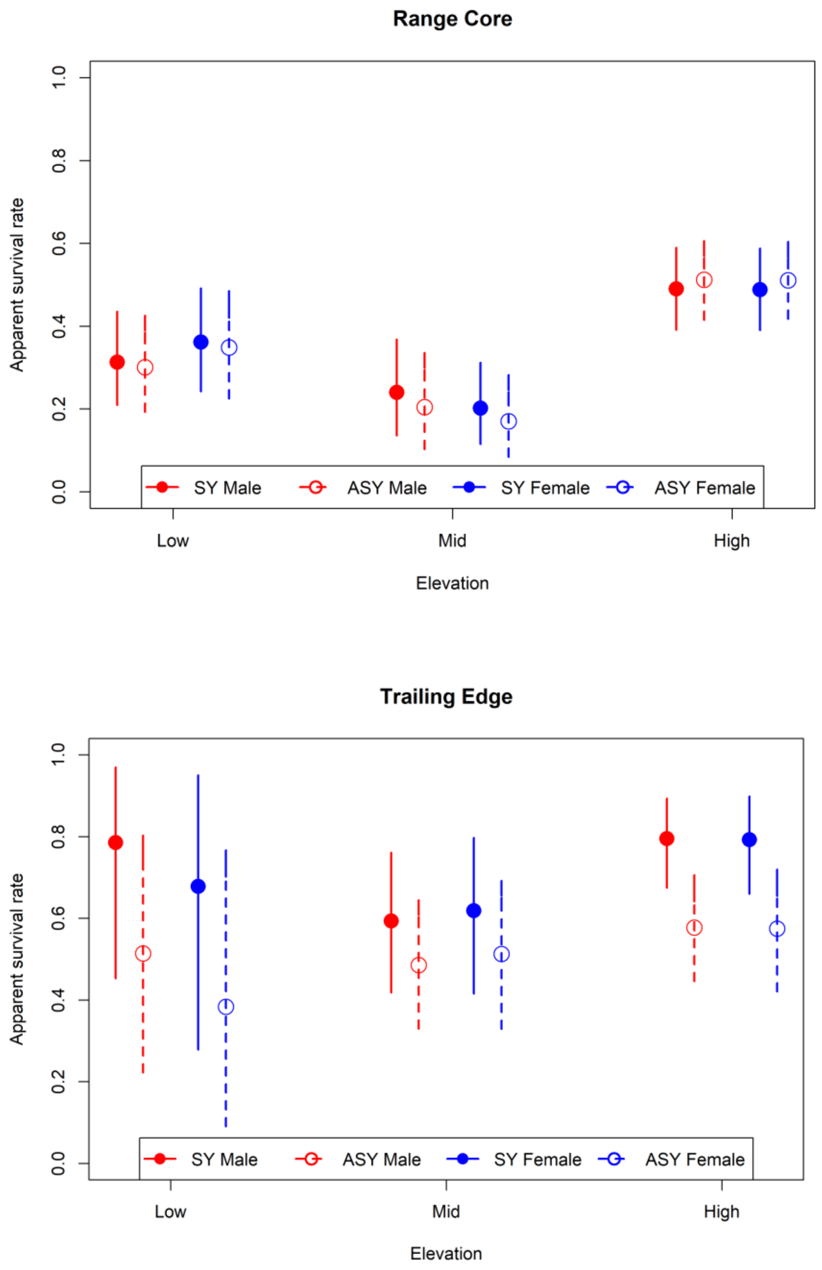


Fig. 5. Elevational variation (+/- 95% credible intervals) in age- and sex- apparent survival of black-throated blue warbler populations at the trailing edge (bottom panel) and core (top panel) of the species’ range. Male survival rates are represented in red, and female are in blue. Yearling survival rates are filled points/lines, and yearlings are open points/lines. Apparent survival rates were estimated using a stage-structured Jolly-Seber model.

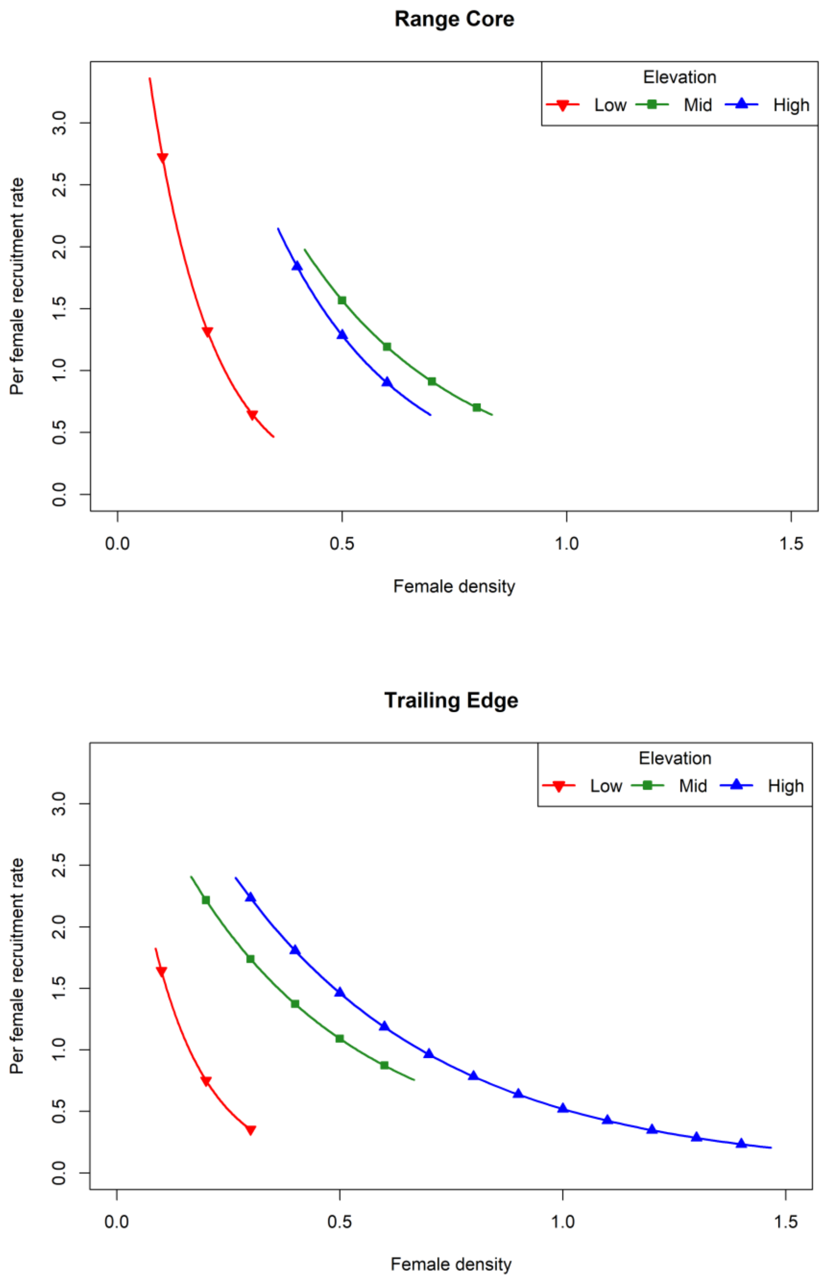


Fig. 6. Variation in recruitment as a function of the previous year's female density for populations at the trailing edge (bottom panel) and core (top panel) of the species' range. Each line represents plots arranged across an elevation gradient: low elevation (red), mid elevation (green), and high elevation (blue). Estimates are plotted across the observed range of density for each site. Recruitment rates were estimated using a stage-structured Jolly-Seber model.

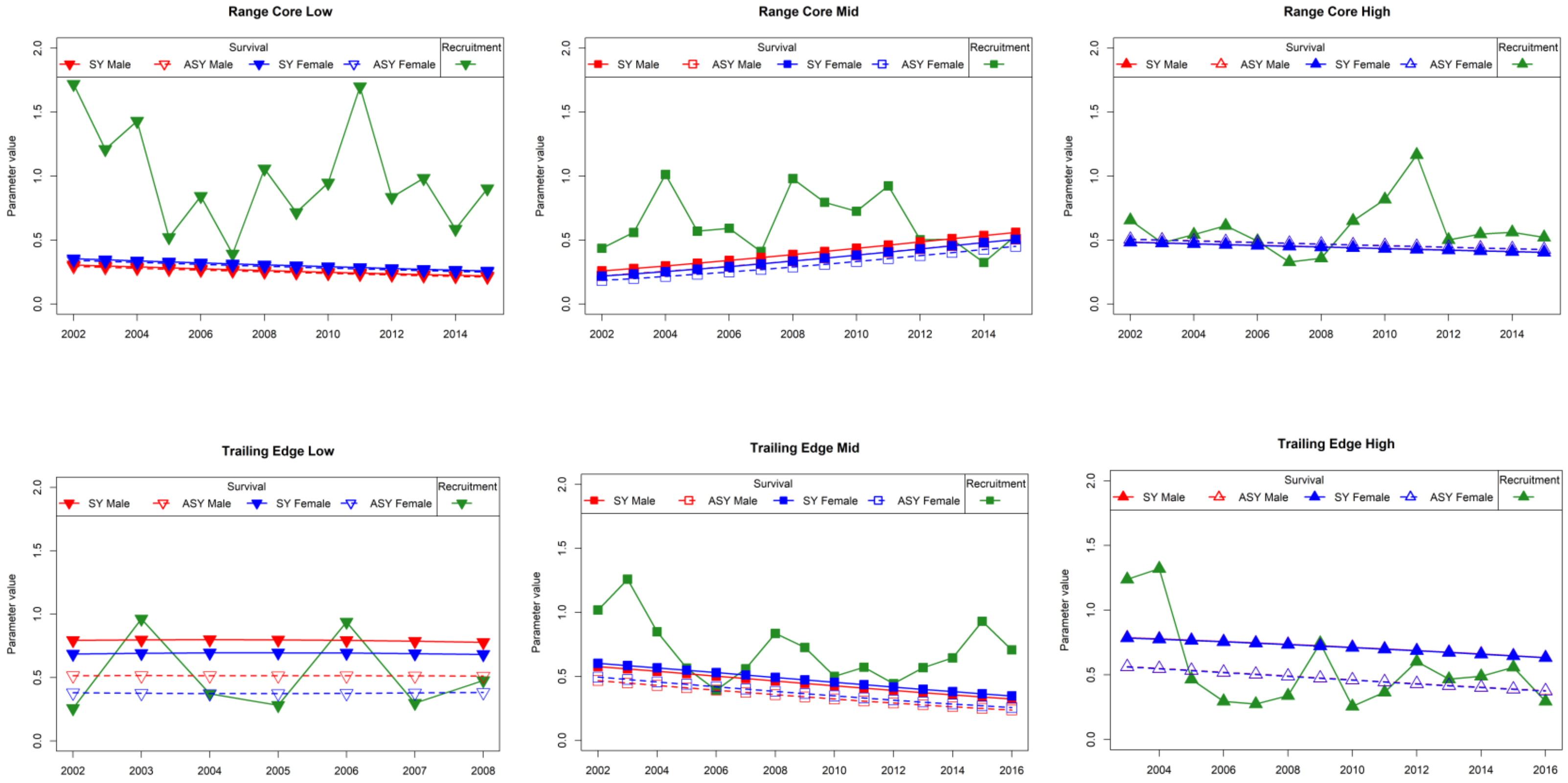


Fig. 7. Annual variation (+/- 95% credible intervals) in recruitment and (green line) age- and sex-specific apparent survival (red and blue lines) of black-throated blue warbler populations at the trailing edge (bottom row of panels) and core (top row of panels) of the species' range. Each column represents plots arranged across an elevation gradient: low elevation (left), mid elevation (middle), and high elevation (right). The solid green line represents recruitment. Male survival rates are represented in red, and female are in blue. Yearling survival rates are filled points/lines, and yearlings are open points/lines.

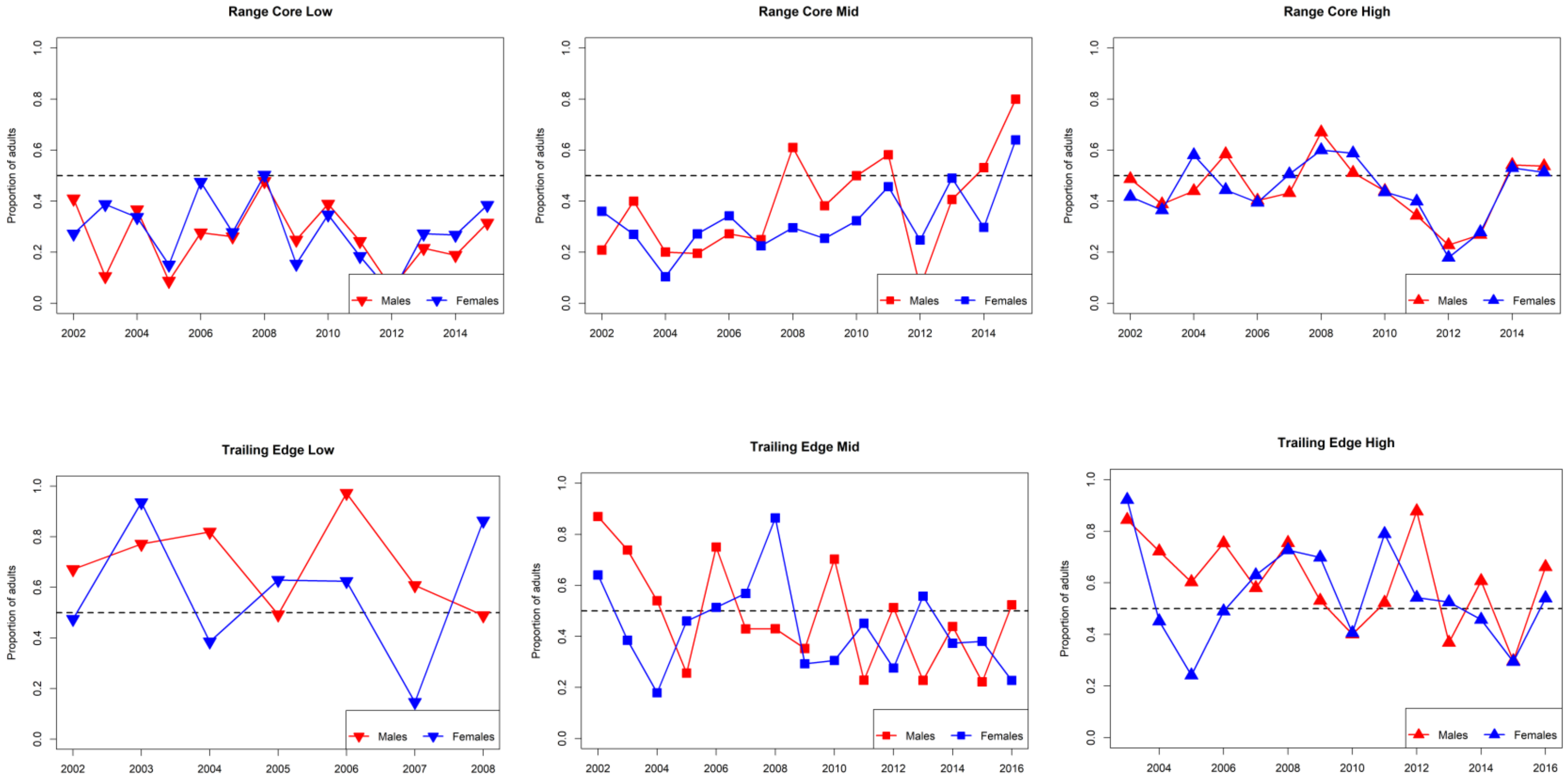


Fig. 8. Annual variation (+/- 95% credible intervals) in the proportion of adults (as opposed to yearlings) of black-throated blue warbler populations at the trailing edge (bottom row of panels) and core (top row of panels) of the species' range. Males are depicted in red, and females are depicted in blue. Each column represents plots arranged across an elevation gradient: low elevation (left), mid elevation (middle), and high elevation (right). The dotted line represents equal age proportions. These were calculated using estimates of age- and sex-specific abundance from a stage-structured Jolly-Seber model.

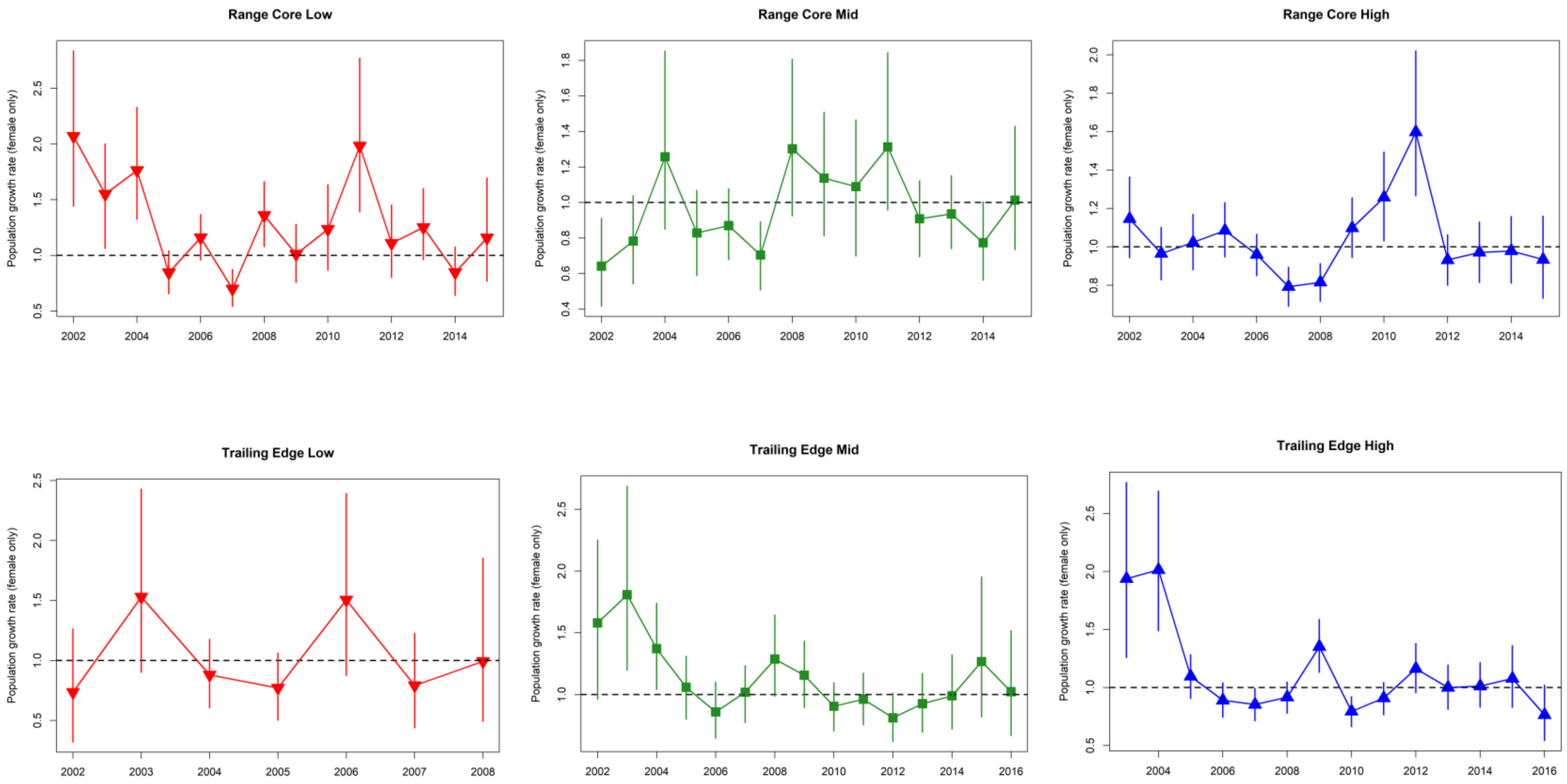


Fig. 9. Annual variation (+/- 95% credible intervals) in asymptotic population growth rate of black-throated blue warbler populations at the trailing edge (bottom row of panels) and core (top row of panels) of the species' range. Each column represents plots arranged across an elevation gradient: low elevation (left), mid elevation (middle), and high elevation (right). The dotted line represents growth rate of 1. Asymptotic population growth rates were calculated using apparent survival and recruitment estimates from a stage-structured Jolly-Seber model in an eigenanalysis approach (Caswell 2001).

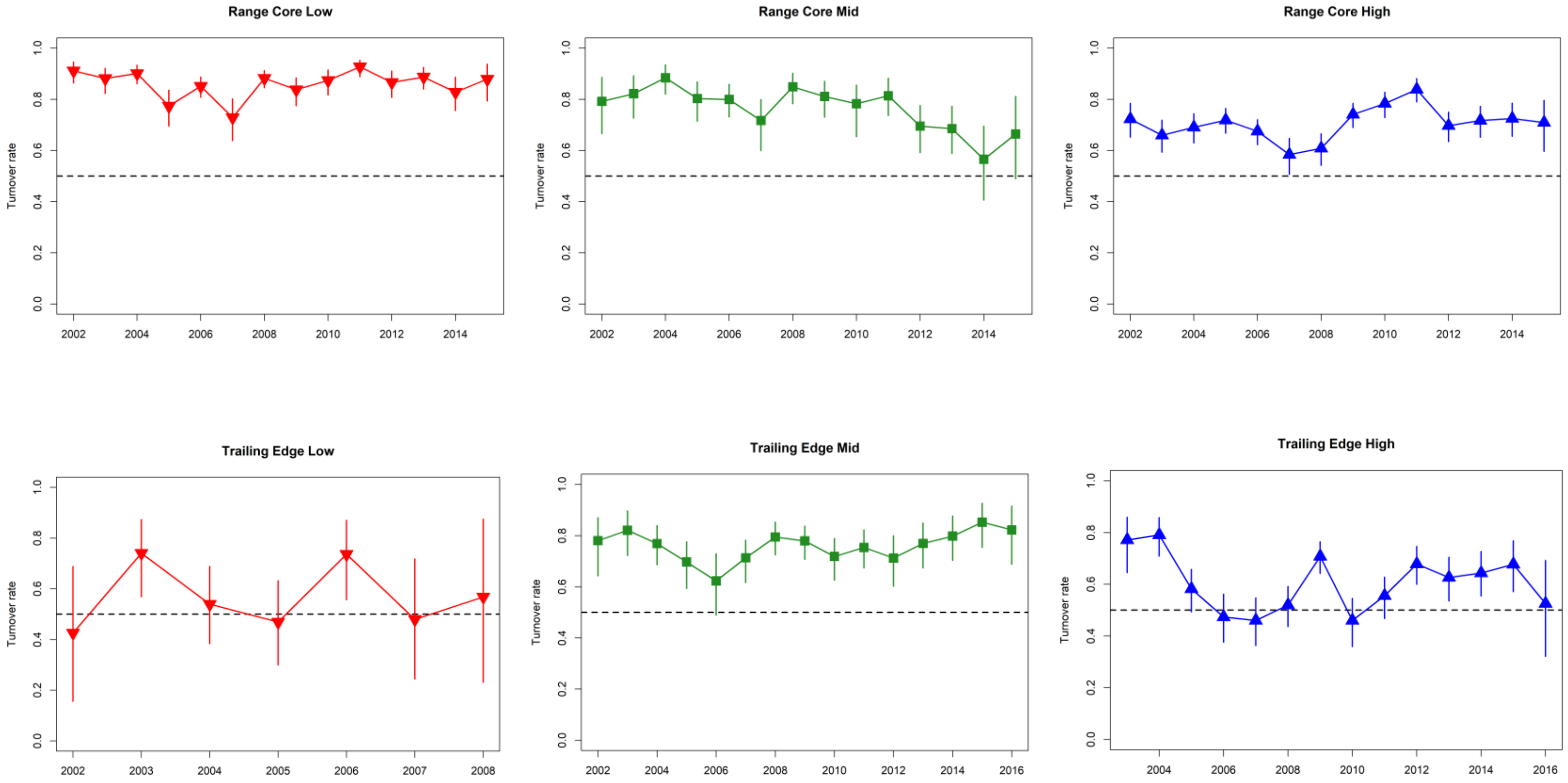
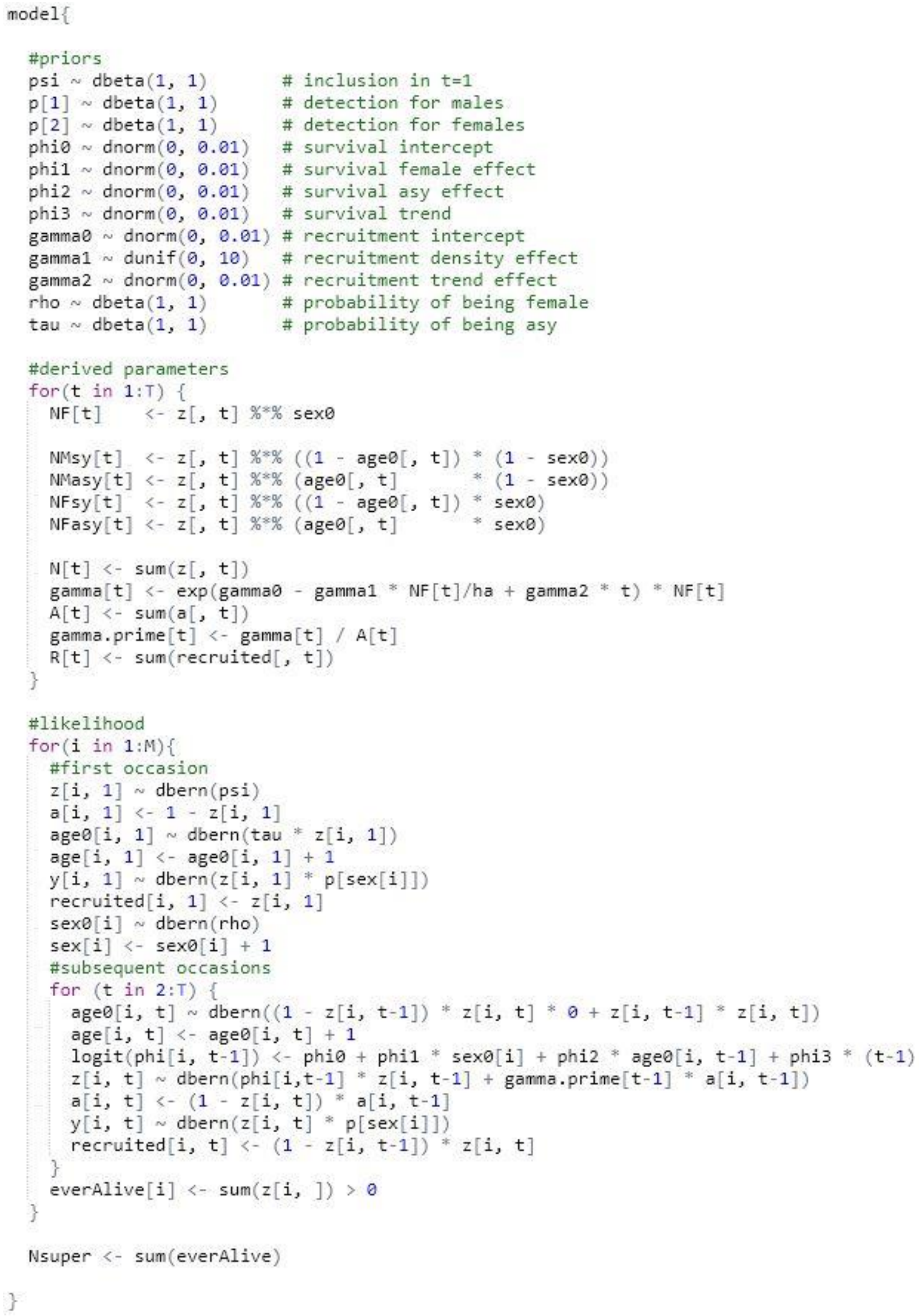


Fig. 10. Annual variation (+/- 95% credible intervals) in turnover rate of black-throated blue warbler populations at the trailing edge (bottom row of panels) and core (top row of panels) of the species' range. Each column represents plots arranged across an elevation gradient: low elevation (left), mid elevation (middle), and high elevation (right). The dotted line represents 50% turnover rate. Turnover rates (Hanski 1999) were calculated using apparent survival and recruitment estimates from a stage-structured Jolly-Seber model.

APPENDIX A

JAGS CODE TO FIT STAGE-STRUCTURED JOLLY-SEBER MODEL



```
model{

  #priors
  psi ~ dbeta(1, 1)       # inclusion in t=1
  p[1] ~ dbeta(1, 1)      # detection for males
  p[2] ~ dbeta(1, 1)      # detection for females
  phi0 ~ dnorm(0, 0.01)   # survival intercept
  phi1 ~ dnorm(0, 0.01)   # survival female effect
  phi2 ~ dnorm(0, 0.01)   # survival asy effect
  phi3 ~ dnorm(0, 0.01)   # survival trend
  gamma0 ~ dnorm(0, 0.01) # recruitment intercept
  gamma1 ~ dunif(0, 10)   # recruitment density effect
  gamma2 ~ dnorm(0, 0.01) # recruitment trend effect
  rho ~ dbeta(1, 1)       # probability of being female
  tau ~ dbeta(1, 1)       # probability of being asy

  #derived parameters
  for(t in 1:T) {
    NF[t]     <- z[, t] %*% sex0

    NMsy[t]  <- z[, t] %*% ((1 - age0[, t]) * (1 - sex0))
    NMasy[t] <- z[, t] %*% (age0[, t]       * (1 - sex0))
    NFsy[t]  <- z[, t] %*% ((1 - age0[, t]) * sex0)
    NFasy[t] <- z[, t] %*% (age0[, t]       * sex0)

    N[t] <- sum(z[, t])
    gamma[t] <- exp(gamma0 - gamma1 * NF[t]/ha + gamma2 * t) * NF[t]
    A[t] <- sum(a[, t])
    gamma.prime[t] <- gamma[t] / A[t]
    R[t] <- sum(recruited[, t])
  }

  #likelihood
  for(i in 1:M){
    #first occasion
    z[i, 1] ~ dbern(psi)
    a[i, 1] <- 1 - z[i, 1]
    age0[i, 1] ~ dbern(tau * z[i, 1])
    age[i, 1] <- age0[i, 1] + 1
    y[i, 1] ~ dbern(z[i, 1] * p[sex[i]])
    recruited[i, 1] <- z[i, 1]
    sex0[i] ~ dbern(rho)
    sex[i] <- sex0[i] + 1
    #subsequent occasions
    for (t in 2:T) {
      age0[i, t] ~ dbern((1 - z[i, t-1]) * z[i, t] * 0 + z[i, t-1] * z[i, t])
      age[i, t] <- age0[i, t] + 1
      logit(phi[i, t-1]) <- phi0 + phi1 * sex0[i] + phi2 * age0[i, t-1] + phi3 * (t-1)
      z[i, t] ~ dbern(phi[i,t-1] * z[i, t-1] + gamma.prime[t-1] * a[i, t-1])
      a[i, t] <- (1 - z[i, t]) * a[i, t-1]
      y[i, t] ~ dbern(z[i, t] * p[sex[i]])
      recruited[i, t] <- (1 - z[i, t-1]) * z[i, t]
    }
    everAlive[i] <- sum(z[i, ]) > 0
  }

  Nsuper <- sum(everAlive)

}
```