POPULATION ECOLOGY OF A LONG-DISTANCE MIGRATORY SONGBIRD IN A CHANGING ENVIRONMENT

by

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(Under the direction of ROBERT J. COOPER)

ABSTRACT

We are living in a time of unprecedented environmental change where species need to respond to many different anthropogenic factors influencing the habitat they depend on. Understanding how species respond to changes in habitat quality is a critical component in understanding and mitigating the detrimental effects associated with future environmental change. Climate change has recently received a lot of attention because of its ability to alter habitat over large swaths of land. In birds, migratory strategy appears to be an important characteristic influencing the ability of a species to respond to climatic change. I investigate this relationship using 40 years of breeding bird survey data and compare and contrast how a community of birds is responding at opposite ends of the Appalachian mountain range. My analysis suggests that long-distance migrants are disproportionately declining in abundance in comparison to short-distance migrants and resident species, yet the disparity is only observed at the southern and not at the northern terminus of the Appalachian Mountains. Although the pattern appears clear, there is little information pertaining to the mechanisms driving these disparate population trends.

The Black-throated Blue Warbler (*Dendroica caerulescens*) is experiencing population declines in the south, similar to many long-distance migrants. I studied its population ecology from 2002–2009 near the southern terminus of the Appalachian Mountains, to investigate the mechanisms driving the decline. This time period coincided with the southward advancement of the hemlock woolly adelgid (*Adelges tsugae*), which provided the opportunity to observe how habitat alteration influenced population demography. The decline of hemlock (*Tsuga canadensis*) had little influence on the reproductive biology or survival of Black-throated Blue Warblers, yet its loss eliminated an important nesting substrate. Lack of nesting substrate probably contributed to the ~70 percent decline in breeding pairs where hemlock was most prevalent and used most often. The decline in breeding pairs was attributable to the failure of new breeders to settle, suggesting that population declines following habitat alteration can be due to changes in the perception of habitat quality by new breeders, and not to outright changes in reproductive performance or adult survival as typically believed.

INDEX WORDS: Black-throated Blue Warbler, *Dendroica caerulescens*, Neotropical migrant, Population trends, Hemlock woolly adelgid, Invasive species, Habitat selection, Age structure, Coweeta

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This project is dedicated to my parents

Frank and Jan Stodola

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

We are living in a time of unprecedented environmental change, in which wildlife species must adapt to many interacting anthropogenic factors that can alter the habitat they depend upon. Climate change and invasive species represent two of these factors and each pose special problems for conservation because of their ability to alter areas otherwise believed to be protected from anthropogenic threats. There have already been noticeable shifts in the distribution and abundance of many species in light of recent climatic changes (Parmesan and Yohe 2003, Root et al. 2003), and future changes will inevitably influence habitat quality (Iverson and Prasad 2002, Iverson et al. 2008, Leithead et al. 2010, Milanovich et al. 2010). Invasive species on the other hand, pose a particular problem in forested areas, because they can cause the loss of foundational tree species which can result in fundamental changes to ecosystem composition and function (Liebhold et al. 1995, Mack et al. 2000, Ellison et al. 2005). These two factors may also interact to further accelerate changes to habitat quality as climatic changes may facilitating the movement of invasive species (Dukes and Mooney 1999, Walther et al. 2009, Bradley et al. 2010). However, the response of wildlife species to these changes in habitat quality, either due to climatic change or invasive species, is still poorly understood.

Climate change has the potential to negatively impact many different species and taxa across wide geographic expanses (Thomas et al. 2004). This influence may already be evident with common observations across broad taxonomic groups indicating that species are moving towards higher latitudes and elevations (Thomas and Lennon 1999, Parmesan and Yohe 2003, Root et al. 2003) and advancing the timing of seasonal life-history events (Crick and Sparks 1999, Menzel and Fabian 1999, Gibbs and Breisch 2001, Parmesan and Yohe 2003, Jonzén et al. 2006). These shifts and changes will inevitably cause many species to come in contact with others with which they have no prior relationship, with the outcomes of many such interactions unknown (Root and Schneider 2006, Walther 2010). Although wholesale extinction in light of recent climatic change has yet to be observed, the warning signs may already be evident through widespread range contractions and extinctions at the population level, most notably in butterflies and frogs (Thomas et al. 2006).

Climate change may also facilitate the movement of invasive species into previously unoccupied areas (Dukes and Mooney 1999, Walther et al. 2009, Bradley et al. 2010), and these invasive species can have far reaching negative effects on biodiversity (Enserink 1999, Pimental et al. 2000, Novacek and Cleland 2001). In particular, introduced pests and pathogens that infect and kill native species are particularly problematic (Castello et al. 1995, Enserink 1999, Everett 2000), especially when associated with the loss of foundational tree species (Ellison et al. 2005). Many notable instances exist where an invasive species has led to the decline or eradication of a foundational tree species, resulting in changes to forest structure and composition (Liebhold et al. 1995, Mack et al. 2000, Ellison et al. 2005). However, despite the fact that these harmful invasions are common, ongoing, and have wide-ranging consequences, little is known about the effects they have on other ecosystem components, such as wildlife species (Orwig 2002).

The manner in which organisms respond to the loss of foundation tree species may provide information on how these organisms will respond to changing climatic conditions. In many respects, habitat change following the invasion of an exotic species is similar to the projected changes expected to occur under climatic warming scenarios, only on an accelerated time scale. As temperatures warm, the distribution of many tree species are expected to shift higher in elevation and latitude (Iverson and Prasad 1998, Morin et al. 2008), changing the functional characteristics of a forest. While this process may take decades to centuries under a gradually changing climate, a similar restructuring of a forest may occur over the course of few years following the loss of foundational tree species (McClure 1991, Liebhold et al. 1995), providing a tractable approach to assessing certain ecosystem changes. Identifying how organisms respond to these ecosystem changes may therefore provide clues pertaining to how they will respond to ecosystem change in general.

Birds are an ideal group of organisms for investigating the impacts of environmental change on ecosystems. They occupy upper trophic levels, so the effects of environmental change on lower trophic levels are often manifested in them. Birds are also relatively easy to obtain detailed demographic information on because they are readily observable and often abundant. These characteristics have facilitated the collection of long-term data sets over large geographic scales that can be used for determining distributional patterns and population trends (Marchant et al. 1990, Desante and Kaschube 2007, Sauer et al. 2008). The availability of this information has led to birds being one of the first and most studied groups of organisms regarding the influence that climatic change has had on vertebrate species (Crick and Sparks 1999, Dunn and Winkler 1999, Thomas and Lennon 1999) and birds have also been useful in examining the patterns of species response to the loss of foundational tree species (Rabenold et al. 1998, Tingley et al. 2002, Monahan and Koenig 2006).

Elucidating the patterns of species response to environmental change is only the first step in understanding the causal mechanisms behind such response. In the case of climatic change, we are beginning to understand the demographic consequences that are associated with a warming climate. For instance, the ability to synchronize breeding season phenology with a food resource base that is altered by climatic change appears to be especially important. When species fail to adequately synchronize breeding season demands with peak breeding resource conditions, they often exhibit increased costs in rearing young (Thomas et al. 2001, Sanz 2003, Sanz et al. 2003), decreased adult survival (Thomas et al. 2001), and reduced offspring quality (Naef-Daenzer and Keller 1999, Sanz et al. 2003). These fitness consequences have also been tied to population persistence, since species that fail to adjust their breeding in a changing environment exhibit the greatest population declines (Møller et al. 2008).

In the case of invasive species and subsequent loss of foundational tree species, the causal mechanisms of population decline remain relatively unknown. Most studies thus far have focused on patterns of species persistence (Rabenold et al. 1998, Tingley et al. 2002, Monahan and Koenig 2006). These studies often correlate areas of high infestation by an exotic pest with population persistence or abundance of the bird communities present. The consensus from such studies is that bird species particularly dependent on a threatened tree species exhibit the largest decline in abundance (Tingley et al. 2002, Becker et al. 2008). Additionally, Allen et al. (2009), showed how the loss of eastern hemlock (*Tsuga canadensis*), due to the invasive hemlock woolly adelgid (*Adelges tsugae*), influenced Acadian Flycatcher (*Empidonax virescens*) abundance by reducing the amount of available nesting substrate. However, while population abundance may decline in response to the loss of a foundational tree species, especially for those with a particular dependence on it, the mechanisms behind such declines are still poorly understood. Furthermore, little information is available on the indirect effect that the loss of foundational tree species has on other species in the community.

The causal mechanisms behind population change may indicate which species are most vulnerable. For instance, the way a bird species responds to a changing climate may depend on migratory strategy (Both et al. 2010). As previously mentioned, the ability to take advantage of a temporally-variable food base can have direct fitness consequences. Properly timing migration to initiate breeding at optimal times is critical in a changing climate and migratory distance appears to influence this ability (Vegvari et al. 2010). While short-distance migrants and resident species can directly assess conditions near to, or on, the breeding grounds to initiate breeding, long-distance migrants must depend on circannual rhythms (Gwinner 1996) and other factors not associated with the breeding grounds (Studds et al. 2008). These cues may preclude long-distance migrants from properly adjusting the start of their breeding season (Both and Visser 2001). Therefore, short-distance migrant and resident species should fare better than long-distance migratory species in a changing climate (Lemoine and Bohning-Gaese 2003, Lemoine et al. 2007, Both et al. 2010, Jones and Cresswell 2010). Although this pattern appears clear for European species, the same level of information is lacking for North American species and what is available is often equivocal (Valiela and Martinetto 2007, Jones and Cresswell 2010).

Understanding the population ecology of species in a changing environment can help biologists understand the mechanisms that influence population persistence. To do so, we need to first identify those species and locations where the influence of environmental change will be most prevalent. By investigating geographic variation in community response to long-term environmental change, we may be able to pinpoint the species and locations of greatest response. Once established, detailed demographic information is necessary to examine the potential causes of population change. Therefore, investigating these same species under conditions of habitat alteration from the loss of a foundational tree species may provide important information relevant to future population changes.

DISSERTATION OBJECTIVES AND STRUCTURE

In Chapter Two of this dissertation, I examine how North American breeding bird communities are responding to recent climatic changes. I investigate population trends with respect to migratory strategy for a community of birds that breed along an elevation gradient in the southern portion of the Appalachian Mountains. I concentrate my analysis on a group of 40 insectivorous and omnivorous species that breed within the same watershed. Average April temperatures (when most bird species begin breeding) in this watershed have increased at the rate of 0.31 °C per decade over the last 40 years (data obtained from: Swift 2010); thus the impact of warming temperatures should be evident in the long-term population trends of the breeding bird community. To investigate this influence, I use 40 years of Breeding Bird Survey (Sauer et al. 2008) data to compare population trends of long-distance migratory species with short-distance migratory and resident species. I first make comparisons across the entire breadth of these species' geographic range and then compare population trends at two different geographic locations along the southwest-northeast axis of the Appalachian mountain range.

The use of long-term descriptive data sets can reveal large-scale patterns of population change across broad groups of species, yet are uninformative concerning the mechanisms of change. For instance, the Breeding Bird Survey is often the principle source of information on population trends for North American breeding birds, and it can be used to examine trends relative to climatic changes (Valiela and Martinetto 2007, Jones and Cresswell 2010) and the influence of invasive species (Monahan and Koenig 2006, Barber et al. 2008). However, lack of information regarding the causal mechanisms behind these trends can lead to erroneous or ambiguous results (Bohning-Gaese et al. 1993, Sauer et al. 1996). Although long-term descriptive data sets can provide a good starting point for investigating the potential impacts of climate change and loss of foundational tree species due to invasive species, understanding the causes behind population change requires long-term intensive study of the demographic and behavioral characteristics of a species.

Chapters Three and Four of this dissertation present detailed demographic and behavioral information for the long-distance migratory Black-throated Blue Warbler (*Dendroica caerules*cens), in the southern Appalachians. The Black-throated Blue Warbler makes an ideal model species for study because of certain population traits and behavioral characteristics. Similar to many forest-dwelling long-distance migratory songbirds, the Black-throated Blue Warbler has been decreasing in abundance over the last 40 years in the southern Appalachians (Figure 1.1). However, the Black-throated Blue Warbler is still relatively abundant, allowing for the collection of detailed demographic information at the population level. In addition, the Black-throated Blue Warbler is sexually dichromatic, nests in the understory, and exhibits high inter- and intra-annual site fidelity (Holmes et al. 2005), all characteristics which facilitate gathering detailed demographic and behavioral information. Therefore, this species may be useful in investigating the possible responses of long-distance migratory birds to environmental change.

Chapter Three presents information on the reproductive output and adult survivorship of the Black-throated Blue Warbler at three study sites in the southern Appalachian Mountains between the years 2002 and 2008. The time frame of the study coincided with the southward advancement of the hemlock woolly adelgid, with 2001 being the first year it was detected in the area of study (USFS 2009). The adelgid quickly spread throughout the region, defoliating and killing eastern hemlocks. Because of the ability of the adelgid to quickly alter forest structure and composition (McClure 1991, Orwig and Foster 1998), this situation provided a unique opportunity to observe how a long-distance migratory species, not generally thought to be hemlock dependent, responded to large-scale habitat alteration.

In Chapter Four, I explore the behavioral response of Black-throated Blue Warblers, as well as long-distance migratory species in general, to declining habitat quality. Habitat quality will inevitably be altered with future climatic change (Iverson and Prasad 2002, Milanovich et al. 2010), as tree species are expected to move higher in elevation and latitude (Iverson and Prasad 1998, Morin et al. 2008). In addition, functional changes to forest structure and will occur following the invasion of invasive pests and pathogens (Castello et al. 1995, Enserink 1999, Everett 2000, Ellison et al. 2005). These movements, along with the shifting of seasonal leaf emergence phenology and growth to different times of the year (Schwartz and Reiter 2000, Chmielewski and Rotzer 2001, Fitter and Fitter 2002), will undoubtedly influence species behavior. Consequently, understanding how long-distance migratory species select and occupy habitat that is declining can provide important clues pertaining to how species will respond to a warming climate.

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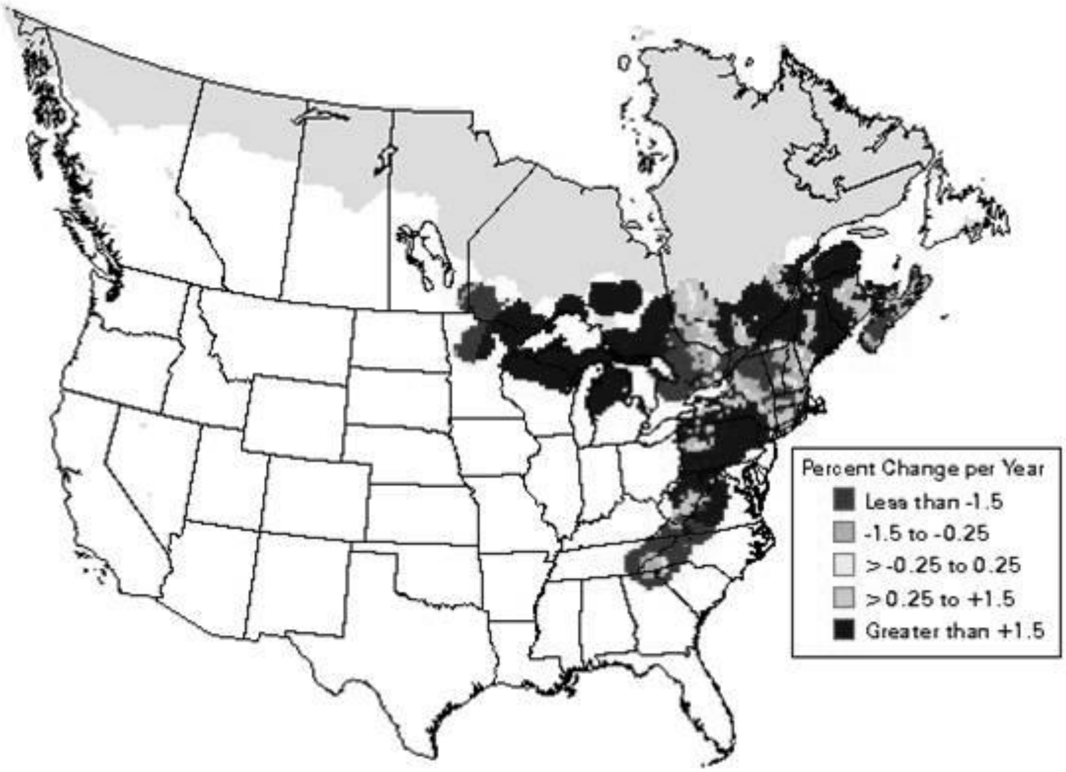

Figure 1.1. Black-throated Blue Warbler distribution and population trend map between the years 1966 to 2003. The map was reproduced from Sauer et al. (2008).

CHAPTER 2

SPATIAL DISTRUPTION OF COMMUNITY STRUCTURE IN LIGHT RECENT CLIMATIC CHANGES [1]

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[1] Stodola, K.W. and R.J. Cooper. To be submitted to *Avian Conservation and Ecology*

ABSTRACT

Climatic change has been linked to geographic range expansions and shifts in the seasonal life-history events of many species. These changes may disrupt community structure if certain organisms are better able to respond to climatic variability than others. In birds, migratory strategy appears to dictate how well a species responds to a changing climate. While the evidence for this is mounting, very little is known about how change in community structure varies across wide geographic expanses. We investigated this issue using population trends for a community of birds all breeding within a relatively small area in a well forested watershed at the southern terminus of the Appalachian mountain range. We used Breeding Bird Survey data for 40 species (20 long-distance migrants, 20 short-distance and resident species) all found breeding at the Coweeta Long Term Ecological Research station in southwestern North Carolina. We compared population trends between the years 1966 – 2007 for these species across their entire geographic range and at two distinct physiographic provinces, the Blue Ridge Mountain and the Northern New England. We found little evidence that long-distance migrants were declining at a greater proportion than resident and short-distance migrant species when viewed across the entire breadth of the geographic range. However, there was evidence that in the Blue Ridge Mountain physiographic province long-distance migrants were declining while resident and short-distance migrant species were increasing. The same pattern was not evident in the Northern New England physiographic province. We believe our results highlight the importance of geographic location pertaining to the influence climate change may have on community structure, and that southern populations may be most vulnerable.

INTRODUCTION

Many organisms have been affected by recent climatic changes (Parmesan and Yohe 2003, Root et al. 2003) and climate change has the potential to become the most serious threat to the biotic communities we observe today (Thomas et al. 2004). While wholesale extinction in response to climate change has yet to occur, the warning signs may already be observed through a multitude of widespread range contractions and extinctions at the population level (Thomas et al. 2006). The corresponding changes to community structure will only be exacerbated when the competitive balance among coexisting species begins to shift (Root and Schneider 2006, Walther 2010). Consequently, to help identify priorities for future conservation work, we need to understand what species are most at risk, where they are at risk, and the mechanisms inducing this risk.

Species are responding to current climatic changes through range expansion towards higher latitudes and elevations (Parmesan and Yohe 2003, Root et al. 2003) and advancement in seasonal life-history events (Crick and Sparks 1999, Menzel and Fabian 1999, Gibbs and Breisch 2001, Jonzén et al. 2006). While often reported separately, these two observations are closely linked. Organisms function most efficiently when environmental conditions are within their physiological tolerance zones (Portner 2002). Consequently, under climatic warming, organisms may need to either move poleward, higher in elevation, or alter the timing of seasonal events towards cooler periods of the year to maintain efficiencies. These shifts may cause novel and unpredictable interactions among species (Root and Schneider 2006, Walther 2010).

Migratory strategies in birds may dictate how well a species responds to a changing climate (Both et al. 2010), which can lead to competitive advantages among coexisting species (Ahola et al. 2007). For instance, short-distance migratory species appear more able to advance their arrival on the breeding grounds compared to long-distance migratory species (Vegvari et al. 2010). This may be due to the ability of short-distance migratory and resident species to directly assess breeding conditions and time the start of their breeding to synchronize with peaks in those conditions. Long-distance migratory species, however, must depend on circannual rhythms (Gwinner 1996) and other cues not associated with the breeding grounds to initiate migration (Studds et al. 2008) and time the start of their breeding season. Therefore, the cues that are favorable for departure from the wintering grounds for long-distance migrants may not be representative of optimal conditions on the breeding grounds and these species may have more difficulty taking advantage of variable peak breeding conditions.

A shifting climatic regime has the potential to disrupt the synchrony between trophic levels (Visser and Both 2005), which can influence individual reproductive performance, population stability, and community structure. Asynchrony between optimal breeding conditions and the timing of peak breeding season demands can influence clutch size, nestling growth, juvenile survival, and reproductive output (Perrins and McCleery 1989, Perrins 1991, Van Noordwijk et al. 1995, Dias and Blondel 1996). Short-distance migrants and resident species may be able to avoid this asynchrony if exposure to the same or similar environmental conditions as that of their food allows them to better time the start of their breeding season. Thus, these species should fare better than long-distance migratory species in light of recent climatic changes (Lemoine and Bohning-Gaese 2003, Lemoine et al. 2007, Both et al. 2010, Jones and Cresswell 2010). While these trends appear clear for European species, the same level of information is lacking for North American species and what is available is equivocal (Valiela and Martinetto 2007, Jones and Cresswell 2010).

Although there is ample documentation of distributional shifts in geographic range (Parmesan and Yohe 2003, Root et al. 2003) and changes to community structure based on life-history strategies (Lemoine and Bohning-Gaese 2003, Vegvari et al. 2010), we know very little about how these patterns are linked and how changes in community structure vary across large geographic expanses in light of current climatic changes. We address this issue by focusing on a group of species breeding along an elevation gradient at the southern terminus of the Appalachian mountain range (Blue Ridge Physiographic Province). We document population trends for this community based on migratory strategy and investigate how these species fare at the northern terminus of the Appalachian mountain range (Northern New England Physiographic Province). Based on previous European research, we expected that (1) a greater proportion of long-distance migratory species would be declining compared to short-distance migrant and resident species, and (2) this disparity would be more pronounced in the north because of both greater warming in this area (Wallace et al. 1996) and longer migratory distance (Vegvari et al. 2010).

METHODS

We analyzed population trends for 40 insectivorous and omnivorous species detected during the breeding season along the elevation gradient (679 – 1,592 m) at the Coweeta Long Term Ecological Research station (35° 07’ N, 83° 31’ W, hereafter Coweeta). We concentrated on this suite of birds because they all bred within a relatively small area in a well forested watershed, and thus have similar habitat preferences. Although this group represented a much smaller sample than other studies that focused on large geographic areas with many species (Valiela and Martinetto 2007, Jones and Cresswell 2010), we were interested in how bird community response varied with geographic location and therefore wanted to constrain our analysis to a distinct community. Coweeta is located near the southern edge of the Blue Ridge physiographic province, was established in 1933, and encompasses a 2,185-ha basin in the Nantahala ranger district, Nantahala National Forest, North Carolina, U.S.A. Average (SE) April (when most birds begin breeding or arrive on the breeding grounds) temperatures at Coweeta have increased at the linear rate of 0.31˚C (0.15) per decade between 1966 and 2007 (Swift 2010).

We used the Breeding Bird Survey's (BBS) trend analysis tool and the estimating equations option (Sauer et al. 2008) to attain estimates of population trend between the years 1966 and 2007 for 40 insectivorous and omnivorous species found breeding at Coweeta (Table 2.1). The group of 40 species consisted of 20 long-distance migratory species (LDM, majority of the population winters south of the Tropic of Cancer) and 20 short-distance migratory and resident species (SDMR, majority of population winters north of the Tropic of Cancer, Table 2.1). To investigate geographic variation in population trends we gathered data on population trends across the entire breadth of the geographic range, in the Blue Ridge physiographic province, and in the Northern New England physiographic province, which is located at the northern terminus of the Appalachian mountain range. Thirty-five of the 40 species breeding at Coweeta are found breed in and around the Hubbard Brook Experimental Forest, which is located in the Northern New England physiographic province. Average (SE) April (when most birds begin breeding or arrive on the breeding grounds) temperatures at the Hubbard Brook Experimental Forest have increased at the linear rate of 0.50˚C (0.18) per decade between 1966 and 2007 (Campbell 2010).

Statistical analysis.- We focused our analyses on whether a species was increasing or decreasing in abundance between the years 1966 – 2007. We took this approach because the magnitude of population trend estimates differed among species and we did not want our results to be overly influenced by the trends of a few species (Table 2.1). To assess whether population stability differed based on migratory strategy, we calculated the binomial likelihood of two competing hypotheses: (H0) the proportion of species with negative population trends do not differ by migratory strategy and (H1) the proportion of species with negative population trends differs by migratory strategy. We investigated these hypotheses at the geographic range scale, for populations in the Blue Ridge Mountain physiographic province, and for populations in the Northern New England physiographic province. We used the likelihoods of each competing hypothesis to calculate Akaike's Information Criterion (AIC, Aikaike 1973) and determine the AIC weight of evidence (Burnham and Anderson 2002) in support of the above hypotheses.

Population trend estimates are often accompanied by uncertainty that we wanted to incorporate into our analyses. Therefore, we employed Monte Carlo simulations where we generated population trend estimates for each species based on a random draw from the normal distribution with the associated mean and variance being attained from BBS analyses. These population trend estimates were used to calculate the likelihood of each competing hypothesis previously put forth concerning the proportion of species in decline. This process was repeated for 10,000 iterations using the Poptools extension in Excel and we calculated the average weight of evidence and 95% confidence limits based on these 10,000 simulations.

RESULTS

We found little evidence that range-wide population trends for the 40 species we analyzed from 1966 - 2007 differed by migratory strategy (Table 2.2). However, this was not the case in the southerly located Blue Ridge physiographic province where we found evidence that LDM species differed in their population trajectories in comparison to SDMR species (Table

2.2). The disparity was not observed in the Northern New England physiographic province (Table 2.2).

The difference in the proportion of species with declining population trends was because of the greater proportion of LDM species declining in the Blue Ridge physiographic province in comparison to the Northern New England physiographic province (Figure 2.1). Not only are LDM species declining at a greater proportion in the south but of the 17 LDM species that bred in both the Blue Ridge physiographic province and the Northern New England physiographic province 66% (95% confidence interval: 47-82) were declining at a greater rate in the south in comparison to the north. The Black-throated Blue Warbler, Black-throated Green Warbler, Eastern Wood-Pewee, Ovenbird, Rose-breasted Grosbeak, and Red-eyed Vireo all fared better in the north with only Wood Thrush exhibiting evidence for the converse (>95% probability). The same disparity in the proportion of species declining was not observed with SDMR species (Figure 2.1). Of the 18 species that bred in both locations 55% (95% confidence interval: 38-67) were exhibiting greater population trends in the north in comparison to the south. American Crow, Blue Jay, Carolina Wren, Downy Woodpecker, Northern Cardinal, and Tufted Titmouse all fared better in the north, while Blue-headed Vireo, Dark-eyed Junco, and Eastern Towhee fared better in the south (>95% probability).

DISCUSSION

Climate change has the potential to influence the competitive relationships among species based on migratory strategy (Ahola et al. 2007), which can alter community structure (Walther 2010). Our analyses indicated that this alteration may depend on geographic location. We found little evidence that population trends differed by migratory strategy when observed across the entire breadth of the geographic range. However, when we constrained our analyses to the Blue

Ridge physiographic province in the southern portion of the Appalachian Mountains we found that a greater proportion of long-distance migrants were declining in comparison to short-distance migrants and resident species. The same pattern did not hold in the Northern New England physiographic province where a greater proportion of long-distance migrants were increasing, suggesting that the ability of long-distance migrants to respond to climatic changes may be hampered at lower latitudes (Jones and Cresswell 2010). Recent shifts in the seasonal phenology of plant species associated with climatic warming (Menzel and Fabian 1999,Schwartz and Reiter 2000, Chmielewski and Rotzer 2001) may be the cause.

Climatic changes may be highly variable across wide geographic expanses (Greene et al. 2006, Christensen et al. 2007) and species may respond more to local climate variation than to continent-wide fluctuations (Dunn and Winkler 1999, Visser et al. 2003, Both et al. 2004). However, failure to adequately respond to changing climatic conditions can have serious consequences for population stability (Møller et al. 2008), because it may lead to a mismatch between peak breeding season demands and peak resource conditions (Visser et al. 2004, Visser and Both 2005). If migratory strategy influences the ability of a species to respond to a changing climate (Vegvari et al. 2010), then long-distance migratory species may decline at a greater proportion or rate. This mismatch has been implicated as the probable cause of population decline for many North American migrant breeding birds (Jones and Cresswell 2010) and may be responsible for the decline in long-distance migrants we observed in the southern region.

Two possible mechanisms may link the response to climatic conditions, asynchrony in food and breeding phenology, and population declines. The first mechanism is centered on the demographic consequences associated with a mismatch in food conditions and breeding needs. The breeding season for most temperate birds is relatively short and food resources are often only abundant for short periods of time; birds attempt to time their breeding to coincide with this peak (Perrins 1970, Daan et al. 1989, Perrins 1991). Asynchrony in this timing, however, can increase the costs associated with rearing young (Thomas et al. 2001, Sanz 2003, Sanz et al. 2003), reduce apparent survival (Thomas et al. 2001), and lead to offspring of lesser quality (Naef-Daenzer and Keller 1999, Sanz et al. 2003), all of which could lead to population declines (Both et al. 2006). Under this mechanism, the geographic differences we observed in population trends would be due to birds in more northerly portions of their range being better able to synchronize their breeding than birds in southern portions of their range. This could occur if northern populations exhibit greater phenotypic plasticity in response to climatic variability (Charmantier et al. 2008).

The second mechanism is centered on the settling patterns of breeding individuals with respect to advanced spring phenology. While short-distance migrants and residents may directly assess resource conditions, long-distance migrants may be unable to synchronize breeding with peak conditions because of arrival time on the breeding grounds (Both and Visser 2001). The only recourse for these individuals, especially younger birds that may not exhibit as much site fidelity as older birds with established territories, is to continue travelling to areas with delayed phenology and more favorable conditions (Studds et al. 2008). This behavior would cause population declines in the south and corroborate evidence pointing to northward shifts in distribution (Parmesan and Yohe 2003, Root et al. 2003, Hitch and Leberg 2007). In addition, under this mechanism populations would remain stable on the continental scale, as we observed.

We predicted that changes to community structure would be greater in the north, yet we observed the opposite pattern. Our prediction of a greater disparity in the north was based on research indicating that migratory distance influences the ability of a species to respond to climate change (Vegvari et al. 2010). However, migratory distance is often calculated using the midpoints of the breeding and wintering range (Jones and Cresswell 2010, Vegvari et al. 2010). This measurement fails to account for geographic variation within a species range, and instead refers to migratory strategy at the species. Consequently, while the ability of a species to respond to climate change may depend on migratory strategy at the species level (Vegvari et al. 2010), the ability of individuals to respond may depend on geographic location. Our results suggest that individuals from more northerly populations of a species may be better able to adjust to a changing climate, potentially through changes in migration behavior (Hedenstrom et al. 2007), which could lead to the geographic differences in population trends we observed.

We also predicted that long-distance migrants would be declining on the continental scale because of research indicating this pattern with European species (Lemoine and Bohning-Gaese 2003, Lemoine et al. 2007, Both et al. 2010). We may not have observed a similar pattern because of landscape-scale changes in habitat availability, changes on the wintering grounds, or habitat differences. Forest cover has increased over much of New England (Foster and Aber 2004) and has remained relatively unchanged in the Blue Ridge Mountain physiographic province over the last 30 years (Napton et al. 2010). Thus, reforestation could potentially increase available habitat and mask any negative effects associated with climate change, in New England. Changes on the wintering grounds could also cause long-distance migratory species to decline at different rates (Sæther 2000), and these changes may have been more severe for European species (Newton 2004). Finally, the tree species composition of forested habitats differ between North America and Europe (Huntley 1993). This difference could influence the phenology and abundance of food, as herbivorous insects would have a greater variety of plant species to choose from. Thus, the timing of breeding may be less important in North America.

Most studies that have investigated community response to climate change have analyzed species population trends in one area or region, with only the geographic scale of inference changing (Lemoine and Bohning-Gaese 2003, Valiela and Martinetto 2007, Jones and Cresswell 2010). We investigated how a community of birds, all with similar habitat requirements and breeding within a small area, changed in abundance by analyzing population trends at the continental-scale and at two distinct geographic regions. Our results signified that a greater proportion of long-distance migrant birds were declining at the southern terminus of the Appalachian mountain range and not at the northern terminus and also when compared with short-distance migrant and resident species. The disproportionate decline in long-distance migrants coincided with increasing spring temperatures, which may have led to the disproportionate decline if a changing climate contributed to either demographic consequences or changes in settling patterns that were not consistent across the geographic range of these species.

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Table 2.1. Population trends and variance estimates for species found breeding along the elevation gradient at the Coweeta Hydrological Laboratory, Macon Co., NC, along with migratory classification[1], and population trends specific to the Blue Ridge Mountain (BRM) and Northern New England (NNE) physiographic provinces.

		Location					
		RANGE		BRM		NNE	
Species		Trend	Var	Trend	Var	Trend	Var
Acadian Flycatcher (*Empidonax virescens*)	LDM	-0.10	0.04	-3.06	0.70	-	-
Black-and-white Warbler (*Mniotilta varia*)	LDM	-0.78	0.06	-3.18	2.00	-2.34	0.42
Blackburnian Warbler (*Dendroica fusca*)	LDM	0.67	0.14	-11.40	117.25	-2.27	2.73
Black-throated Blue Warbler (*Dendroica caerulescens*)	LDM	0.92	0.48	-2.38	1.37	0.38	1.26
Black-throated Green Warbler (*Dendroica virens*)	LDM	0.57	0.21	-2.12	3.65	1.68	2.08
Canada Warbler (*Wilsonia canadensis*)	LDM	-2.33	0.49	-5.06	49.85	-3.04	2.78
Chestnut-sided Warbler (*Dendroica pensylvanica*)	LDM	-0.68	0.09	-0.97	0.99	-2.15	0.18
Chimney Swift (*Chaetura pelagic*)	LDM	-1.85	0.02	-2.43	0.70	-2.64	0.32

Eastern Wood-Pewee (*Contopus virens*)	LDM	-1.67	0.02	-7.37	1.68	-2.81	0.37
Hooded Warbler (*Wilsonia citrina*)	LDM	0.84	0.55	1.16	0.58	-	-
Indigo Bunting (*Passerina cyanea*)	LDM	-0.54	0.01	-1.22	0.09	0.75	2.60
Northern Parula (*Parula americana*)	LDM	0.80	0.12	-1.52	1.56	0.00	9.60
Ovenbird (*Seiurus aurocapilla*)	LDM	0.27	0.02	-1.28	0.91	0.61	0.09
Red-eyed Vireo (*Vireo olivaceus*)	LDM	1.19	0.03	-0.77	0.30	0.34	0.14
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	LDM	-0.74	0.08	-3.55	3.27	0.20	0.84
Ruby Throated Hummingbird (*Archilochus colubris*)	LDM	2.19	0.11	4.27	19.21	1.59	2.18
Scarlet Tanager (*Piranga olivacea*)	LDM	-0.08	0.03	-1.82	1.52	-0.97	0.27
Veery (*Catharus fuscescens*)	LDM	-1.45	0.04	8.82	72.09	-1.73	0.09
Wood Thrush (*Hylocichla mustelina*)	LDM	-1.74	0.03	-1.01	1.46	-3.00	0.16
Worm-eating Warbler (*Helmitheros vermivorum*)	LDM	0.70	0.56	-3.12	2.03	-	-
American Crow (*Corvus brachyrhynchos*)	SDMR	1.95	0.07	1.56	0.34	2.55	0.08
Blue Jay (*Cyanocitta cristata*)	SDMR	-1.11	0.02	-0.81	0.34	0.34	0.16
Blue-headed Vireo (*Vireo solitaries*)	SDMR	4.52	0.35	4.57	5.05	3.92	1.34
Brown Creeper (*Certhia americana*)	SDMR	0.60	0.59	13.73	141.56	-0.22	3.62

Carolina Chickadee (*Poecile carolinensis*)	SDMR	-0.81	0.04	-0.13	0.87	-	-
Carolina Wren (*Thryothorus ludovicianus*)	SDMR	0.64	0.02	1.29	0.21	10.76	3.11
Dark-eyed Junco (*Junco hyemalis*)	SDMR	-1.30	0.06	2.25	0.33	-3.78	2.16
Downy Woodpecker (*Picoides pubescens*)	SDMR	-0.26	0.02	-1.73	1.91	2.47	0.82
Eastern Phoebe (*Sayornis phoebe*)	SDMR	0.83	0.04	0.38	0.90	0.51	0.23
Eastern Towhee (*Pipilo erythrophthalmus*)	SDMR	-1.61	0.02	0.22	0.37	-8.38	0.85
Golden-crowned Kinglet (*Regulus satrapa*)	SDMR	0.50	0.05	4.89	14.11	3.62	32.22
Hairy Woodpecker (*Picoides villosus*)	SDMR	1.34	0.07	0.53	1.92	0.14	0.72
Northern Cardinal (*Cardinalis cardinalis*)	SDMR	0.19	0.01	0.35	0.85	7.07	1.07
Northern Flicker (*Colaptes auratus*)	SDMR	-1.79	0.02	-3.31	3.85	-3.83	0.15
Pileated Woodpecker (*Dryocopus pileatus*)	SDMR	1.81	0.05	2.85	0.88	4.79	3.82
Red-bellied Woodpecker (*Melanerpes carolinus*)	SDMR	0.71	0.02	4.37	1.92	-	-
Tufted Titmouse (*Baeolophus bicolor*)	SDMR	0.89	0.02	0.04	1.09	16.52	2.19
White-breasted Nuthatch (*Sitta carolinensis*)	SDMR	-1.04	0.33	5.33	1.25	4.00	0.72
Wild Turkey (*Meleagris gallopavo*)	SDMR	12.93	0.63	14.03	215.00	30.63	35.47
Winter Wren (*Troglodytes hiemalis*)	SDMR	1.33	0.64	-1.23	0.91	-3.72	7.65

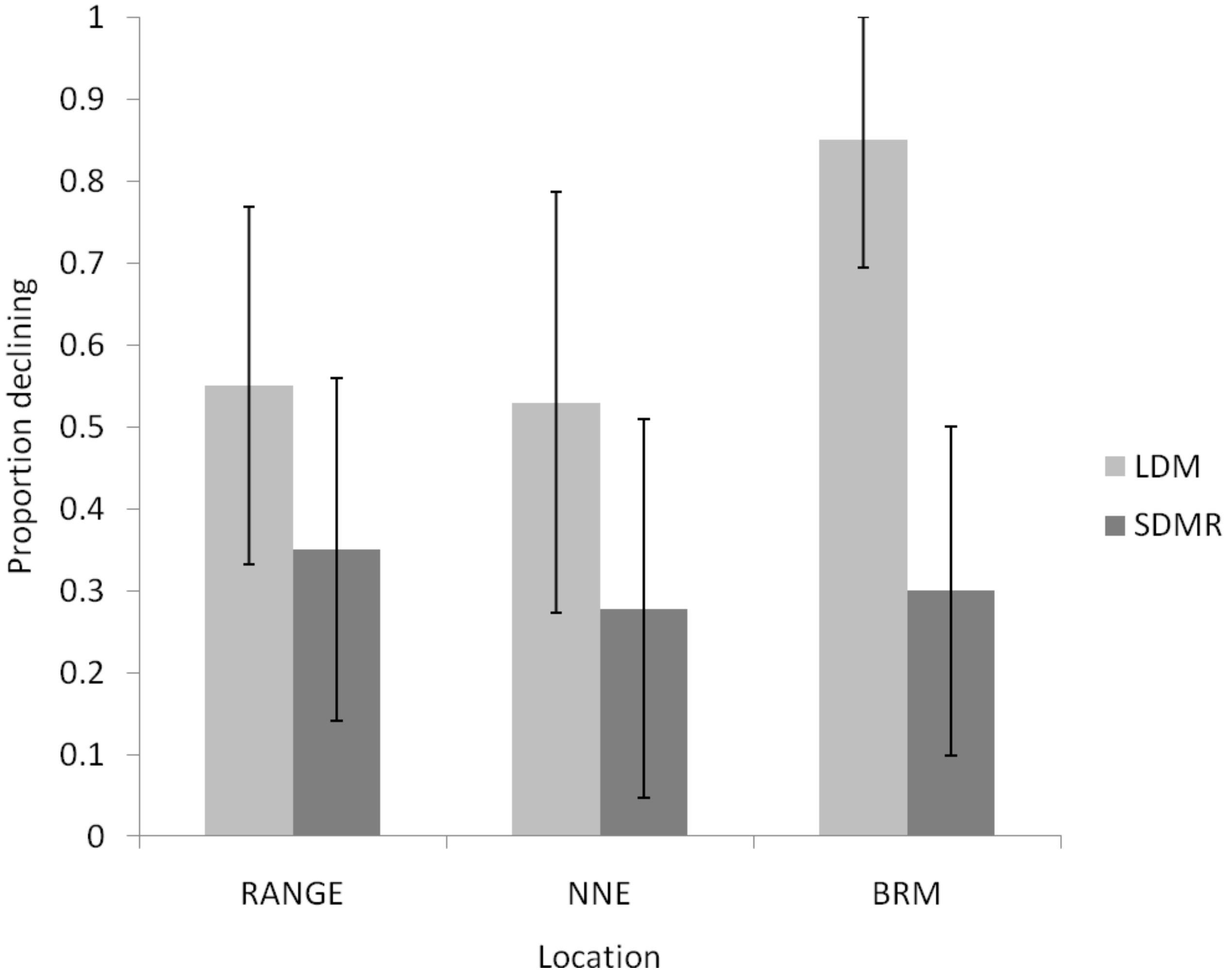
[1] LDM = Long-distance migrant; SDMR = Short-distance migrant & Resident

Table 2.2. Weight of evidence supporting disparate population trends for LDM species in comparison to SDMR species across the entire breadth of their geographic range (RANGE), in the Blue Ridge physiographic province (BRM), and the Northeast New England physiographic province (NNE), along the 95% confidence intervals.

Location	Evidence[1]
RANGE	0.44 (0.31–0.70)
BRM	0.94 (0.70-1.00)
NNE	0.55 (0.29-0.92)

[1] Weight of evidence and confidence intervals obtained via 10,000 Monte Carlo simulations

Figure 2.1. Proportion of Long-distance migrant (LDM) and short-distance migrant and resident species (SDMR) declining across their entire range (RANGE), Northern New England physiographic province (NNE), and Blue Ridge Mountain physiographic province (BRM). Error bars represent 95% confidence intervals



CHAPTER 3

INDIRECT EFFECTS OF AN INVASIVE EXOTIC SPECIES ON A LONG-DISTANCE MIGRANT SONGBIRD

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[1] Stodola, K.W., E.T. Linder, and R.J. Cooper. To be submitted to *Conservation Biology*

ABSTRACT

The loss of native species to exotic invasive pests and pathogens is an ongoing and serious threat to biodiversity. These threats are particularly detrimental when associated with the loss of foundational tree species, which can have far reaching consequences for forest composition and function. We had the opportunity to observe how the loss of eastern hemlock (*Tsuga canadensis*), due to the invasive hemlock woolly adelgid (*Adelges tsugae*), influenced the population ecology of a long-distance migratory songbird in the southern Appalachian mountains. We studied the breeding demography of Black-throated Blue Warblers (*Dendroica caerulescens*) at three study sites between 2002 and 2008, a time period that coincided with the invasion of the hemlock woolly adelgid and subsequent decimation of eastern hemlock. Although this warbler is not considered a hemlock–dependent species, hemlock provided an important nesting substrate at one of our three sites because it helped compensate for the lack of *Rhododendron maximum*, which is the preferred nesting substrate. Over the seven years of our investigation we noticed a precipitous decline in breeding pairs at the site where hemlock was most important and noticed little change at our other two sites. We observed no changes in reproductive output or apparent survival at this site suggesting that this decline was because of the lack of colonization by new breeders. New breeders were likely excluded from this site because of the lack of available nesting substrate caused by the hemlocks demise, as well as increased territory size needed by returning adults. Our results show that the indirect effects of an invasive species have wide ranging consequences, even for bird species not generally believed to be susceptible.

INTRODUCTION

Invasive non-native species represent one of the greatest threats to biodiversity (Enserink 1999, Pimental et al. 2000, Novacek and Cleland 2001). In particular, introduced pests and pathogens that infect and kill native species have wide-ranging detrimental effects (Castello et al. 1995, Enserink 1999, Everett 2000). These consequences are especially negative when associated with the loss of foundational tree species, which can result in fundamental changes to ecosystem composition and function (Ellison et al. 2005). The changes brought forth by exotic species can cascade throughout an ecosystem, thus affecting all organisms, and may be a major driver of environmental change, even in areas presumably protected from other threats (Vitousek et al. 1996).

Invasive pests and pathogens have decimated many foundational tree species, resulting in altered ecosystems and landscape patterns. In the eastern deciduous forests, the invasion of the chestnut blight fungus (*Cryphonectria parasitica*) reduced the once dominant American chestnut (*Castenea dentata*) down to a forest understory shrub (Liebhold et al. 1995). In the western United States, the white pine blister rust (*Cronartium ribicola*) has decimated western white (*Pinus monticola*) and sugar pine (*P. lambertiana*) forests (Liebhold et al. 1995). Other examples, such as Dutch elm disease (*Ophiostoma ulmi*) and gypsy moth *(Lymnatria dispar*) abound (Liebhold et al. 1995, Mack et al. 2000, Ellison et al. 2005). Despite the fact that the invasions of harmful pests and pathogens are common, ongoing, and have wide-ranging effects, little is known about the effects these invasions have on other ecosystem components such as wildlife species (Orwig 2002).

The eastern hemlock (*Tsuga canadensis*) is currently at risk of complete eradication from eastern deciduous forests because of the introduction of a destructive non-native insect.

Hemlock is a foundational tree species (Rogers 1978) that provides a unique microhabitat and an important structural component to a forest community (Kincaid and Parker 2008). Because of these qualities, hemlock stands harbor unique assemblages of birds and other taxa (Snyder et al. 2002, Tingley et al. 2002, Ross et al. 2003, Ross et al. 2004, Becker et al. 2008). However, the communities dependent on hemlock forests are threatened by the introduction of the hemlock woolly adelgid (*Adelges tsugae*). The adelgid was first introduced into the northeast and quickly spread, eliminating large stands of eastern hemlock (Orwig et al. 2002) and currently threatens hemlock stands as far south as Georgia (USFS 2009). Hemlock die-off following adelgid infestation occurs quickly, with needle loss beginning within a few years (Nuckolls et al. 2009), and mortality occurring within four years (McClure 1991). The adelgid attacks hemlocks of all age classes and can change the functional characteristics of a forest within a few years (Orwig and Foster 1998).

To date, a few studies have investigated the effects of adelgid infestation and subsequent hemlock loss on forest birds and found that species with a high dependence on hemlock, specifically Acadian Flycatcher (*Empidonax virescens*), Black-throated Green Warbler (*Dendroica virens*), Blackburnian Warbler (*Dendroica fusca*), and Hermit Thrush (*Catharus guttatus*), are least abundant where adelgid infestation is high (Tingley et al. 2002, Becker et al. 2008). The loss of hemlock as a nesting substrate has been proposed as a possible mechanism causing these declines, at least in Acadian Flycatchers (Allen et al. 2009). While these findings have helped our understanding of how the adelgid and the loss of hemlock can indirectly influence bird communities and populations, all studies compared the response variable (e.g., community structure or species performance) among areas of varying infestation (Tingley et al. 2002, Becker et al. 2008, Allen et al. 2009). An alternative approach towards understanding the causal mechanisms of species decline due to the invasion of an exotic species would be to collect detailed demographic information on a single population, from adelgid infestation to complete hemlock loss.

We were presented with a unique situation similar to the one described above, in which we could monitor the loss of hemlock and the effects it had on a long-distance migratory songbird. Beginning in 2002, we established three study sites in the Nantahala National Forest in Macon Co., North Carolina (which is located near the southern terminus of the Appalachian mountain range) focused in part on monitoring the demography of the Black-throated Blue Warbler (*Dendroica caerulescens*). The time frame of our study coincides with the southward advancement of the hemlock woolly adelgid, with 2001 being the first year it was detected in Macon county (USFS 2009). The adelgid quickly spread throughout this region, defoliating and killing hemlocks. We first observed it on our study sites in July of 2002 and by 2008 nearly all hemlocks were dead.

We focus on the patterns of Black-throated Blue Warbler abundance relative to hemlock loss and investigate the processes driving these patterns. The Black-throated Blue Warbler is a particularly valuable species for this investigation because of its dependence on large tracts of healthy mature forest (Holmes et al. 2005), which hemlock loss can alter (Orwig and Foster 1998). The Black-throated Blue Warbler also uses Lepidoptera larvae as its main prey resource, an important herbivore in eastern deciduous forests whose abundance may be altered with the loss of hemlock (Rohr et al. 2009), and nests in understory shrubs (Holmes et al. 2005) that may change in distribution following the loss of hemlock (Eschtruth et al. 2006, Spaulding and Rieske 2010). Consequently, the loss of hemlock has the potential to influence many facets of the Black-throated Blue Warblers’ breeding biology. However, unlike the Acadian Flycatcher or other hemlock associated species, the Black-throated Blue Warbler uses a variety of nesting substrates (Holmes et al. 2005) and therefore the loss of hemlock may not negatively affect it. Consequently, understanding how the Black-throated Blue Warbler responds to the loss of hemlock can provide valuable information on the potential consequences associated with the loss of foundational tree species to forest interior songbirds.

METHODS

We conducted this study within the Nantahala National Forest in the southern Appalachian Mountains, Macon County, North Carolina. We established three study sites at approximate elevations of 1050m (LOW), and 1200m (MID), and 1350m (HIGH) and all three study sites were within 15 km of one another. The LOW and MID elevation sites were established in 2002, while the HIGH elevation site was added in 2003. This forest is characterized by cove hardwood and northern hardwood forest vegetation (Day et al. 1988), with an understory dominated by *Rhodendron maximum* and *Kalmia latifolia* (Day and Monk 1974).

Study Species

The Black–throated Blue Warbler is a 9 – 10 g insectivorous Nearctic-Neotropical migrant that winters in the Greater Antilles and breeds from the southern Appalachian Mountains of Georgia northward to Nova Scotia and as far west as northeast Minnesota (Holmes et al. 2005). Inter-annual site fidelity is high (Holmes et al. 1992) and males defend non–overlapping territories, typically remaining in these territories for the duration of the breeding season (Holmes et al. 2005, Stodola *personal observation*). The sexually dichromatic Black–throated Blue Warbler forages mainly in the understory. In studies conducted in New Hampshire, Lepidoptera larvae made up >80% of the prey items taken (Robinson and Holmes 1982) and 60–87% of the estimated prey biomass brought to nestlings (Goodbred and Holmes 1996). The

Black-throated Blue Warbler has been extensively studied at Hubbard Brook Experimental Forest in New Hampshire (e.g., Rodenhouse and Holmes 1992, Holmes et al. 1996, Sillett and Holmes 2002, Rodenhouse et al. 2003, Sillett et al. 2004), yet little demographic data are available from the southern portion of its breeding range.

Habitat Assessment

Vegetation composition.– We focused our vegetation measurements on woody-stemmed species and gathered information on their abundance at 74, 69, and 36 systematically placed locations on the LOW, MID, and HIGH sites, respectively. Each location was separated by approximately 70 m and arranged in a checker board pattern that encompassed the area where Black-throated Blue Warblers nested. We measured basal area for all tree species >10 cm diameter at breast height (dbh) within 11.3-m-radius plots, and counted all saplings (3 cm – 10 cm dbh) and stems from shrubs (< 3 cm in width, > 0.3 m in height) within 3m radius vegetation plots.

Hemlock decline.– The process of hemlock loss is well understood and consistent, ending in massive needle loss and tree death within approximately four years (McClure 1991, Nuckolls et al. 2009); thus our estimates of hemlock loss are mainly qualitative. We did estimate hemlock defoliation in 2007 because this year represented the time period of 3-5 years following infestation (when hemlock death would be most noticeable); by 2008 nearly all hemlocks were completely decimated, which limited the utility in estimating defoliation. We gathered our 2007 estimates on 52, 50, and 50 haphazardly chosen hemlocks at the LOW, MID, and HIGH sites respectively. We estimated percent needle loss (percent defoliated over a 200 cm^2 area) on the lower branches (~1m high) on three different sides of each hemlock, and averaged these to estimate defoliation.

Population Demography

Survival.– We attempted to band all singing males and nesting females at each site in each year. Both males and females were fitted with unique combinations of color bands. In each year, we relocated all banded individuals on our study sites, and searched surrounding areas for individuals that may have moved off our plots.

Breeding density.– To facilitate territory mapping and location of breeding males, we gridded each study plot by flagging trees every 25 or 50 meters. The grid was then superimposed onto a topographic map of the study area where we marked territory observations. Although not every territorial male or female was banded, unbanded individuals were usually surrounded by color-banded ones and were easy to identify. In addition, we visited each site nearly every day, which allowed us to learn individual territories and territory boundaries. We feel confident that we located all individual territorial males and focal females because we were able to locate nests for every territorial male, although we may have missed some nests of secondary females of bigamous males. Territory size for each breeding male was estimated from the territory maps.

Reproductive Output.– Several demographic parameters (clutch size, number of fledged young, number of nesting attempts and broods, time to renest, and duration of the breeding season) are required to estimate annual reproductive output (Farnsworth and Simons 2001) and we made every effort to locate all nesting attempts to estimate these parameters. We monitored nests every 2 – 4 days to ascertain the date of clutch initiation, clutch size, start of incubation, hatching date, and number of young fledged. We used parental behavior to ascertain fledging status if fledglings were not seen and assumed fledging had occurred if parents were seen carrying food or were agitated at the presence of an observer for an extended period of time (>10 min). Unsuccessful nests were determined by loss of nest, eggs, or nestlings prior to day 8 (hatch day = day 0) of the nesting cycle, which is the earliest Black-throated Blue Warblers fledged young during the course of this study. Nest cycle length was calculated as the difference in days between the start of incubation and the successful fledging of young.

We used the Farnsworth and Simons model (2001, 2005) to estimate annual reproductive output (ARO, defined as the number of young fledged per pair per season), instead of our empirical estimates of ARO, because we did not feel confident we found every nesting attempt for every focal pair, especially later in the breeding season. Consequently, while we recognize the concern that the Farnsworth-Simons (2001, 2005) model may overestimate ARO, especially at lower levels (Jones et al. 2005b), we believe the issue of bias in our empirical estimates of ARO to be a bigger problem. However, the Farnsworth-Simons model (2001, 2005) exhibited a strong positive relationship with observed ARO for a population of Black-throated Blue Warblers in New Hampshire (Jones et al. 2005a, b).

Statistical analyses

We estimated apparent survival using Cormack-Jolly-Seber models (Lebreton et al. 1992) by implementing the recaptures option in Program MARK (White and Burnham 1999). We took an iterative approach to modeling apparent survival by first fitting four models where survival was held constant ($\Phi_.$) and detection was either constant ($P_.$), a function of site (P_{SITE}), gender (P_{GENDER}), or their interaction ($P_{SITE \times GENDER}$). Model fit was evaluated using Akaike's Information Criterion (AIC; Akaike 1973) adjusted for small sample size (AICc; Burnham and Anderson 2002). The weight of evidence (Wi; Burnham and Anderson 2002) for each model was used to compare among sets of competing models. We then used the best fitting detection model when investigating apparent survival. For this analysis we fit seven different models where survival was constant across years, sites, and gender ($\Phi_{.}$), a function of site (Φ_{SITE}), a function of gender (Φ_{GENDER}), and a function of year (Φ_{YEAR}), along with the interaction of site and gender ($\Phi_{\mathrm{SITE\ x\ GENDER}}$), site and year ($\Phi_{\mathrm{SITE\ x\ YEAR}}$), and gender and year ($\Phi_{\mathrm{GENDER\ x\ YEAR}}$). We estimated territory size by fitting a general linear model relating territory size to year, site, year and site, and their interaction, along with a constant model with no difference in territory size among years or sites. Territory size was log transformed prior to analysis.

Breeding parameters of interest were estimated by fitting generalized linear models relating clutch size and fledged young per successful nest to site, year, site and year, the interaction of site and year, along with a constant model with no difference among sites or years. We estimated time to renest in a similar fashion but included an additional predictor indicating if the attempt followed a successful or unsuccessful nest attempt. Time to renest was modeled using a Poisson distribution and log link in Proc Genmod (SAS Institute 2007). We controlled for underdispersion of the data using the dscale option, which computes an additional scale parameter and adjusts the standard errors of the regression coefficients. Clutch size and number of fledged young per successful nest were modeled using a beta-binomial distribution and the logit link in Proc Genmod (SAS Institute 2007), where the maximum clutch size and fledged young were set to five. A Hosmer and Lemeshow test of goodness of fit failed to indicate any lack of fit. We calculated daily nest survival using the logistic exposure method (Shaffer 2004). The last day the nest was observed active was used to calculate exposure days for nests with uncertain fates (Manolis et al. 2000). Nests were considered successful if at least one young fledged.

We used a similar information theoretic approach described for estimating apparent survival where model fit was evaluated using Akaike's Information Criterion (AIC; Akaike

1973) adjusted for small sample size (AICc; Burnham and Anderson 2002). The weight of evidence (Wi; Burnham and Anderson 2002) for each model was used to compare among sets of competing models and we used model averaging (Burnham and Anderson 2002) to incorporate uncertainty about our estimates for clutch size, fledged young per successful nest, breeding cycle length, time between breeding events, and probability of nest survival. We did not incorporate model averaging for parameters that were best explained by the constant model. These estimates were then incorporated in the Farnsworth and Simons model (2001, 2005) for calculating ARO, along with a nesting cycle of 21 days (12 day incubation, 9 day nestling period), maximum number of two broods in a season, and five total nesting attempts, which represented the maximum number of nests we observed females attempting. Breeding season length for each site and year was estimated as the difference between the average date of clutch initiation for the first five nesting attempts and the average date of clutch initiation for the last three nest attempts (e.g. Marshall et al. 2002) plus 25 days, which corresponded to a clutch size of four, an incubation period of 12 days, and a nestling period of nine days.

To incorporate the uncertainty in our demographic estimates we recalculated ARO under 10,000 Monte Carlo simulations where each iteration represented a random draw from the normal distribution with the mean and standard error coming from the untransformed model-averaged beta estimates for the respective parameter of interest: clutch size, number of fledged young per successful nest, time between breeding events, and daily probability of nest survival. The randomly generated beta estimate was then back-transformed and used in Monte Carlo simulations for estimating ARO. Simulations were performed using the POPTOOLS add-in for Microsoft Excel and interpretations of ARO were performed using the Monte Carlo 95% confidence intervals. Interpretations of vegetation differences among sites were performed using approximate confidence intervals derived from the normal distribution and all other parameters of interest are reported with 95% confidence intervals calculated using asymptotic maximum likelihood standard error estimates (Gerrard et al. 1998, Johnson 1999).

RESULTS

Habitat assessment

Vegetation composition.– Average (95% confidence interval) basal area was 32.4 (30.3, 34.4) cm^2/m^2 at the LOW site, 34.2 (31.4, 37.0) cm^2/m^2 at the MID site, and 28.3 (23.4, 33.2) cm^2/m^2 at the HIGH site. *Liriodendron tulipifera* was the most dominant tree at the LOW site, *Quercus rubra* was the most dominant tree at the MID site, and *Acer rubrum* was the most dominant tree at the HIGH site (Figure 3.1). *Tsuga canadensis* was prevalent on the LOW and HIGH sites, but relatively sparse at the MID site (Figure 3.1). Sapling density (95% confidence interval) was slightly greater at the HIGH site with 6.9 (4.7, 9.0) saplings per 3m radius vegetation plot, in comparison to the MID and LOW sites, 6.3 (4.1, 8.4), 5.3 (3.3, 7.3) per 3m radius vegetation plot respectively. *R. maximum* was the most abundant sapling across all sites with an average (95% confidence interval) abundance per 3m radius vegetation plot being 1.7 (1.0, 2.3). This abundance varied by site, however, and it was more numerous at the HIGH and MID sites in comparison to the LOW site (Figure 3.2). Overall, hemlock was the fourth most abundant sapling across all sites, although it was second most abundant at the LOW site (Figure 3.2). Average shrub density (95% confidence interval) was much greater at the HIGH site in comparison to the MID and LOW sites, with 51.5 (37.2, 65.7), 34.2 (26.2, 42.1), and 37.9 (28.6, 47.2) shrubs per 3m radius vegetation plot at the HIGH, MID, and LOW sites respectively. *Gaylusaccia* species were the most abundant shrub across all sites, with an average (95% confidence interval) of 10.3 (5.9, 14.7) per 3m vegetation plot, followed by *R. maximum* 8.7 (5.6, 11.7), and *Q. rubra* seedlings 3.1 (1.7, 4.5), with the distribution varying across sites (Figure 3.3a). Hemlock, at the shrub level, was less abundant across all sites, with an average (95% confidence interval) of 0.6 (0.2, 1.0) per 3m radius vegetation plot, but much more prevalent at the LOW site in comparison to the MID and HIGH sites (Figure 3.3b).

Hemlock decline.– We first detected the aldegid at the LOW site at the end of 2002, and on the MID and HIGH sites in the beginning of 2003. While the adelgid was ubiquitous by 2004, we only observed needle loss at one very localized 2 ha patch on the LOW site, which is where we first located the adelgid. However, by 2007 the average needle loss was approximately 80% at the LOW site, 70% at the MID site, and 85% at the HIGH site. In 2008, nearly all hemlocks were dead or defoliation was over 80%.

Population demography

Survival.– We banded 163 males and 122 females over the seven years of this study across all sites. The best fitting detection model received 78% of the weight of evidence and indicated that detection was a function of gender, with the probability (95% confidence interval) of detection being 0.82 (0.67 – 0.91) for females and 0.97 (0.84 – 0.99) for males. The constant detection model received 11% of weight of evidence, while the interaction of site and gender received 8%, and site received 2%. The best fitting survival model indicated the influence of site, although model uncertainty was high (Table 3.1). Estimates from the constant survival model indicated that apparent survival (SE) was 0.53 (0.48–0.58), irrespective of site, gender, and year, while the site effects model indicated that apparent survival was 0.52 (0.41 – 0.63) at the LOW site, 0.47 (0.38 – 0.55) at the MID site, and 0.59 (0.51 – 0.67) at the HIGH site.

Nest placement and Breeding density.– We monitored 562 nests across all years and sites. The majority of nests were placed in *Rhododendron maximum* (71%), followed by *Tsuga* *canadensis* (hemlock) (6%), *Gaylussacia* spp. (6%), *Rubus* spp. (4%), and *Kalmia latifolia* (2%); with 28 other species making up the other 11 percent. However, the proportion of nests in hemlock was much greater at the LOW site (23%), than at the MID (0%) and HIGH (2%) sites. Furthermore, the proportion at the LOW site declined precipitously after 2003, going from approximately 50% of all nests in the first two years to approximately 10% in the final three years (Figure 3.4). The loss of hemlock at the LOW site coincided with a 70% decline in the density of breeding males (Figure 3.5), with the average territory size for a breeding pair nearly doubling (Table 3.2, Figure 3.6). While density of breeding males fluctuated yearly, there was no concomitant decline at the MID and HIGH sites (Figure 3.5; 2009 density estimates at the MID and HIGH sites are provided for comparison), nor was there a similar increase in territory size (Figure 3.6).

Annual Reproductive Output.– Days between renests varied by site and year (Table 3.3) and it took females approximately 6.5 (5.3 – 7.8) days following a nest failure and 10.5 (8.4 – 13.1) days following a successful nest. Clutch size and number of fledged young per successful nest were best explained by the constant model with no difference between sites and years (Table 3.2). Clutch size was 3.68 (3.59 – 3.76) irrespective of site and year, while the number of fledged young per successful nest was 3.39 (3.27 – 3.51), irrespective of site and year. The probability of daily nest survival varied by site and year (Table 3.2), with the probability of survival being consistently lowest at the MID site (Figure 3.7). Breeding season length was longer at the MID and HIGH sites in comparison to the LOW site, although there was no change over time (Table 3.4). Finally, while ARO differed by site, it was consistently lowest at the MID site and greatest at the HIGH site, and there did not appear to be any clear pattern throughout the duration of our study coinciding with the loss of hemlock (Figure 3.8).

DISCUSSION

Our three study sites provided a contrast in the availability and importance of hemlock to the Black-throated Blue Warbler. Hemlock was present in the overstory at all three sites, most notably at the LOW and HIGH sites, yet its presence in the understory (saplings and shrubs) was much more pronounced at the LOW site. The LOW site also differed from the other two sites in that *R. maximum* was much less abundant there. *R. maximum* is clearly the preferred nesting substrate for Black-throated Blue Warblers in our study area and its relative scarcity at the LOW site required breeding females to place a greater proportion of nests in other species of understory shrub. Prior to hemlock decline, the best alternative nesting substrate was hemlock, which provides dense, near-ground foliage similar to *R. maximum*. However, as hemlock declined and became scarce, breeding individuals needed to use other nesting substrates.

While the Black-throated Blue Warbler is generally not considered a hemlock associated species (Holmes et al. 2005, Becker et al. 2008), our results indicated a substantial decline in breeding pairs at our LOW site, in conjunction with the loss of hemlock. We observed no concomitant loss at our other two sites where *R. maximum* was abundant. The disparity between sites indicates that hemlock loss may be the probable cause for decline in breeding pairs. Thus, much like the Acadian Flycatcher (Allen et al. 2009), the decline in density we observed at our LOW site was likely due to the loss of hemlock as nesting substrate. However, because we were able to follow this process from infestation through near complete hemlock loss, our data may explain the link between loss of hemlock and a substantial decline in breeding pairs in certain habitats.

Three possible mechanisms may be driving the population decline we observed at the LOW site: birds leaving because of reduced reproductive performance, reduced survival precluding individuals from returning, or inadequate immigration into the area by new breeders to compensate for birds that do not return. Site fidelity in birds is often predicated on breeding success in the previous year (Greenwood and Harvey 1982, Hoover 2003, Porneluzi 2003, Sedgwick 2004) and the loss of hemlock in our study area could have directly influenced fidelity by decreasing the availability of food resources or increasing nest depredation rates. The Black-throated Blue Warbler forages primarily in the understory (Robinson and Holmes 1982) and loss of hemlock in our area could reduce available foraging substrate. This in turn could reduce food availability and reproductive output (Martin 1987, Nagy and Holmes 2005). In addition, because hemlock provides a dense understory (Kincaid and Parker 2008), and its loss reduces understory density (Kizlinski et al. 2002), nest depredation rates could increase with greater nest visibility. Yet, we failed to detect any reduction in reproductive output that could be related to the adelgid.

A reduction in birds returning to breed at the LOW site could also occur via outright mortality for many of the same reasons provided in the preceding paragraph. Reduced food availability could negatively impact survival through increased time spent searching for prey (Naef-Daenzer and Keller 1999), increased daily energy expenditures, and reduced body condition (Nagy et al. 2007). In addition, the loss of hemlock and its dense understory branches may eliminate safe resting and roosting locations, thus subjecting breeding birds to higher predation rates. However, while these scenarios are possible, we failed to observe any reduction in Black-throated Blue Warbler survival associated with the invasion of the hemlock woolly adelgid and the subsequent loss of hemlock.

Failure of new birds to settle on the LOW site remains the last plausible mechanism inducing a decline in breeding pairs following the loss of hemlock. Site fidelity in the Black-throated Blue Warbler has been tied to habitat quality (Holmes et al. 1996), and habitat quality declined at our LOW site. As the adelgid spread and defoliated hemlock throughout the LOW site, areas that may have once been suitable for breeding now lacked suitable nesting substrate. Territory size of breeding adults increased as well during this time period, potentially to gain access to suitable nesting areas. Anecdotally, areas with high hemlock densities that supported multiple breeding pairs during the first few years of our study, supported only one pair during the last couple of years. Thus, younger birds may have chosen not to settle, or were excluded from breeding, at the LOW site because the lack of available nesting substrate caused by hemlock loss. The relatively constant population densities at the MID and HIGH sites corroborate the idea that a lack of available nesting areas caused new breeders not to settle at the LOW site. Hemlock declined at the MID and HIGH sites but *R. maximum* remained abundant. Breeding density remained stable and males did not increase their territory size. Because adults returned at similar rates at the MID and HIGH sites in comparison to the LOW site populations must have remained stable by new birds filling in opened territories from birds that failed to return. Therefore, by process of elimination, we believe our results suggest the cause of population decline at the LOW site is due to a failure by new breeders to immigrate and set up territories.

Many other species of birds are expected to decline as the adelgid spreads and eliminates the remaining hemlock stands throughout the southeast. Not surprisingly, bird species tied to hemlock may be at special risk to the changes caused by the introduction of this invasive species (Ross et al. 2004, Becker et al. 2008, Allen et al. 2009). However, as we have shown, the negative consequences associated with the infestation of the adelgid and loss of hemlock may go beyond just those species believed to be hemlock associates. For the Black-throated Blue Warbler, hemlock was only important at one of our three study sites where it was disproportionately used as a nesting substrate. Other bird species may also use hemlock in ways, means, and locations where its importance may not be expected nor readily observed. Under this scenario, hemlock loss may have far reaching yet very local, species-specific consequences.

Eastern deciduous forests have been decimated by the hemlock woolly adelgid (Kizlinski et al. 2002, Orwig et al. 2002, Spaulding and Rieske 2010); what replaces hemlock is yet to be seen, and other potential threats to the forest are looming. Following the loss of hemlock, projections of future forest structure suggest replacement by black birch (*Betula lenta*), oak (*Quercus*), and hickory (*Carya*) species (Eschtruth et al. 2006, Spaulding and Rieske 2010). Although it is unknown how other bird species will respond to the structural changes associated with the loss of hemlock, our data indicate that the Black-throated Blue Warbler infrequently nests in the species expected to replace hemlock. Consequently, the unique structural component that hemlock provides will be hard to replace and will ultimately change community structure. Furthermore, threats from other non-native species appear on the horizon (Loo 2009, Gandhi and Herms 2010). For Black-throated Blue Warblers, sudden oak death (*Phytophthora ramorum*) may provide an even more severe challenge because it can infect *R. maximum* (Tooley and Browning 2009), a preferred nesting material. As our study indicates, Black-throated Blue Warblers are especially sensitive to the loss of important nesting substrates, which can influence the immigration of new breeders.

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Table 3.1. Comparison of candidate Cormack-Jolly-Seber models investigating apparent survival (Φ) in the Black-throated Blue Warbler. Detection was modeled as a function of gender. Number of model parameters (K), Akaike Information Criterion adjusted for small sample size (AICc), and AICc weight of evidence are included (Wi).

Model	K	AICc	Wi
Φ_{SITE}, $P_{.}$	5	566.7	0.28
$\Phi_{.}$, $P_{.}$	3	566.8	0.27
Φ_{GENDER}, $P_{.}$	4	567.5	0.19
$\Phi_{YEAR\ x\ GENDER}$, $P_{.}$	14	567.9	0.15
Φ_{YEAR}, $P_{.}$	8	568.9	0.09
$\Phi_{GENDER\ x\ SITE}$, $P_{.}$	8	571.7	0.02
$\Phi_{YEAR\ x\ SITE}$, $P_{.}$	19	581.1	0.00

Table 3.2. Comparison of candidate models investigating the influence of year and site on territory size, clutch size, number of fledged young per successful nest, and probability of daily nest survival. Number of model parameters (K), sample size (N), AICc, and AICc weight of evidence (Wi) are provided. The best fitting model is bolded.

	Territory Size				Clutch Size				Fledged Young				Fledged Young			
	K	N	AICc	Wi	K	N	AICc	Wi	K	N	AICc	Wi	K	N	AICc	Wi
CONSTANT	2	236	360.8	0.00	**1**	**520**	**3008.8**	**0.70**	**1**	**284**	**1795.4**	**0.74**	1	4217	2100.2	0.00
YEAR	8	236	363.7	0.00	7	520	3010.9	0.24	7	284	1797.7	0.24	7	4217	2074.1	0.00
SITE	4	236	204.8	0.00	3	520	3014.2	0.04	3	284	1803.4	0.01	3	4217	2066.9	0.13
YEAR + SITE	12	236	180.3	0.00	11	520	3016.4	0.02	11	284	1805.8	0.00	**11**	**4217**	**2063.1**	**0.87**
YEAR X SITE	**20**	**236**	**165.6**	**1.00**	19	520	3033.6	0.00	19	284	1821.7	0.00	19	4217	2096.0	0.00

Table 3.3. Comparison of candidate models investigating the influence of year and site, on the time to renest. Whether the nest followed a successful or unsuccessful nest (AFTER) was included in all models except the constant model. Number of model parameters (K), sample size (N), AICc, and AICc weight of evidence (Wi) are provided.

	K	N	AICc	Wi
YEAR X SITE	21	217	-3723.7	1.00
YEAR + SITE	11	217	-3469.2	0.00
YEAR	9	217	-3456.0	0.00
SITE	5	217	-3408.7	0.00
AFTER	3	217	-3404.3	0.00
CONSTANT	2	217	-2407.4	0.00

Table 3.4. Breeding season length at the LOW, MID, and HIGH sites across all years. Breeding season length was estimated as the difference between the mean date of the first 5 nests initiated in a season and the mean date of the last 3 nests (e.g. Marshall et al. 2002).

	Site			
Year	LOW	MID	HIGH	Average
2002	60.7	60.8	-	
2003	63.2	73.5	71.1	69.3
2004	66.1	71.5	81.4	73.0
2005	56.2	63.7	69.7	63.2
2006	70.1	82.9	75.5	76.2
2007	68.9	68.5	63.5	67.0
2008	65.2	70.2	73.5	69.6
Average	63.9	72.9	74.4	

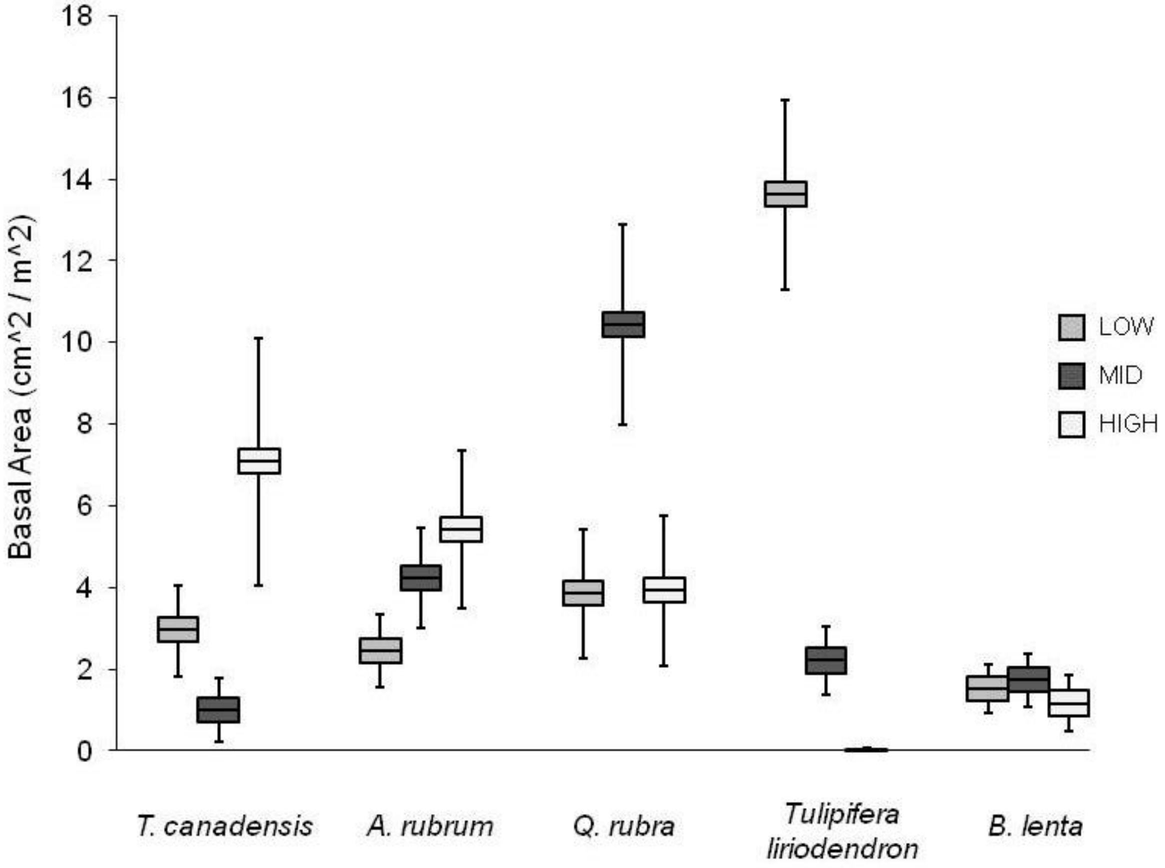

Figure 3.1. Average basal area (cm^2 / m^2) of the five most abundant tree species across all sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. Error bars represent 95 % confidence intervals.

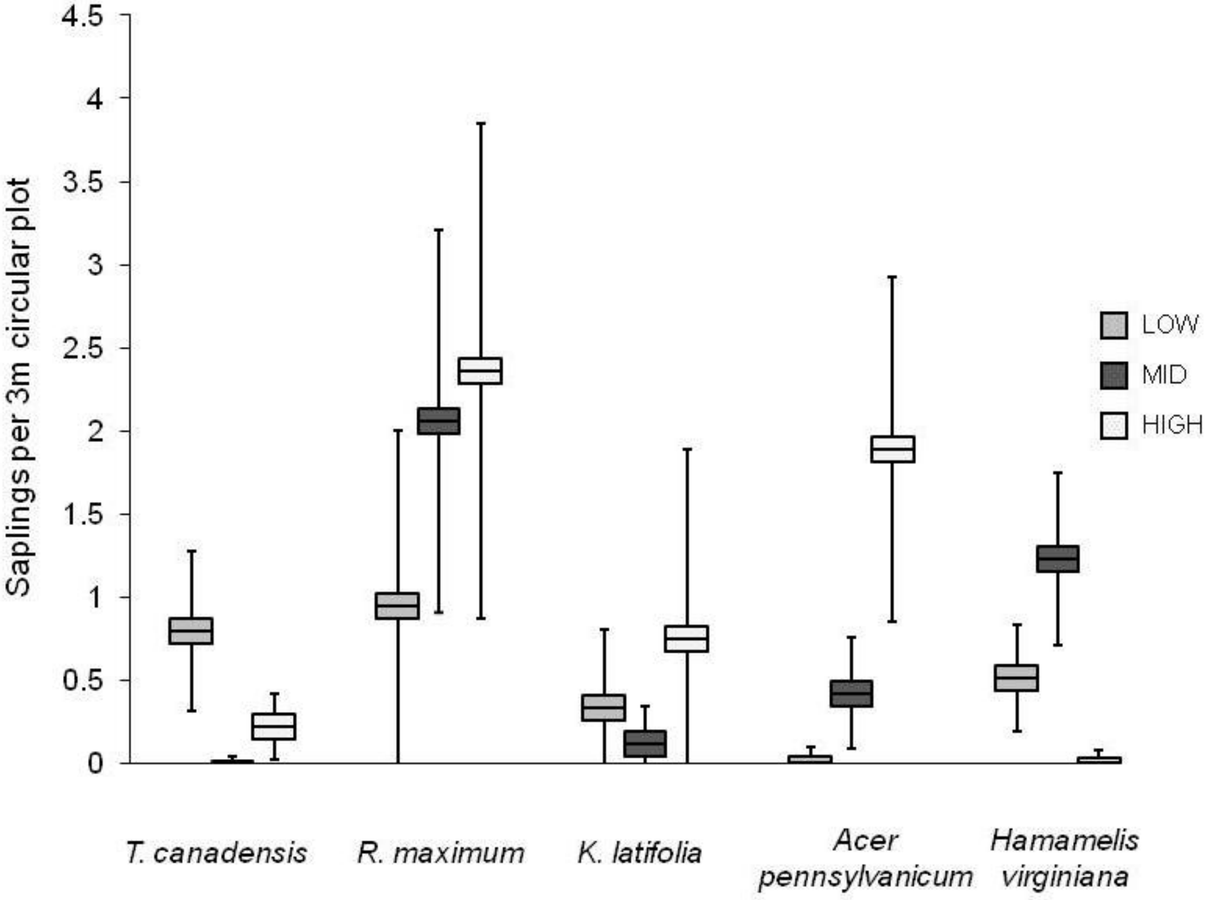

Figure 3.2. Average number of the five most abundant saplings (3 cm – 10 cm dbh) in 3 m radius vegetation plots across all sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. Error bars represent 95 % confidence intervals.

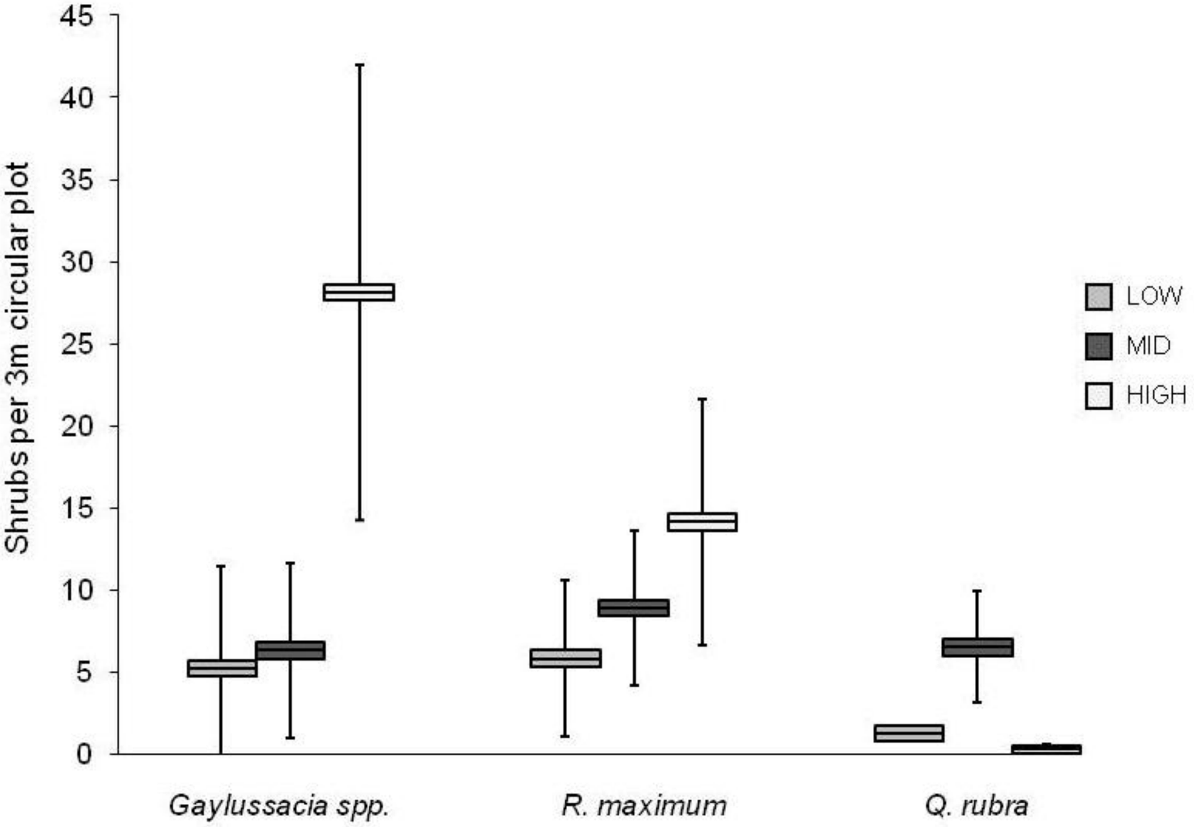

Figure 3.3a. Average number of the three most abundant woody shrub (< 3 cm in width, > 0.3 m in height) species found in 3 m radius vegetation plots across all sites. Error bars represent 95% confidence intervals.

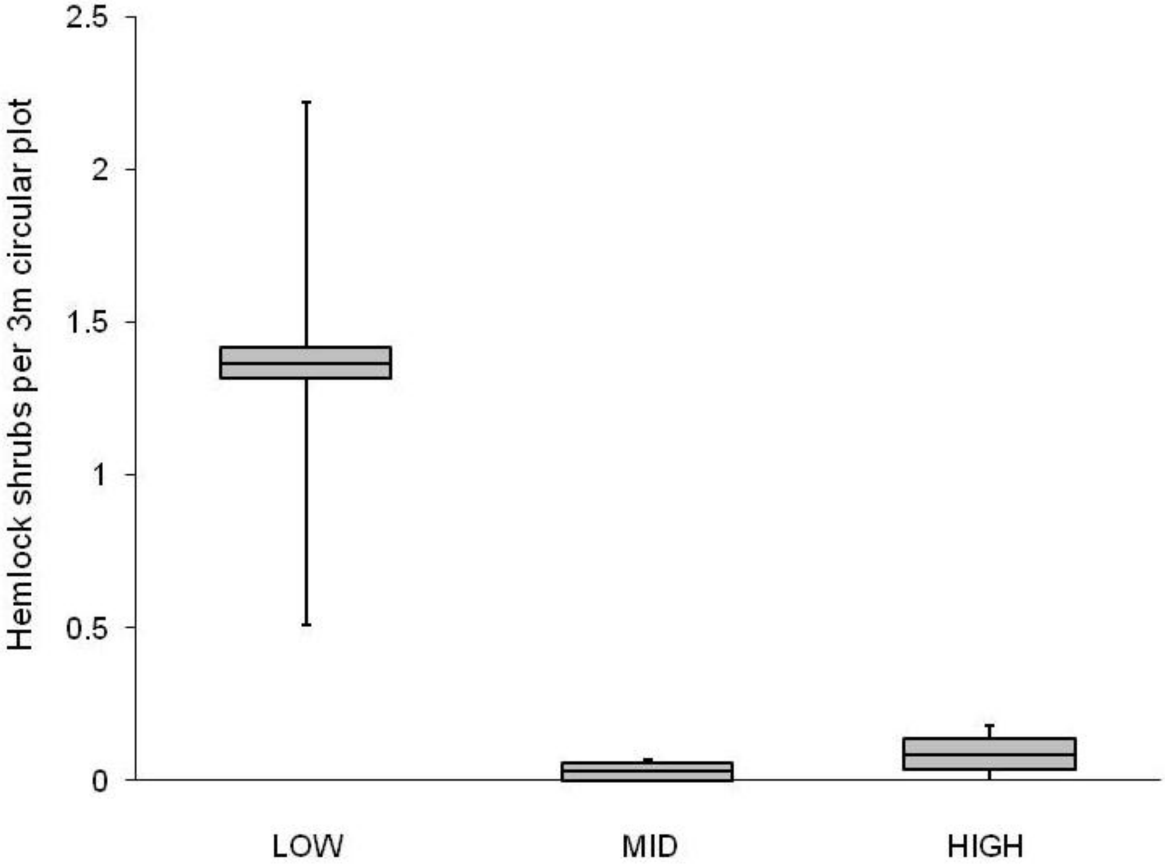

Figure 3.3b. Average number of hemlock shrubs (< 3 cm in width, > 0.3 m in height) found in 3 m radius vegetation plots across all sites. Error bars represent 95% confidence intervals.

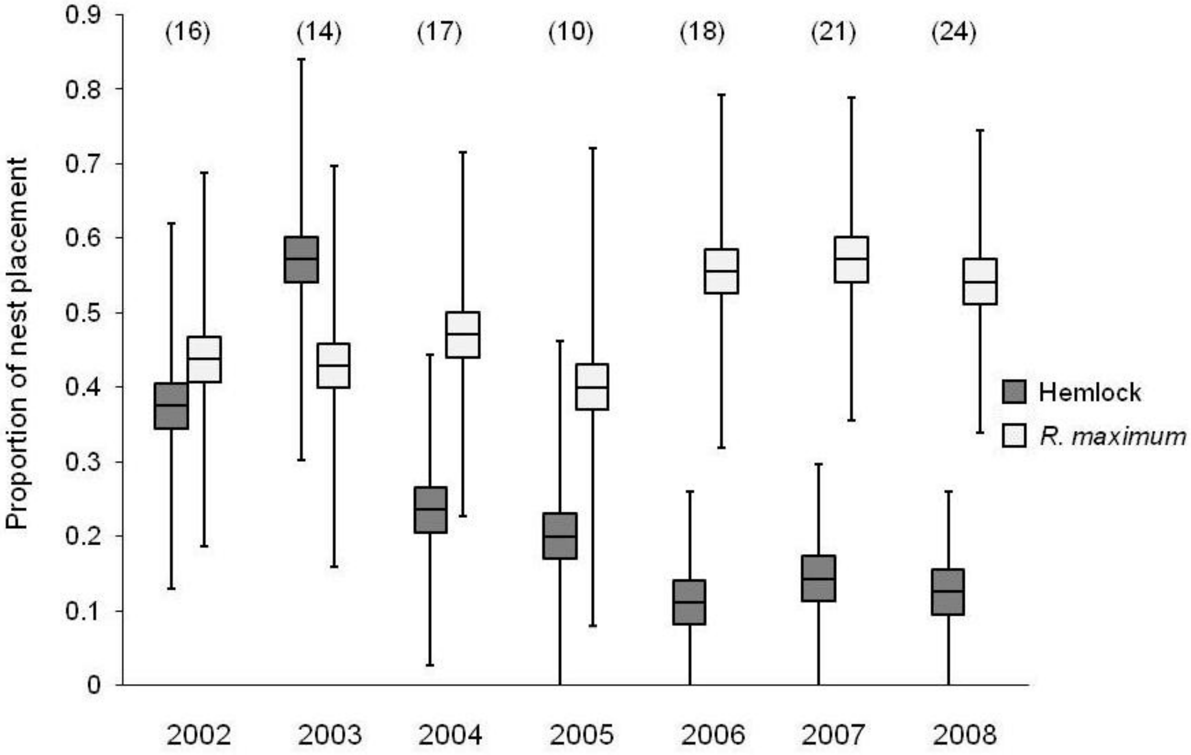

Figure 3.4. Proportion of nests found in *Tsuga canadensis* (Hemlock) and *Rhododendron maximum* (Rhodo) at the LOW site between the years 2002 – 2008. Total nests found in that year are provided in parentheses.

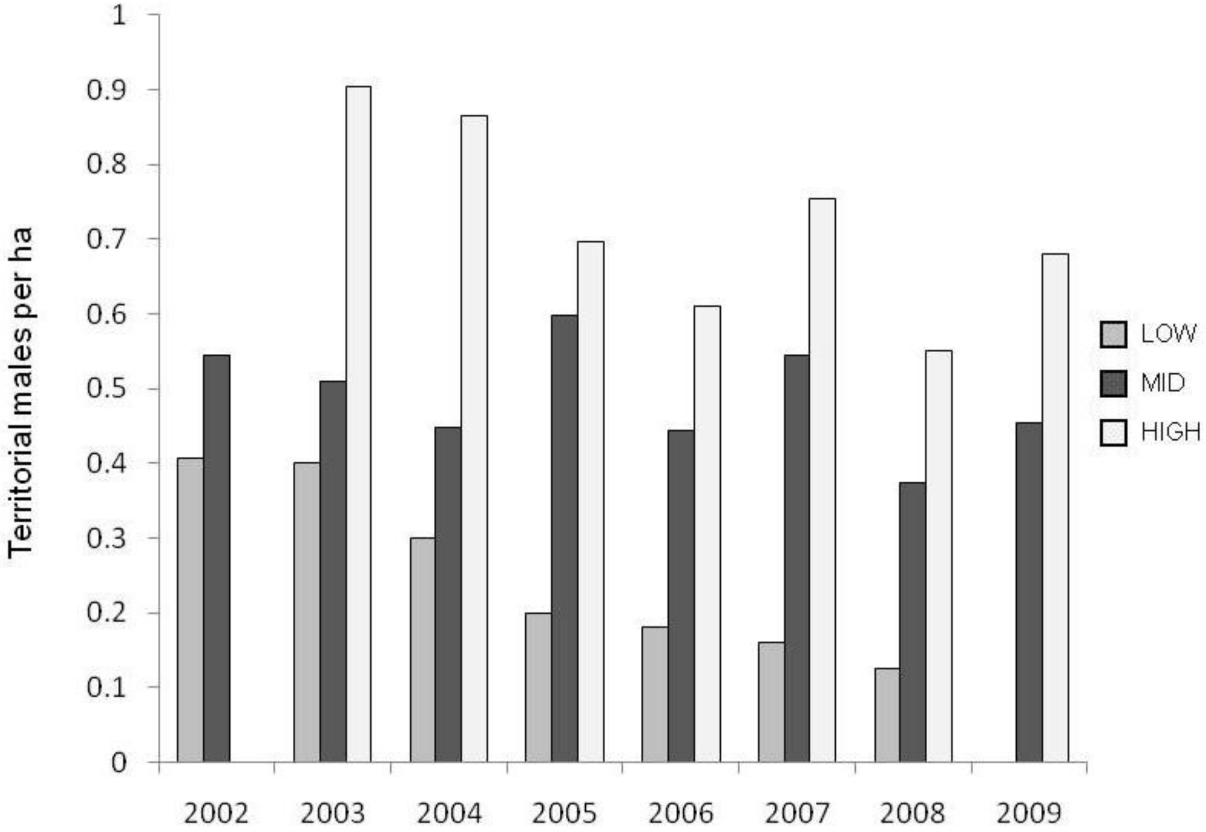

Figure 3.5. Density of territorial male Black-throated Blue Warblers across sites and years, 2009 data is presented for comparison reasons.

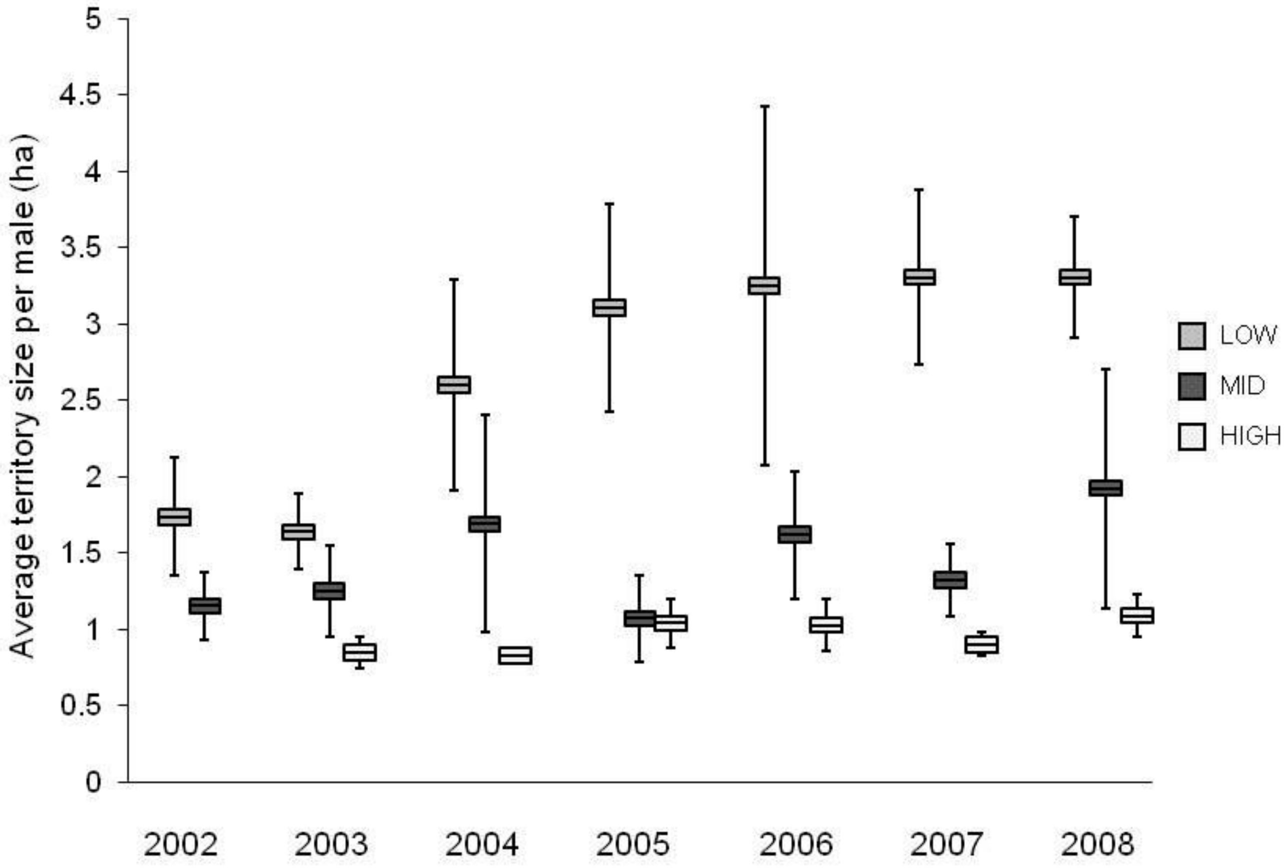

Figure 3.6. Average territory size (ha) for breeding Black-throated Blue Warblers across sites and years. Error bars represent 95% confidence intervals.

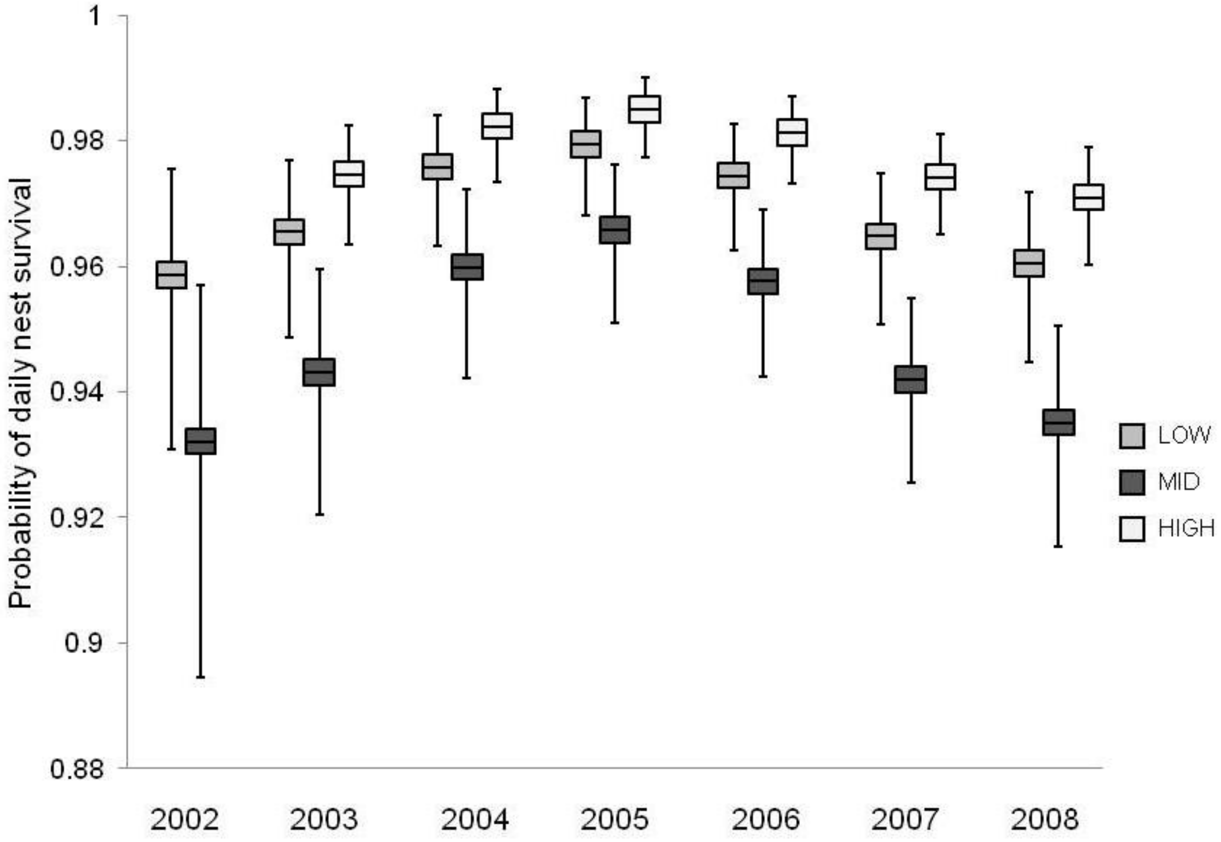

Figure 3.7. Probability of daily nest survival across sites and years. Error bars represetn 95% confidence intervals.

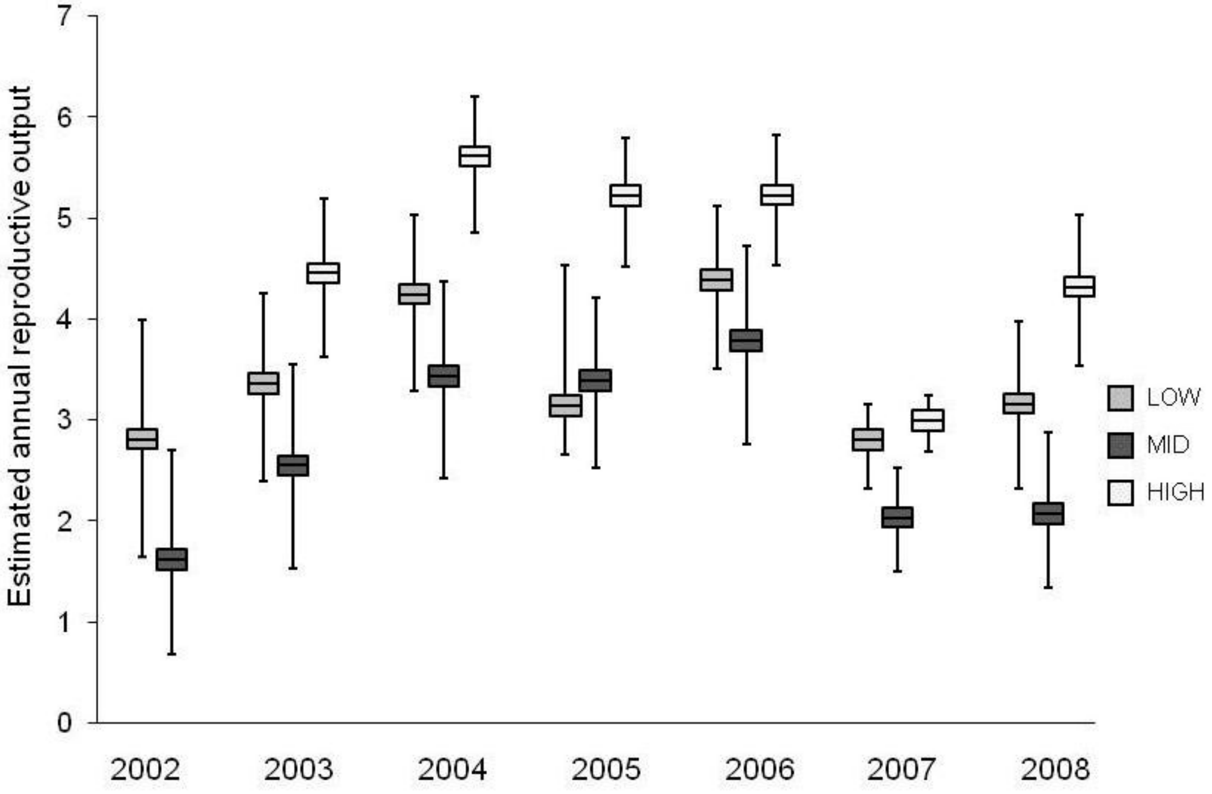

Figure 3.8. Estimated annual reproductive output per breeding pair, across all sites and years. Error bars represent 95% confidence intervals.

CHAPTER 4

AGE STRUCTURE IN A DECLINING HABITAT: DO OLDER BIRDS REFLECT BETTER HABITAT?[1]

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[1] Stodola, K.W. and R.J. Cooper. To be submitted to *Auk*

ABSTRACT

Evaluating habitat quality requires an understanding of how organisms select habitat and are distributed across the landscape. Current theory suggests that the distribution of older individuals should be a good means of assessment, because older more dominant individuals often sequester the best areas or territories, and preclude younger individuals from these areas. The relationship between habitat quality and age structure has been investigated many times and the predictions have mainly held. However, age structure has rarely if ever been investigated in habitat that is changing in quality. We show how age structure of a population can be older in habitat that is declining in quality for species that exhibit high degrees of site fidelity. We begin with a conceptual argument demonstrating how this distribution would occur and then follow with empirical evidence from a population of Black-throated Blue Warblers (*Dendroica caerulescens*) where habitat quality has recently been altered by an exotic invasive species. Changes to the physical make up of the forest at one of our long-term study sites led to a significantly older age structure during the period when habitat declined the fastest. This finding was in contrast to many different indices indicating habitat quality was greater elsewhere, yet where age structure was younger. We point out how an older age structure in habitat that is declining may be fairly common and also point out how this can influence measures of individual fitness, which is what habitat evaluation should ultimately rest upon.

INTRODUCTION

Evaluation of habitat quality is basic to the study and application of ecology and requires an understanding of how organisms select habitat and are distributed across the landscape. Differences in habitat quality stem from the variability in biotic and abiotic conditions, which can influence an organism's fitness (Block and Brennan 1993). Thus, many different factors influence habitat selection (Cody 1985), but the process should ultimately lead to individuals occupying areas most suitable to their needs. Fretwell and Lucas (1970) formalized this relationship with the ideal free distribution, in which individuals first select the highest quality habitat and then settle into areas of lesser quality as population density increases and fitness decreases. Inter- and intra-specific competition will not only influence the distribution of a species (Svärdson 1949) but the relationship between habitat and fitness (Sillett et al. 2004, Wilkin et al. 2006, Skagen and Adams 2010).

Habitat quality is often evaluated based on the models of habitat selection put forth by Fretwell and Lucas (1970). Under these models, habitat quality is related to the fitness of an organism, with organisms distributing themselves in a manner that maximizes their fitness. However, evaluating habitat quality based on detailed demographic work that evaluates fitness is time and energy intensive and other methods are sought (Johnson 2007). Population density is often used in lieu of detailed demographic information because higher quality areas should be preferred, leading to greater population density (Van Horne 1983, Bock and Jones 2004, Johnson 2007). Bock and Jones (2004) investigated the support for this relationship and found that greater recruitment per capita and greater recruitment per unit of land area were associated with greater density in 72% and 85% of all studies respectively. However, population density is not always correlated with fitness (Van Horne 1983), and this appears to be especially problematic in habitats altered by anthropogenic processes (Kristan 2003, Battin 2004, Bock and Jones 2004).

Other means for evaluating habitat quality have been sought as a result of the conflicting information concerning population density and habitat quality. The ideal despotic distribution is an extension of the ideal free distribution in which highest quality habitat is selected and occupied first, precluding others from the area (Fretwell and Lucas 1970, Pulliam and Danielson 1991). It has long been noted that older and more dominant individuals are better at sequestering territories in higher quality sites (Noble 1939). Therefore, dominant individuals should be more numerous in higher quality habitat, and this relationship has been well documented (Holmes et al. 1996, Petit and Petit 1996, Marra 2000, Fernandez and Lank 2006). Consequently, age structure of a population may be a useful means of assessing habitat, assuming an established despotic distribution exists and age is correctly identified at appropriate times (Johnson 2007). However, age ratios have rarely, if ever, been studied under conditions of habitat change.

Habitat characteristics of an area are always changing through succession processes, even when not affected by human disturbance, and bird species and communities respond to these changes. For instance, change in a mature hardwood forest is often a slow process, yet noticeable shifts in bird abundance are apparent when viewed over decades of change (Holmes and Sherry 2001). A faster response is observed when fire is removed from longleaf pine (*Pinus palustris*) systems; some species can decline rapidly and community composition is quickly changed (Engstrom et al. 1984). A similar response is observed in regenerating clearcuts where shrubland species may only be present for less than 20 years, with many species only being abundant in 10 of those years (Schlossberg and King 2009). Clearly, changes in habitat quality affect the distribution and abundance of species as expected. Current theory also suggests similar patterns in the age structure of a population. Yet, how age structure of a population changes under conditions of habitat change is still relatively unknown.

We explore the use of age structure as an indicator of habitat quality under conditions in which habitat quality changes over time. We first present a conceptual argument that demonstrates how one may actually observe an older age structure in an area where habitat quality is in decline. We then present information on habitat quality and age structure for a long-distance migratory songbird in the southern Appalachians whose breeding habitat has changed because of the newly arrived invasive hemlock woolly adelgid (*Adelges tsugae*). The adelgid has decimated eastern hemlock (*Tsuga canadensis*) in this region, eliminating an important nesting substrate and altering habitat quality (Stodola Chapter 3). We show how site fidelity and habitat alteration interact to influence age structure and discuss the implications it may have for evaluating habitat quality. Finally, we predict how habitat change may influence age structure over different scales of interest.

CONCEPTUAL ARGUMENT

Many migratory passerines exhibit a high degree of breeding site fidelity (Greenwood and Harvey 1982), which influences the age structure of a population at a given site. Consider an area occupied by a migratory species that exhibits a high degree of site-fidelity. Territories in this area will be filled by those individuals that survive and return, along with new individuals settling into vacated territories created by individuals that did not survive or return. For simplicity, set the number of territories in this area at 10 and assume that the migratory species has a return rate of 50 percent. Under this scenario we would expect to observe five older returning individuals and five new breeders, presumably first-year breeders due to high site fidelity of older individuals at other locations. We would continue to observe this pattern as long as there was no change in the carrying capacity of the area, in site fidelity, or in survival of the species in question. Of course, this relationship is a simplified example, as landscape features and behavioral characteristics will inevitably vary over time and abundance will fluctuate regionally.

Let us now consider an area with similar initial habitat quality to the one described above, but where quality and the number of territories diminish over time. This scenario could occur because of the introduction of an invasive pest, loss of a foundational species, successional changes, or climatic changes. If carrying capacity of this area declines by 20% from one year to the next, then the number of territories the area could hold would decrease from 10 to eight between years. However, we may still expect the same proportion of breeding individuals to return if site fidelity remains high. Thus, we would expect that five older individuals would return on average, with only three new breeders able to settle into the remaining available territories. Consequently, if we were to assess habitat quality using age structure as our metric, we would observe ~62% older individuals. In comparison to the unaltered location described in the preceding paragraph, with approximately 50% older individuals, we may conclude that habitat quality was greater at the altered location if age structure was the metric used to evaluate quality. Furthermore, because older individuals typically exhibit greater reproductive success and survival (Lack 1966, Clutton-Brock 1988, Newton 1989, Martin 1995), estimates of population fitness may be greater at the altered site as well. This scenario is illustrated in Figure 4.1 and we follow with a field study that demonstrates this phenomenon in a long-distance migratory songbird.

METHODS

Study species.– We investigated the breeding demography and behavior of the Black–throated Blue Warbler (*Dendroica caerulescens*) between the years 2002 – 2008. The Black-throated Blue Warbler is a small insectivorous Nearctic-Neotropical migrant that winters in the Greater Antilles and breeds from the southern Appalachian Mountains of Georgia northward to southern Canada (Holmes et al. 2005). Inter-annual site fidelity in this species is high and males defend non–overlapping territories (Holmes et al. 2005), typically remaining in these territories for the duration of the breeding season (Stodola *personal observation*). The sexually–dichromatic Black–throated Blue Warbler builds its nest in the understory, with most nests being found between 0.95 – 1.30 m high (Stodola et al. 2010).

Field site.– Our study area was located within the Nantahala National Forest in the southern Appalachian Mountains, Macon County, North Carolina (35° 07' N, 83° 31' W). The vegetative composition of this forest is dominated by cove hardwood and northern hardwood forest vegetation (Day et al. 1988), with an understory dominated by *Rhodendron maximum* and *Kalmia latifolia* (Day and Monk 1974). We established three study plots in this area at approximate elevations of 1050m (LOW), and 1200m (MID), and 1350m (HIGH) with all three study plots being located within 15 km of one another. The LOW and MID elevation sites were established in 2002, while the HIGH elevation site was added in 2003. The time frame of our study happened to coincide with the advancement of the hemlock woolly adelgid (*Adelges tsugae*) into the region, with it being first detected in Macon County in 2001 (USFS 2009). The hemlock woolly adelgid is an introduced aphid-like insect that can quickly defoliate and kill eastern hemlocks (*Tsuga canadensis*) soon after infestation (Nuckolls et al. 2009), and it can change the functional characteristics of a forest (Orwig and Foster 1998).

Habitat quality.– We evaluated habitat quality among sites using a number of different habitat and demographic metrics. First, we evaluated the structural vegetative characteristics of the three sites, because habitat quality for the Black-throated Blue Warbler is related to the density of understory shrubs (Holmes et al. 1996). Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. At each location we counted the number of woody saplings (3-10 cm in diameter at breast height) and woody shrub stems (< 3 cm in width, > 0.3 m in height) within a 3 m circular vegetation plot. We highlight *Rhododendron maximum* in the results, because it is the preferred nesting substrate of the Black-throated Blue Warbler at our study area (Stodola Chapter 3). Second, we estimated food differences among sites by counting Lepidoptera larvae, which constitute the majority of prey items fed to nestlings (Goodbred and Holmes 1996, Stodola unpublished data). We conducted three bi-weekly samples during the period when Black-throated Blue Warblers were provisioning young (the beginning of June, middle of June, and beginning of July). Each sample consisted of approximately 80 locations per site distributed across four parallel 500 m transects. At each location we conducted two counts, each of 50 leaves, where we counted clinging larvae on three of the most ubiquitous understory saplings, American chestnut (*Castenea dentata*), red maple (*Acer rubrum*), and northern red oak (*Quercus rubra*).

Demographic indicators of habitat quality.– We monitored nest survival at all three sites to attain an index of predation pressure. Nests were monitored every 2 – 4 days to ascertain the date of clutch initiation, clutch size, start of incubation, hatching date, and number of young fledged. We used parental behavior to ascertain fledging status if fledglings were not seen and assumed fledging had occurred if parents were seen carrying food or were agitated at the presence of an observer for an extended period of time (>10 min). Unsuccessful nests were determined by loss of nest, eggs, or nestlings prior to day 8 (hatch day = day 0) of the nestling cycle, which is the earliest Black-throated Blue Warblers fledged young during the course of this study. We estimated breeding season length to determine difference in habitat quality among sites under the assumption that a longer breeding season relates to higher quality habitat. Breeding season length was estimated as the difference in days between the laying dates of the first five nests attempted and fledging dates of the last three nesting attempts per year (e.g. Marshall et al. 2002), plus 25 days, which corresponds to a clutch size of four, an incubation period of 12 days, and a nestling period of nine days. Finally, we estimated annual reproductive output (ARO) per pair for each study site using the Farnsworth-Simons model (Farnsworth and Simons 2001, 2005). We caution the reader that this model may overestimate ARO, especially at lower levels of ARO, and may not be an exact representation of population health (Jones et al. 2005a, b). However, the model exhibited a strong positive relationship with observed ARO for a population of Black-throated Blue Warblers in New Hampshire (Jones et al. 2005a, b).

Territoriality and Age structure. – To facilitate territory mapping and location of breeding males, we gridded each study plot by flagging trees every 25 or 50 meters. This grid was then superimposed onto a topographic map of the study area where we marked territory observations. We used targeted mist-netting and call playback to capture and band territorial males. We aged all males using unique plumage characteristics that are diagnostic of second year birds (SY – second year, or first breeding season) in comparison to older individuals (ASY – after second year) which have experienced at least one previous breeding season (Holmes et al. 2005). We gave each male on each plot a unique color band combination that allowed us to follow them throughout the breeding season and to delineate territory boundaries. We also visited each plot nearly every day, which allowed us learn individual territories and territory boundaries. Thus, we feel confident that we located and mapped all individual territorial males within the study sites.

Statistical analyses

We estimated Lepidoptera larvae abundance at a site by fitting a repeated measures generalized linear model with a Poisson distribution and log link. We controlled for year, sample, and tree species by including them as fixed effects and the repeated measure was necessary to control for the replicate counts at a location. We estimated daily nest depredation rates for each site using the logistic exposure method (Shaffer 2004) and included year as a fixed effect. The last day the nest was observed active was used to calculate exposure days for nests with uncertain fates (Manolis et al. 2000). Breeding parameters of interest (Farnsworth and Simons 2001, 2005) were estimated by fitting generalized linear models relating clutch size and fledged young per successful nest to site and year. We estimated time to renest in a similar fashion but included an additional predictor indicating if the attempt followed a successful or unsuccessful nest attempt. Clutch size and number of fledged young per successful nest were modeled using a beta-binomial distribution and the logit link in Proc Genmod (SAS institute 2007), where the maximum clutch size and fledged young were set to five. A Hosmer and Lemeshow goodness of fit test failed to indicate any lack of fit. Time to renest was modeled using a Poisson distribution and log link in Proc Genmod (SAS Institute 2007). We controlled for underdispersion of the data using the dscale option, which computes an additional scale parameter and adjusts the standard errors of the regression coefficients.

To incorporate the uncertainty in our demographic estimates we recalculated ARO under 10,000 Monte Carlo simulations where each iteration represented a random draw from the normal distribution with the mean and standard error coming from the untransformed model-averaged beta estimates for the respective parameter of interest: clutch size, number of fledged young per successful nest, time between breeding events, and daily probability of nest survival. The randomly generated beta estimate was then back-transformed and used in Monte Carlo simulations for estimating ARO. Simulations were performed using the POPTOOLS add-in for Microsoft Excel. Interpretations of vegetation differences among sites were performed using 95% confidence intervals approximated using the normal distribution and interpretation of ARO differences were performed using the Monte Carlo 95% confidence intervals (Gerrard et al. 1998, Johnson 1999). Finally, we tested for difference among sites in the proportion of ASY males during the period of hemlock decline (2004-2007) using a Cochran-Mantel-Haensel test, to control for year specific effects.

RESULTS

Habitat quality.– Vegetation characteristics differed among the three study sites with understory vegetation generally increasing with elevation. Sapling density (95% confidence interval) was slightly greater at the HIGH site with 6.9 (4.7, 9.0) saplings per 3 m radius vegetation plot, in comparison to the MID and LOW sites, 6.3 (4.1, 8.4), 5.3 (3.3, 7.3) per 3 m radius vegetation plot respectively. This relationship was most notable with *R. maximum* (Figure 4.2a). Average shrub density (95% confidence interval) was much greater at the HIGH site in comparison to the MID and LOW sites, with 51.5 (37.2, 65.7), 34.2 (26.2, 42.1), and 37.9 (28.6, 47.2) shrubs per 3m radius vegetation plot at the HIGH, MID, and LOW sites respectively. Woody stems of *R. maximum* increased with elevation as well (Figure 4.2b). Lepidoptera larvae availability increased with elevation at the time adults were provisioning young (Figure 4.3).

Demographic indicators of habitat quality.– Breeding season length was approximately 10 days longer at the HIGH and MID sites in comparison with the LOW site (Figure 4.4). Nest depredation was least frequent at the HIGH site, followed by the LOW and MID sites (Figure 4.5). Estimates of ARO indicate that 0.4 more young were produced per pair at the HIGH site in comparison with the LOW site, and 1.2 more in comparison with the MID site (Figure 4.6), probably because of the difference in nest survival among sites.

Territoriality and Age structure. – The density of singing males varied annually but fluctuated around 0.5 males per ha on the MID plot and 0.7 males per ha on the HIGH site over the seven-year observation period (Figure 4.7a). However, density at the LOW plot decreased by approximately 60 percent over the same time period from approximately 0.4 males per ha in 2002 and 2003 to approximately 0.1 in 2007 and 2008 (Figure 4.7a). The change in breeding density was also reflected in larger territory size for males at the LOW site (Figure 4.7b). The decline in breeding abundance beginning in 2004 coincided with a decrease in the proportion of nests placed in eastern hemlock at the LOW site (Figure 4.8). The breeding season of 2004 also coincided with the first year where we noticed differences in the proportion of older males among the three study plots; this trend continued throughout the period of hemlock decline, 2004-2007 (Figure 4.9). During this period, the proportion of ASY males at the LOW study site was significantly greater than that observed on the MID and HIGH sites ($X^2_{\mathrm{cmh}} = 7.71$, P=0.021). By the end of 2007, nearly all eastern hemlocks were defoliated and the number of territorial birds changed little at the LOW site between 2007 and 2008. Coinciding with this observation, the proportion of ASY males decreased at the LOW site to levels previously observed at the other study sites.

DISCUSSION

In this study we provide a conceptual argument describing how age structure can be a misleading indicator of habitat quality, and provide an example that supports our argument.

Several direct measures of habitat quality (vegetation characteristics, food availability, and population demographic characteristics) indicated that quality was greatest at the HIGH site, yet we did not observe an older age structure as would be predicted under the ideal despotic distribution. First, previous studies indicate that habitat quality for the Black-throated Blue Warbler is related to the density of understory vegetation (Holmes et al. 1996), which increased with elevation at our study, most notably with *R. maximum* being most abundant at the HIGH site. Second, food availability was greatest and nest depredation lowest at the HIGH site, suggesting favorable bottom-up and top-down conditions. Third, breeding season length was greatest at the HIGH site, indicating favorable resource conditions over the entire breeding season. Finally, annual reproductive output was greatest at the HIGH site, suggesting that all these characteristics lead to greater fitness. However, while we believe habitat quality was greatest at the HIGH site, age structure of the population at the LOW site was skewed towards older birds during the period when habitat quality at that site was declining most quickly.

The vegetation characteristics of our sites not only contributed to differences in habitat quality but also determined the influence that the hemlock woolly adelgid and loss of hemlock had on Black-throated Blue Warblers. *R. maximum* is most ubiquitous at the HIGH site, and consequently the high site has the best vegetation structure. However, in comparison to the HIGH site, *R. maximum* is restricted to cool wet areas near ephemeral springs and creeks at the LOW site. Consequently, Black-throated Blue Warblers at the LOW site must utilize other nesting substrates. Eastern hemlock was a commonly used alternative nesting substrate, as its abundance in the understory was much greater at the LOW site in comparison to the MID and HIGH sites (Stodola Chapter 3). Furthermore, the proportion of nests placed in hemlock is much greater at the LOW site in comparison to the other two sites. This proportion was most pronounced in the first two years of our study in which approximately 50% of all nests at the LOW site were placed in hemlock. The introduction of the adelgid altered the availability of hemlock and the proportion of nests placed in hemlock dwindled to only 10% in the last few years of our study, with these being mainly dead to dying saplings. Yet, with this decline in habitat quality, we observed a greater proportion of older birds settling and breeding at this site.

Theory of habitat selection and our basic understanding of social dominance hierarchy suggests that age structure of a population should be a good indicator of habitat quality (Fretwell and Lucas 1970, Pulliam and Danielson 1991, Johnson 2007), yet we illustrate that this may not always be the case. Over the course of our study, the adelgid eliminated most of the hemlock and led to a decrease in the breeding density of Black-throated Blue Warblers at the site where hemlock was an important breeding substrate. Similar declines in abundance did not occur at the other two sites where hemlock was less important, which suggests that the decline in habitat quality was not a region-wide phenomenon. Because hemlock was an important breeding substrate at the LOW site, returning individuals needed access to additional areas and increased territory size to compensate. In addition, other areas were less favorable due to hemlock loss and scarcity of other suitable nesting substrates, leaving first-year breeders with less available area to settle in. Consequently, we observed an older age structure at our LOW site where habitat quality was the least favorable.

The high degree of breeding philopatry in the Black-throated Blue Warbler led to our observation of an older age structure in lower quality habitat. In many species, site fidelity is related to breeding experience in the previous year, with birds that breed successfully returning the following year (Greenwood and Harvey 1982, Hoover 2003, Porneluzi 2003, Sedgwick 2004). Because returning birds have the advantage of familiarity with food resources and refuges from predators (Greenwood and Harvey 1982), fitness benefits may accrue (Blancher and Robertson 1985, Desrochers and Magrath 1993, Hoover 2003) that override other consequences associated with habitat change. While we observed a change in habitat conditions, the change mainly occurred in the loss of breeding substrate and not in the conversion or alteration of the structural make-up of the forest, as hemlock was loosely scattered throughout the plots in small saplings to trees. The loss of hemlock did not alter resource availability nor nest depredation rates, and breeding success remained relatively constant (Stodola Chapter 3). Therefore, adults returned to breed at similar proportions across sites, even though habitat quality from the perspective of the population was changing.

Habitat quality differs between the individual- and population-levels (Pidgeon et al. 2006), which can influence the evaluation of habitat quality. Assessing habitat quality is a critical but difficult proposition that would ideally incorporate the demographic characteristics of a population (Battin 2004, Johnson 2007). Yet, fecundity or survival estimates of a population may be influenced by its age structure, as older birds exhibit greater reproductive success and survival (Lack 1966, Clutton-Brock 1988, Newton 1989, Martin 1995). Older birds, if more prevalent in declining habitat, may skew the estimates of demographic parameters of the population higher. Our own estimates of reproductive output and survival at our LOW site (i.e. lower quality habitat), where habitat quality was declining, were very similar to that observed at our HIGH site (i.e. greater habitat quality) where we deemed habitat quality to be greatest.

The habitat quality of the area we surveyed likely declined because the adelgid eliminated hemlock over the course of a few years (Nuckolls et al. 2009), the rapidity of which may be similar to other systems. In many respects the pattern we observed in habitat change is similar to change in habitat for species that rely on early successional vegetation. Species that breed in these areas respond rapidly to vegetation changes, with changes in abundance and distribution being observed over a period of a few years (Engstrom et al. 1984, Schlossberg and King 2009). Because these species exhibit similar rates of site fidelity to those that inhabit mature forests (Schlossberg 2009), we predict that the age structure of birds in regenerating habitats would be older as successional changes occur. This could influence estimates of population demography and lead to erroneous assessments of habitat quality, a situation similar to what we observed.

The prediction of an older age structure associated with declining habitat could also be extended to reflect perceived habitat changes associated with perturbations that occur over larger scales such as those associated with climate change. For instance, the phenology of spring events have recently been advancing (Menzel and Fabian 1999, Schwartz and Reiter 2000, Parmesan and Yohe 2003), which may change the perception of habitat quality for migrating individuals. If first-year breeding individuals arrive on the breeding grounds and are greeted by vegetation that is advanced beyond what they prefer they may elect to continue travelling, as demonstrated by Studds et al. (2008). This could lead to noticeable northward shifts in the geographic distribution of many species due to recent climatic changes (Parmesan and Yohe 2003, Root et al. 2003). We therefore may expect to observe a younger age structure with increasing latitude, especially in abnormally warm years with advanced spring phenology. Graves (1997) investigated the age structure of the Black-throated Blue Warbler across eastern North America and found a greater proportion of older birds in the south with the age structure of populations becoming progressively younger at higher latitudes. While Graves (1997) surmised that this pattern was due to differences in habitat quality, our findings suggest this pattern may have been due to large scale movement of younger birds in response to spring phenology.

Developing a good indicator of habitat quality is often time and energy intensive. Alternative measures of assessment have been sought, mainly relying on density or abundance as a means of inferring habitat quality (Bock and Jones 2004). While this approach may often result in a correct assessment, density and abundance are not always an accurate reflection of habitat quality (Van Horne 1983, Bock and Jones 2004). Thus researchers have sought other indirect means of assessing habitat quality (Johnson 2007), which includes age structure. The pervading view, however, is that none of these metrics alone are a sufficient means of habitat assessment and must be combined with other measures, namely measurements of outright fitness (Battin 2004). Although there are likely few studies that document change in demography during habitat alteration, we were able to record population parameters during abrupt habitat change and point out a potential flaw in current habitat assessment procedures. As we show, outright fitness consequences may not be observed in a declining habitat because an older age structure of the population could potentially mask their estimation.

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Table 4.1. Number of color banded males on each plot in each year.

YEAR	LOW	MID	HIGH
2002	7	7	-
2003	11	15	25
2004	7	14	18
2005	6	15	14
2006	9	20	19
2007	7	20	22
2008	8	15	17

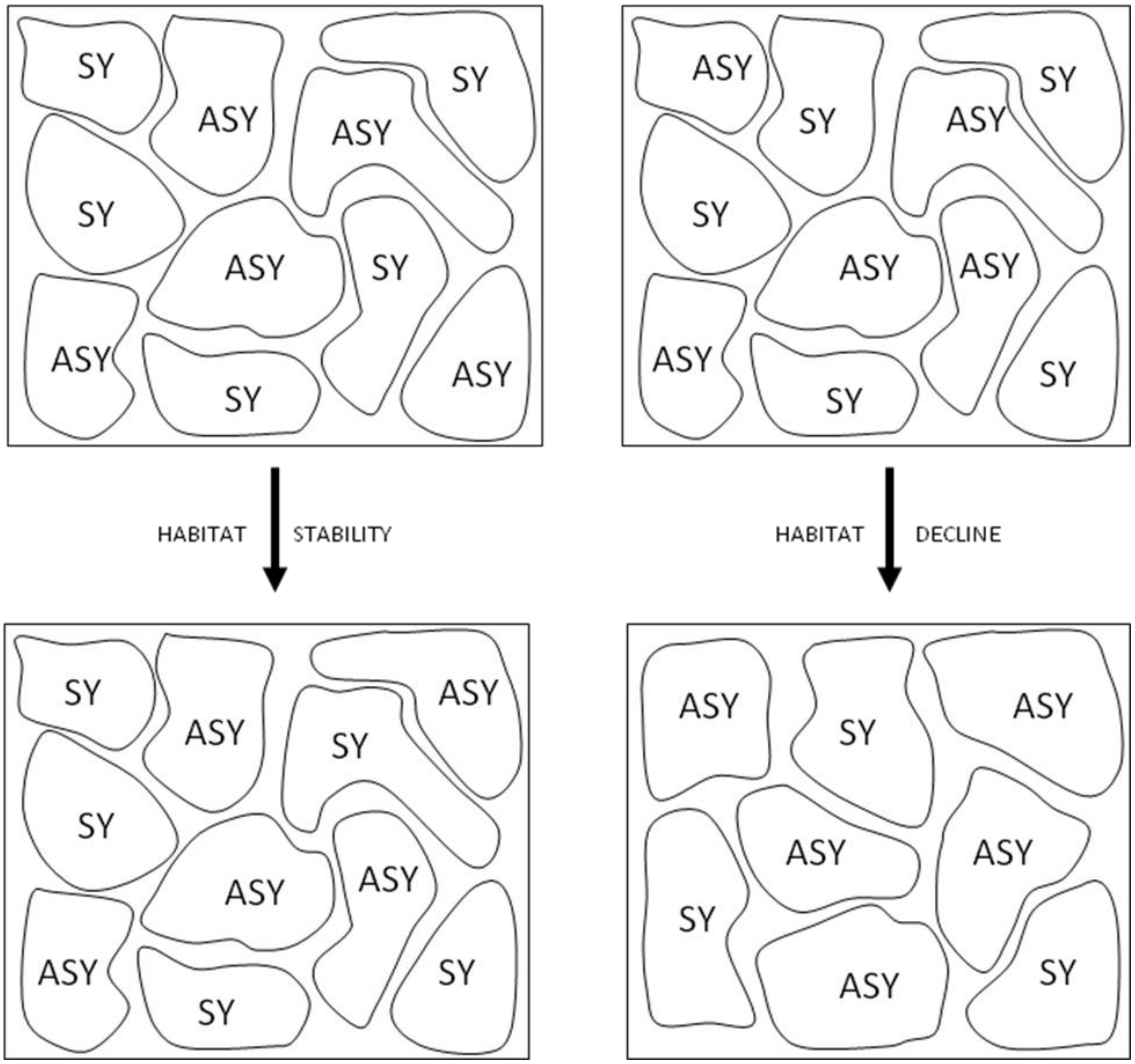

Figure 4.1. Age-structure for a migratory songbird in two similar areas where one declines in habitat quality by 20 percent or reducing carrying capacity by two territories. Age structure under habitat stability remains the same at 5 old to 5 young birds. Age structure under habitat decline will exhibit a greater proportion of older individuals 5 old to 5 young birds. ASY refers to After Second Year breeding adults while SY refers to Second Year breeding adults which represent their first breeding attempt.

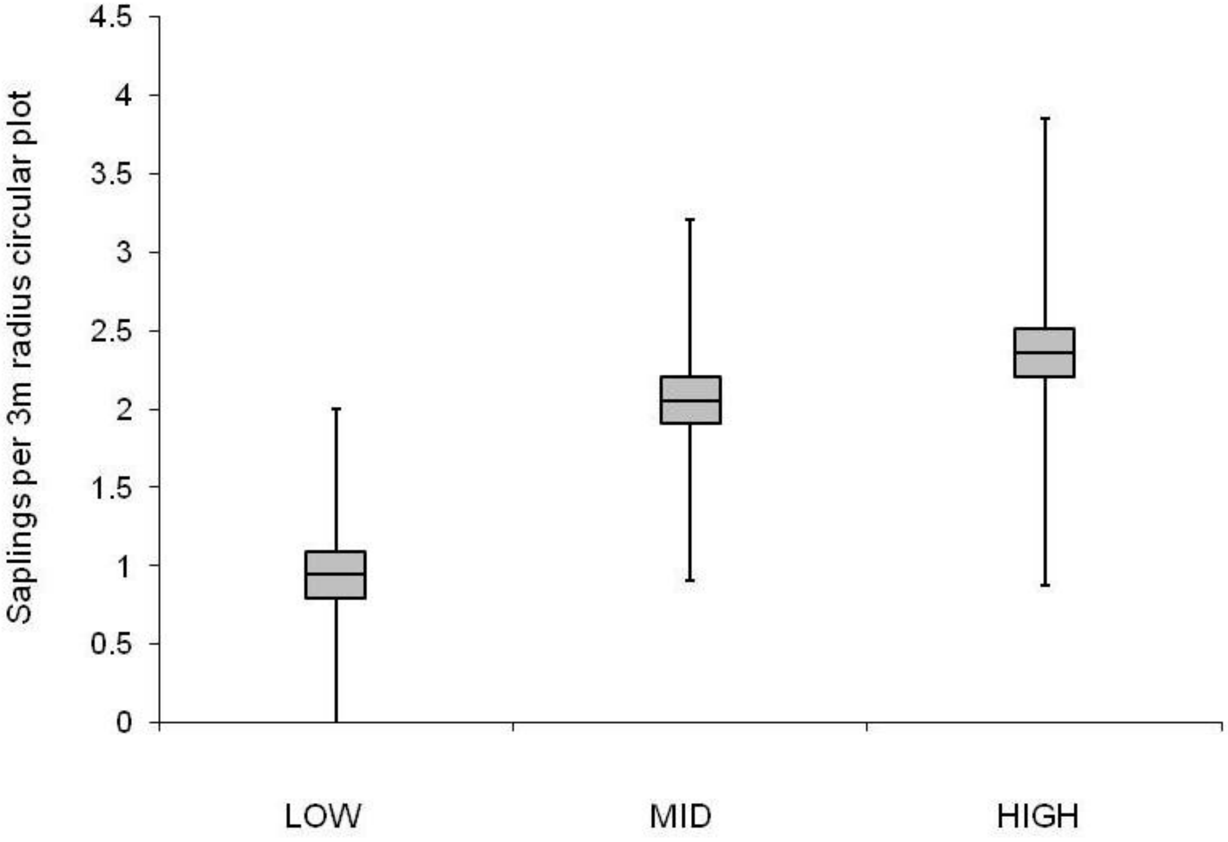

Figure 4.2a. Average number of *R. maximum* saplings (3 – 10 cm diameter at breast height) in 3 m circular vegetation plot across three study sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. Error bars represent 95% confidence intervals.

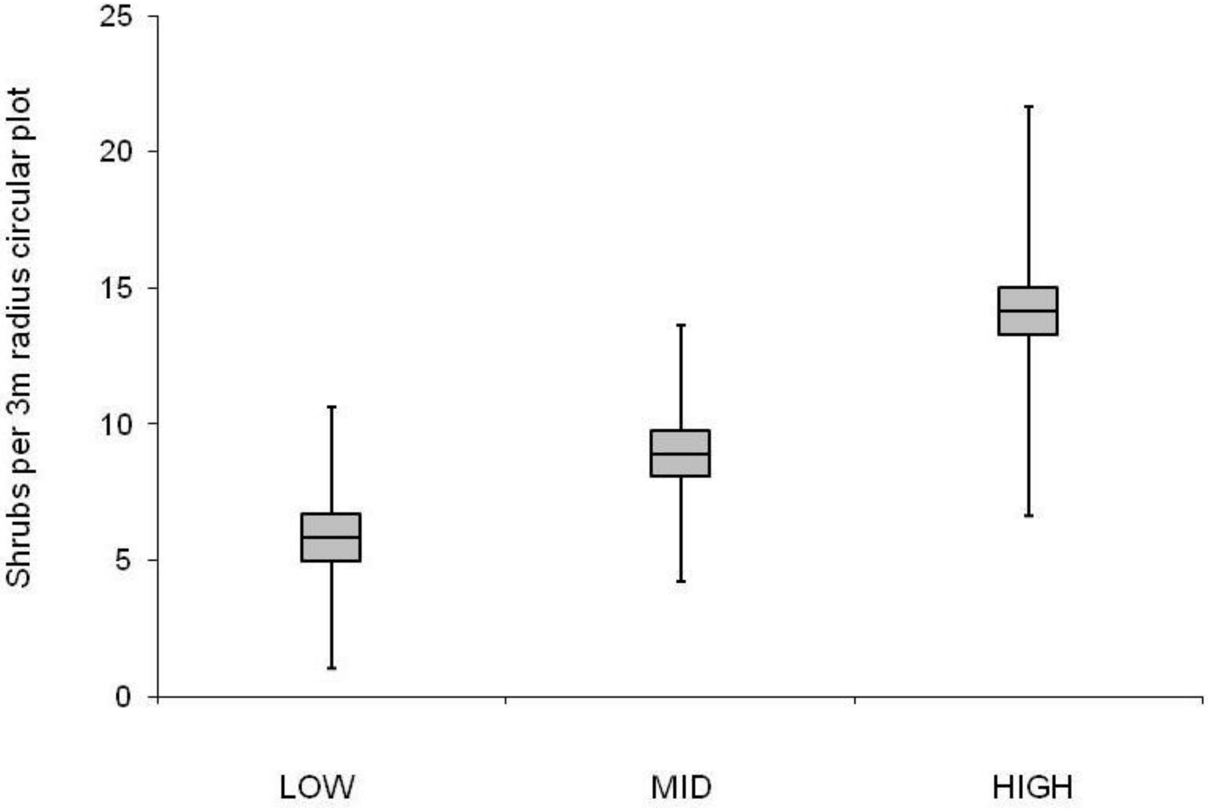

Figure 4.2b. Average number of *R. maximum* stems in 3 m radius circular vegetation plot across three study sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. Error bars represent 95% confidence intervals.

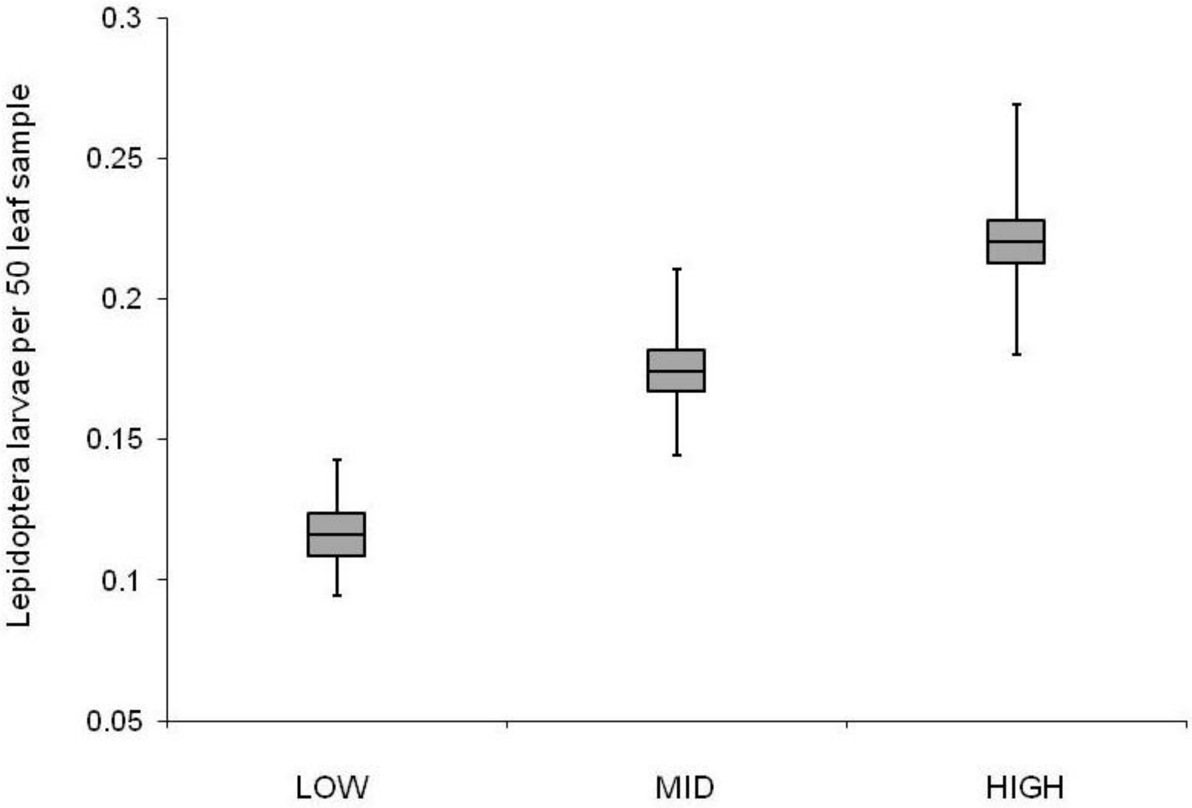

Figure 4.3. Lepidoptera larvae found per 50 leaf sample, controlling for tree species (*A. rubrum*, *Q. rubra*, and *C. dentata*), sampling period (beginning of June, middle of June, beginning of July), and year. Error bars represent 95% confidence intervals.

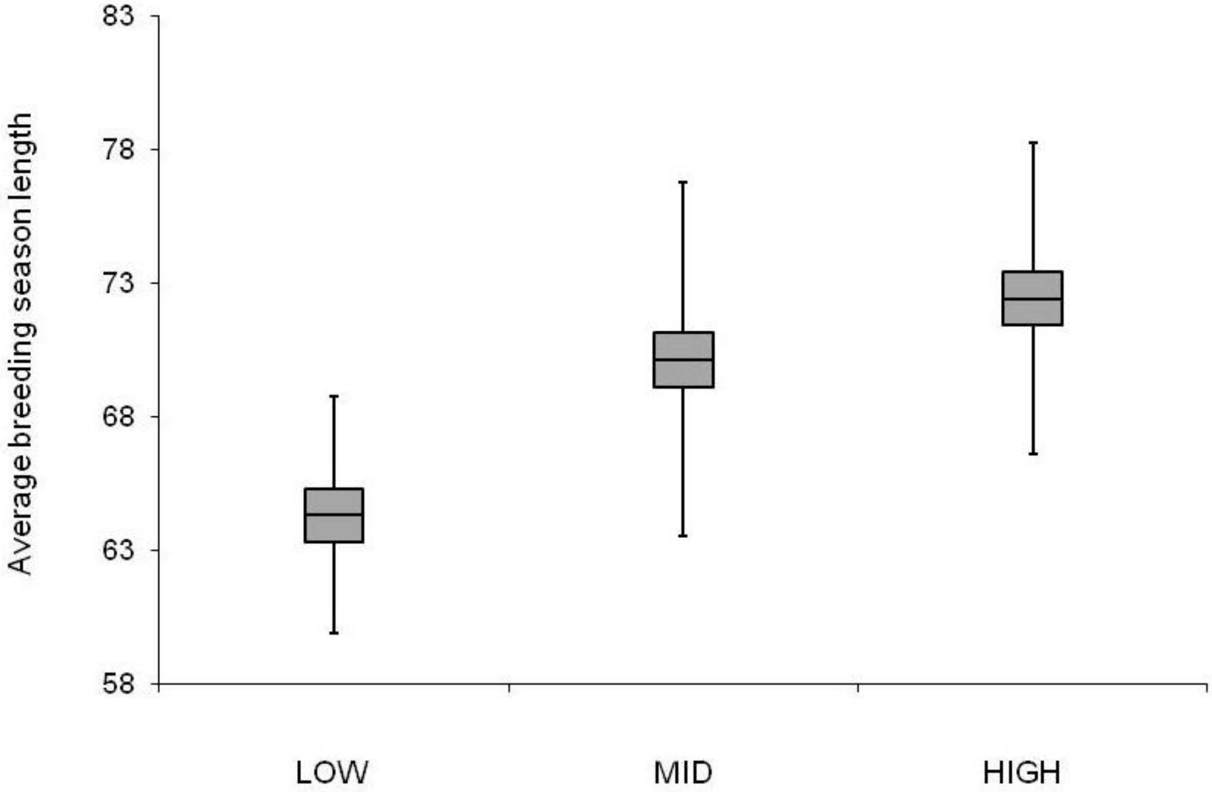

Figure 4.4. Average breeding season length at the three study sites between the years 2002 – 2008. Breeding season length was estimated as the difference between the average of first 5 nests initiated in a season and the average of the last 3 nests (e.g. Marshall et al. 2002). Error bars represent 95% confidence intervals.

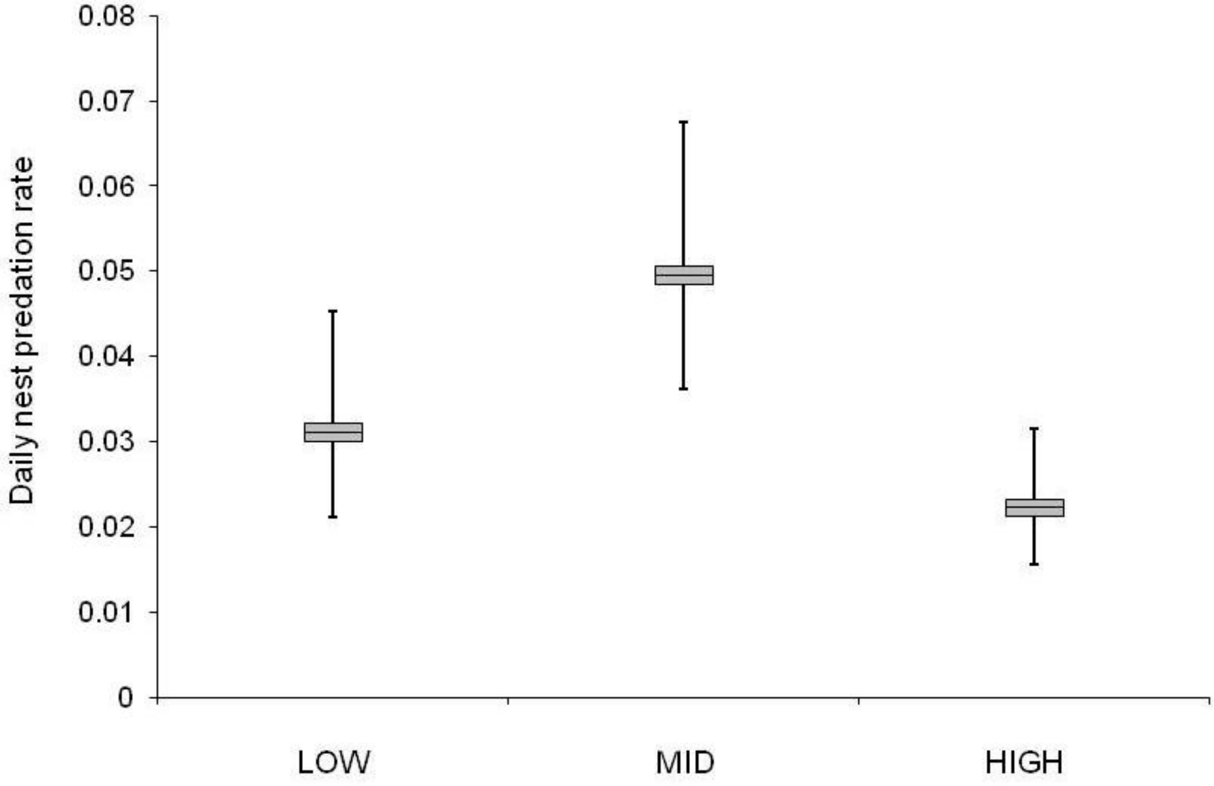

Figure 4.5. Daily nest depredation rates across the three study sites between the years 2002 – 2008. Error bars represent 95% confidence intervals.

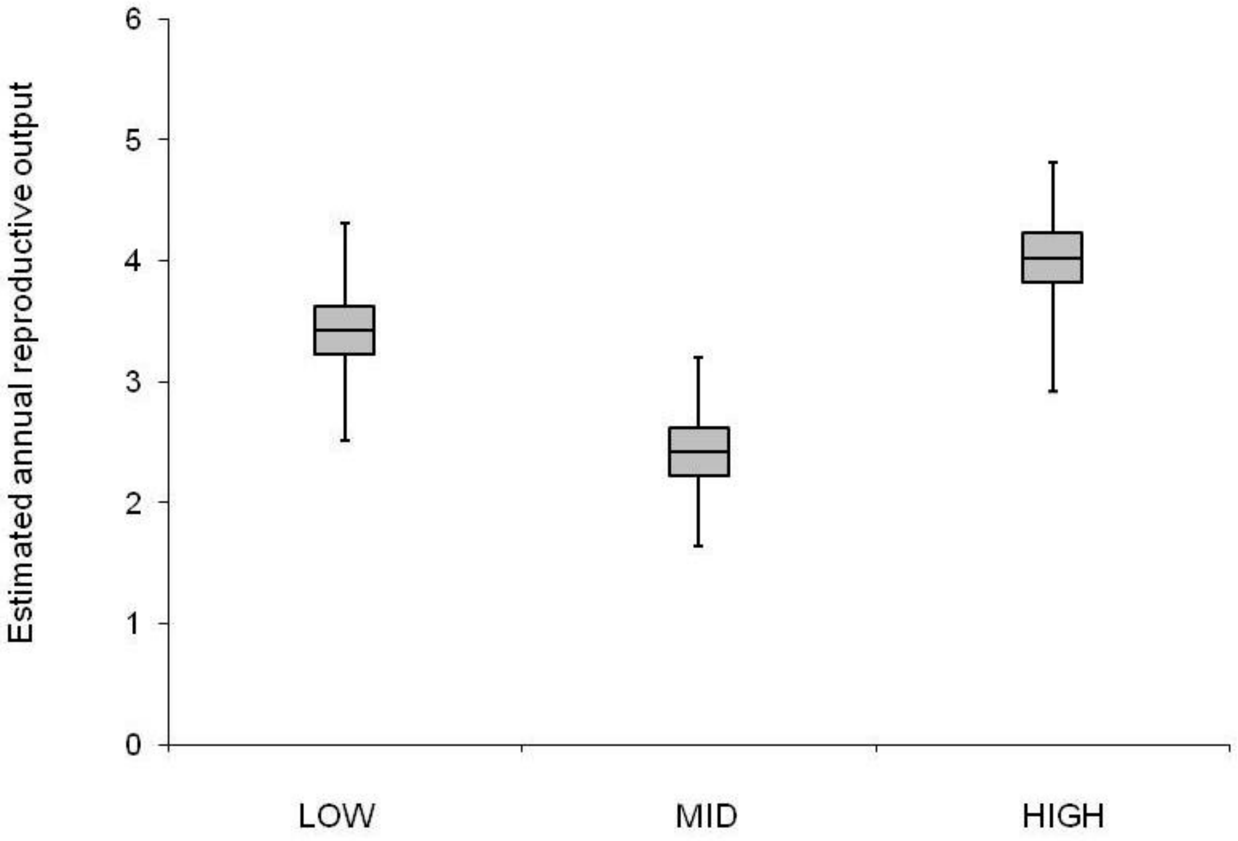

Figure 4.6. Annual reproductive output per breeding pair across the three study sites between the years 2002 – 2008. Error bars represent 95% confidence intervals.

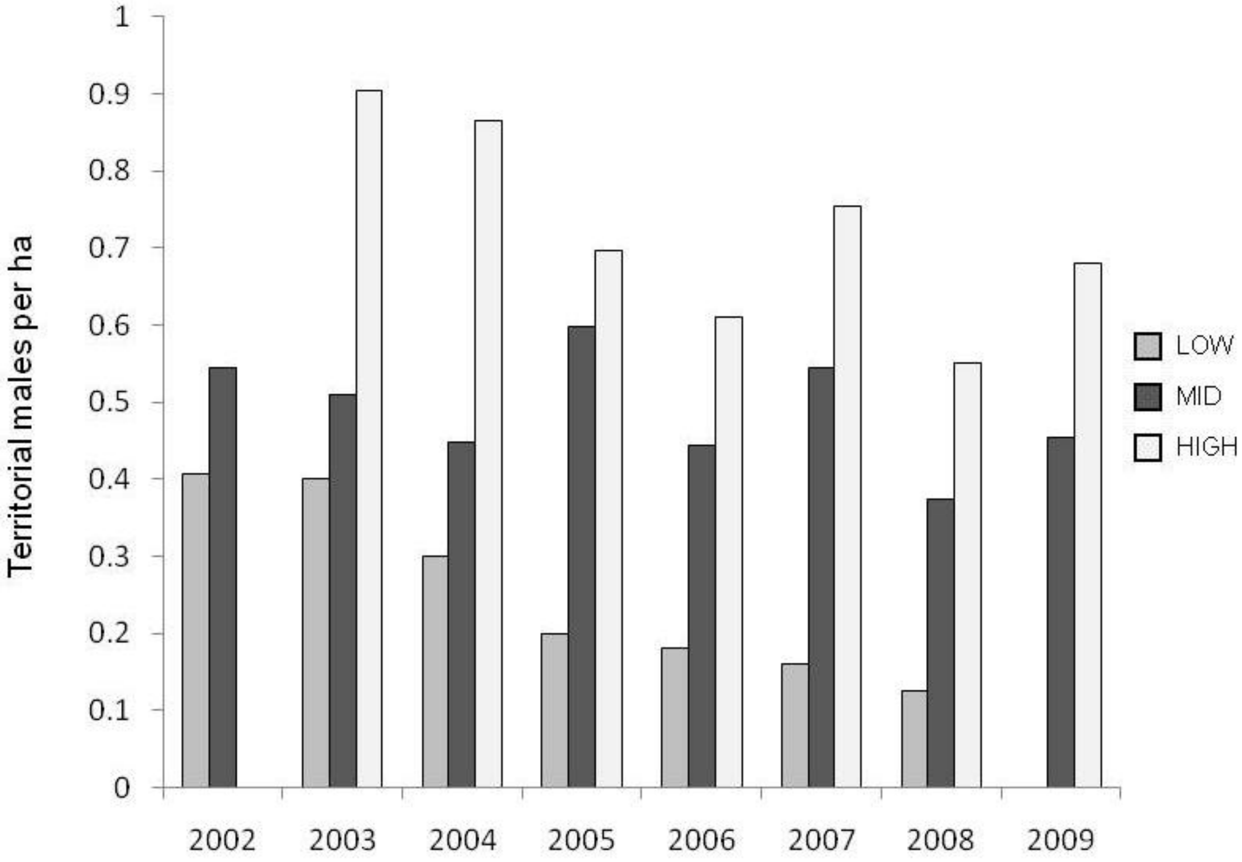

Figure 4.7a. Breeding density (males per ha) of Black-throated Blue Warblers across the three study sites and between the years 2002 – 2008, 2009 data is presented for comparison reasons, although no data extists for the LOW site.

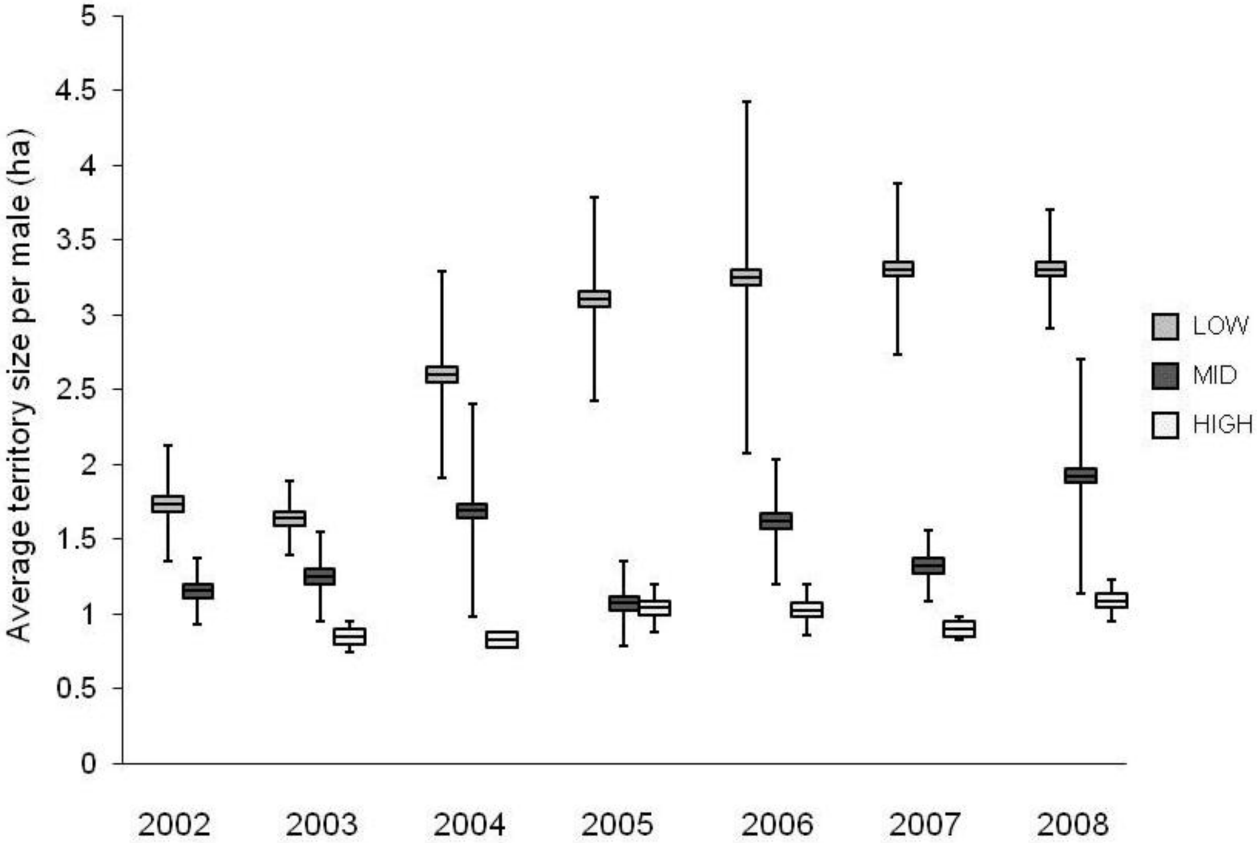

Figure 4.7b. Average territory size (ha) of Black-throated Blue Warblers across the three study sites and between the years 2002 – 2008. Error bars represent 95% confidence intervals.

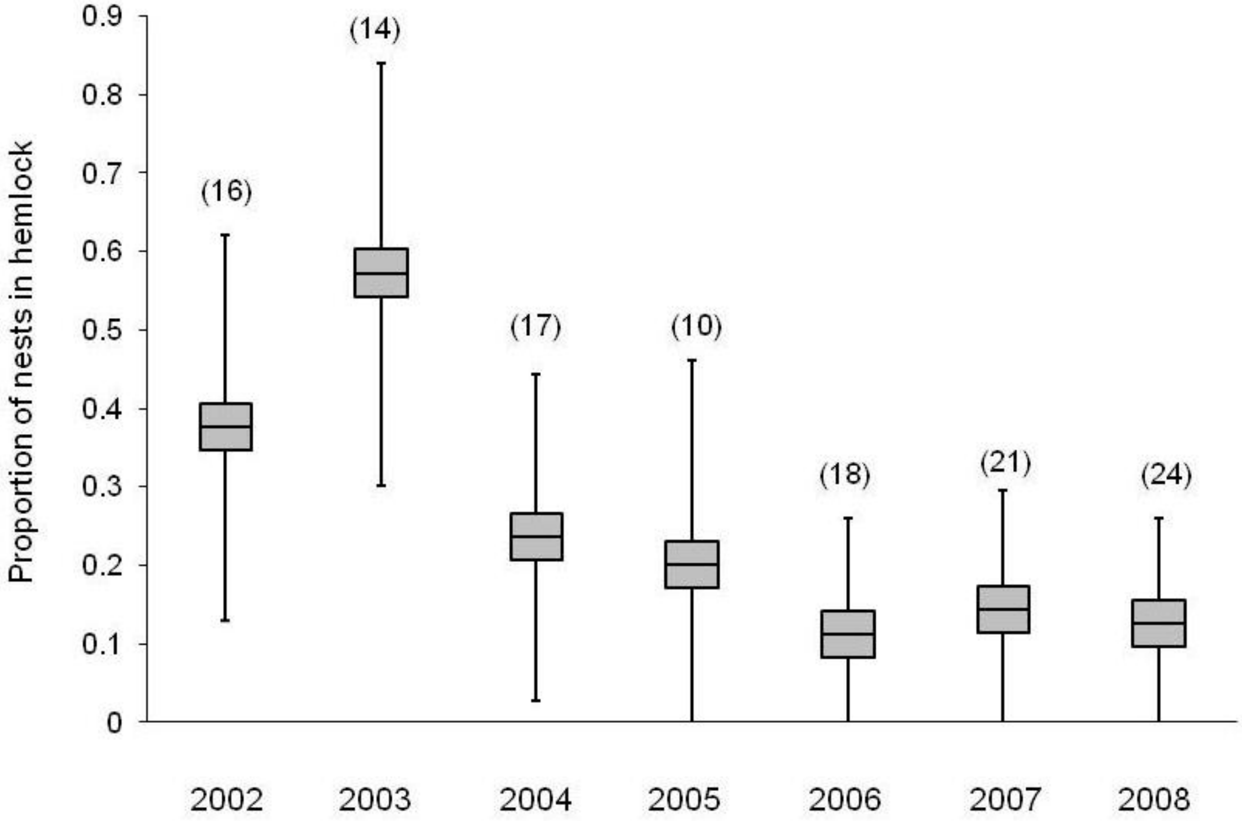

Figure 4.8. Proportion of nests placed in eastern hemlock at the LOW site between the years 2002 – 2008. Sample sizes are provided in parentheses and error bars represent 95% confidence intervals.

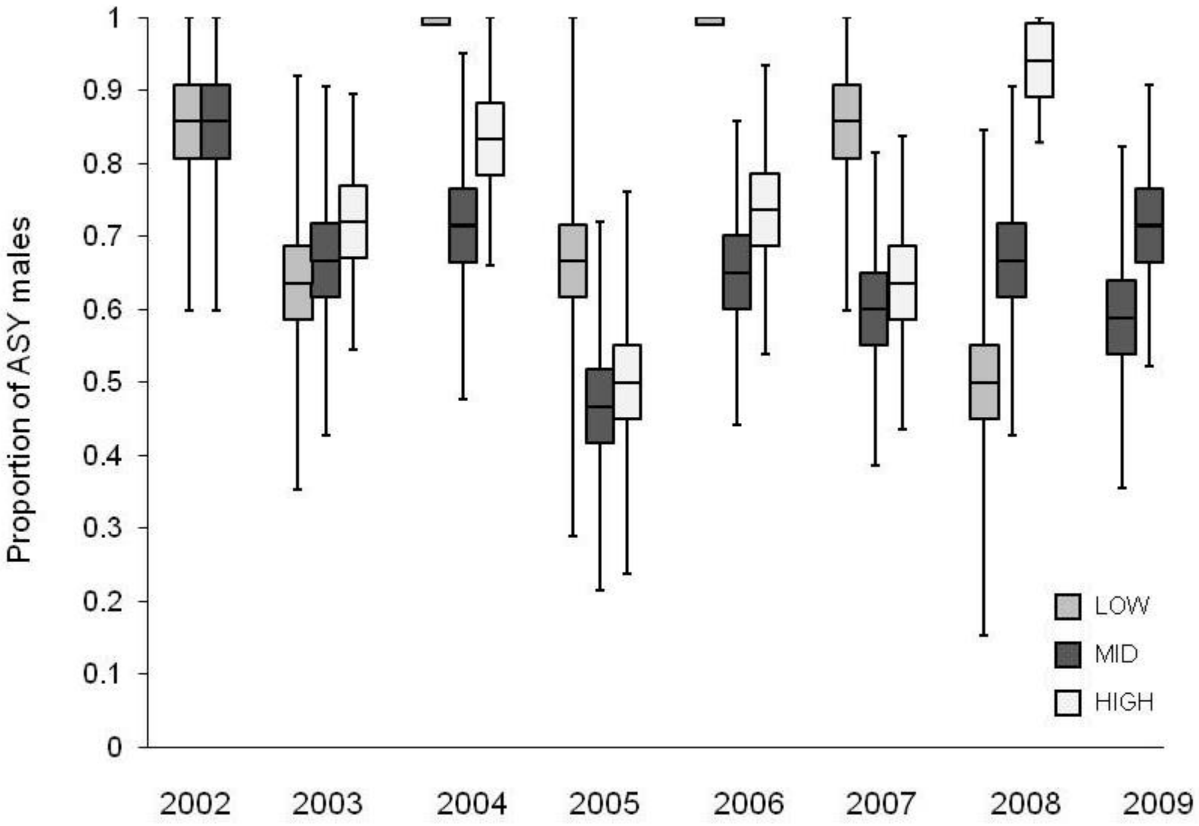

Figure 4.9. Proportion of after second year (ASY) breeding males in relation to first year breeding males (SY) across and the three study sites and between the years 2002 – 2008, 2009 data is presented for comparison reasons, although no data extists for the LOW site. Error bars represent 95% confidence intervals.

CHAPTER 5

CONCLUSION AND SYNTHESIS: UNDERSTANDING COMMUNITY AND POPULATION RESPONSE TO A CHANGING ENVIRONMENT

This dissertation focused on how a community of forest breeding birds and a particular member of that community are responding to recent climatic change and habitat alterations in the southern Appalachian Mountains of southwestern North Carolina. Long-term data indicate that temperatures have been steadily increasing in this area over the past few decades (Trenberth et al. 2007, Swift 2010). This region is located at the southern edge of Appalachian Mountain range and thus represents the southern terminus of the geographic range for numerous species. Because species are shifting their geographic distributions towards higher elevations and latitudes (Parmesan and Yohe 2003, Root et al. 2003) and this pattern is expected to continue (Iverson and Prasad 2002, Iverson et al. 2008, Leithead et al. 2010), the effects of climatic changes may manifest itself here first. In addition to recent climatic changes, the southern Appalachian Mountains have been subjected to numerous invasions of exotic pests and pathogens that have changed forest structure by decimating several foundational tree species (Liebhold et al. 1995, Rabenold et al. 1998, Koch et al. 2006). The recent invasion of the hemlock woolly adelgid (*Adelges tsugae*), which defoliates and kills eastern hemlocks (*Tsuga canadensis*), provided an opportunity to investigate the response of a forest breeding bird to the loss of this important forest community member.

COMMUNITY RESPONSE TO A CHANGING ENVIRONMENT

Climate change has the potential to alter habitat quality by shifting the geographic distribution of species (Iverson and Prasad 2002, Iverson et al. 2008, Leithead et al. 2010) and changing the seasonal phenology of life-history events, such as leaf-out (Menzel and Fabian 1999, Ibanez et al. 2010) and insect emergence and growth (Robinet and Roques 2010). These factors can disrupt the links between different trophic levels (Visser and Both 2005, Both et al. 2009, Walther 2010) with implications for species persistence (Møller et al. 2008). Long-distance migratory species appear to be most vulnerable to such changes, at least in Europe (Lemoine and Bohning-Gaese 2003, Lemoine et al. 2007, Both et al. 2010, Jones and Cresswell 2010). However, the same type of evidence was often lacking from North America and what was available was often equivocal (Valiela and Martinetto 2007, Jones and Cresswell 2010). In Chapter 2, I point out a potential reason for the discrepancy in evidence between North American and European breeding birds. I demonstrate that populations of long-distance migratory birds in eastern North America are disproportionately declining in comparison to short-distance migratory and resident birds, but only in more southerly portions of their geographic ranges. Therefore, studies that investigate many species over broad geographic scales may fail to observe this subtle response.

I conclude Chapter 2 by suggesting two potential mechanisms driving the disparate pattern in population trends of long-distance migratory species between southern and northern populations. The first mechanism is an ability to adjust the start of the breeding season to properly coincide with changing conditions on the breeding grounds. As I point out in Chapter 2, the failure to adjust the timing of breeding to coincide with peak breeding season resource conditions can lead to outright fitness consequences (Naef-Daenzer and Keller 1999, Thomas et al. 2001, Sanz et al. 2003), and population declines (Møller et al. 2008). However, northern populations may be better able to adjust to climatic changes if they exhibit greater phenotypic plasticity in response to climatic variability, which may be expected given their history with past climatic fluctuations (Charmantier et al. 2008). Thus, populations in the north may fare better in a changing climate in comparison to populations in the south, much like what we observed. The second mechanism dealt with the perception of habitat quality by breeding individuals. Climatic warming can lead to an advance in the timing of spring phenological events (Menzel and Fabian 1999) potentially causing migrating individuals to perceive habitat quality differently than they have in the past. If individuals are more likely to settle at higher latitudes that have more favorable spring phenology (Studds et al. 2008), then the disparate population trends we observed between geographic regions may reflect a unilateral movement of birds towards higher latitudes.

SPECIES RESPONSE TO A CHANGING ENVIRONMENT

The ability to observe the effects of environmental change on the geographic distribution of species and population persistence may depend on the nature of the change. For instance, distributional shifts and restructuring of forest assemblages under global climatic change may only be evident over long temporal scales. The ability to detect these changes on wildlife species generally requires long-term data sets. However, this may not be the case with the direct effects that invasive species can have on forest structure. Invasive exotic pests and pathogens, especially those that infect and kill foundation tree species, often alter the structure of a forest within a few years (McClure 1991, Liebhold et al. 1995, Ellison et al. 2005), similar to what we observed with the loss of eastern hemlock due to the invasive hemlock woolly adelgid. Therefore, how species respond to altered habitat quality due to invasive species and loss of foundational tree species may help reveal patterns concerning the potential impacts of global climate change.

We were presented with a unique situation in which we could monitor the loss of hemlock and how the Black-throated Blue Warbler (*Dendroica caerulescens*), a species not generally believed to be hemlock dependent, was affected. We observed this response on three study sites in the southern Appalachian Mountains. The time frame of our study coincided with the southward advancement of the hemlock woolly adelgid, with 2001 being the first year it was detected in the county where this research took place (USFS 2009). The adelgid quickly spread throughout this region, defoliating and killing hemlocks. We first observed it on our study sites in July of 2002 and by the end of 2007 nearly all hemlocks were defoliated or dead. We found that breeding density declined precipitously at one of the three study sites where hemlock was an important breeding substrate because it substituted for the more preferred *Rhododendron maximum.* This decline in breeding pair abundance, however, was not associated with any observable changes to individual measures of fitness (e.g., reproductive output or survival), or with emigration by breeding adults, as I point out in Chapter 4. Instead, the decline in abundance was likely caused by a reduction in first-year breeders settling at that site.

The manner in which the Black-throated Blue Warbler responded to the loss of hemlock may provide insight into population persistence in light of other habitat changes. Many migratory bird species, including the Black-throated Blue Warbler, exhibit high rates of site fidelity between years (Greenwood and Harvey 1982, Hoover 2003, Porneluzi 2003, Sedgwick 2004). If older birds return to areas where habitat is declining, they may alter the age-structure of the population in a way that is inconsistent with current theory (Fretwell and Lucas 1970, Johnson 2007). As I documented in Chapter 4, the age-structure of Black-throated Blue

Warblers at the one site where habitat changed the most was skewed towards older birds. Because older birds generally experience greater reproductive performance and survival (Lack 1966, Clutton-Brock 1988, Newton 1989, Martin 1995), per capita estimates of reproductive performance may actually be greater in areas of declining habitat. Therefore, these populations may persist for longer periods than would be expected given habitat quality.

BIOLOGICAL IMPLICATIONS

Understanding all facets of species ecology may provide a clearer picture pertaining to how they respond to a changing environment. As I demonstrated, populations of long-distance migratory species breeding at the southern edge of the Appalachian Mountain range have been declining over the past few decades, potentially in response to recent climatic changes. To date, most studies have focused on the fitness consequences attributable to climatic change, by pointing out the negative effects associated with the decoupling of breeding season demands and breeding season resource conditions (e.g. Thomas et al. 2001, Sanz et al. 2003, Visser and Both 2005, Walther 2010). However, as I demonstrate, outright fitness consequences may not always occur in habitat that is changing in quality. Instead population declines may be the result of a reduction in the immigration rate, especially by younger individuals. This may be especially prevalent for species that exhibit high rates of site fidelity, such as the Black-throated Blue Warbler and other long-distance migratory songbirds.

The older age-structure we observed in a population of Black-throated Blue Warblers in response to habitat decline was caused by the lack of first-year individuals settling in that area. In response to large-scale climatic change this behavior may induce a unilateral movement by young first-year breeding individuals towards higher latitudes. The shift in settling patterns would then support our findings that long-distance migrants are declining at the southern portions of the Appalachian Mountain range while remaining stable in the northern portions. Support for this unilateral movement of young birds may come from Graves (1997), who noted a greater proportion of older birds in the south with the age structure of populations becoming progressively younger with increasing latitude. While Graves (1997) surmised that this pattern was due to greater habitat quality in the south, this dissertation suggests the opposite pattern may be true. If climatic conditions have altered the perception of habitat quality by first-year breeding individuals, they may be more likely to continue traveling and settle in concert with local vegetation phenology, as demonstrated by Studds et al. (2008). Consequently, this would also corroborate evidence indicating that species are shifting their distributional ranges towards higher latitudes (Parmesan and Yohe 2003, Root et al. 2003), and provide a mechanism for why this is occurring.

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