INTRINSIC AND EXTRINSIC FACTORS THAT INFLUENCE FLEDGLING SURVIVAL OF A MIGRATORY SONGBIRD IN THE SOUTHERN APPALACHIANS

by

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(Under the Direction of Robert J. Cooper and Jeffrey Hepinstall-Cymerman)

ABSTRACT

The Black-throated Blue Warbler (*Setophaga caerulescens*) is a Neotropical migrant songbird that breeds in eastern North America. From 2011-2012, I examined fledgling survival and habitat selection for this species at the southern limit of its breeding range in the Nantahala National Forest, North Carolina, USA. I observed 222 uniquely-marked Black-throated Blue Warbler fledglings and collected data on habitat characteristics and food availability (larval insects). An interaction between fledge date and food was most important in explaining fledgling survival, indicating a potential sensitivity of survival to phenological mismatches caused by climate change. To investigate fledgling habitat use, I compared shrub density at fledgling locations with available habitat. Fledglings of older warblers were found in areas of greater evergreen shrub density than fledglings of younger parents. My results suggest that intrinsic individual qualities and extrinsic habitat characteristics can affect fledgling survival and should be simultaneously considered in future studies.

INDEX WORDS: Black-throated Blue Warbler, Fledgling survival, Habitat selection, Climate change

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INTRODUCTION AND LITERATURE REVIEW

Introduction and Literature Review

Global climate change

Annual average temperature has risen 2°F in the southeastern United States since 1970, and precipitation during summer months has decreased over nearly the entire region (Karl et al. 2009). Global climate change model projections show continued warming trends for the Southeast, with annual temperatures increasing between 4.5 and 10.5 °F by 2080 with the greatest increases occurring during the summer months (Karl et al. 2009). These changes are unparalleled in recent climate history, and will have a major influence on the distribution, abundance, and behavior of many species (Brown et al. 1999, Forchhammer et al. 2002, Parmesan and Yohe 2003, Saino et al. 2004, Both et al. 2006, Hitch and Leberg 2007, Balbontin et al. 2009). Furthermore, as overall temperature increases drive changes in timing of seasonal life-history events and distribution of geographic ranges for various species, it is likely that different species will not collectively adapt to changes at the same rates or magnitudes. Such mismatches in responses between trophic levels could lead to reduced reproductive fitness and survival of individuals and result in population declines (Walther et al. 2002). Long-term studies are needed to examine the effects of climate change on the fitness and survival of organisms and the mechanistic responses of individuals and species (Pearce-Higgins and Gill 2010). To date, very few studies have investigated such effects.

The implications of a changing climate are still largely unknown, because organisms, communities, and ecosystems will respond differently, and the degree of the response will also vary. Until recently, research of climate change effects on organisms has been largely restricted to localized areas, with regional studies mainly limited to the United Kingdom and Germany (Parmesan 2006). Even fewer of these studies have involved migratory birds, because it is often challenging to study these species across the range of an annual cycle that spans multiple continents. Limited information exists regarding the effects of global climate fluctuations on any one particular part of the annual cycle for most bird species, with few exceptions (Dunn and Winkler 1999, Both et al. 2006). Previous studies have highlighted variability in responses among avian species to climate change (Brown et al. 1999, Strode 2003, Both et al. 2006). Many species differ in dispersal abilities and probabilities of population extinctions and colonizations (Parmesan 2006). Furthermore, life-history strategies or constraints placed on migratory species at other times in their annual cycle could also confound the evolution of a uni-directional response to changes in habitat caused by global climate shifts (Both and Visser 2001, Studds and Marra 2007).

To determine the ability of an individual to respond to environmental changes, the mechanisms that influence such response must be understood first. A range of factors likely influences timing of migration and breeding for a variety of species, including both biotic and abiotic factors, such as the North American Oscillation (Forchhammer et al. 2002, Gordo et al. 2005). It is possible that climate change could directly shift timing of arrival on the breeding grounds through changes to both forage and weather conditions during migration (Forchhammer et al. 2002). Range shifts and localized population extinctions have been documented as a result of increased variability in weather conditions for certain organisms (Ehrlich et al. 1980, Parmesan 1996, Singer and Thomas 1996, Thomas et al. 1996, Parmesan et al. 1999, Pounds et al. 1999, van Herk et al. 2002, Crozier 2003), although avian taxa are underrepresented in this research. For most species, changes in global climate will have an indirect influence on fitness and survival through habitat alteration and in concert with landscape-scale changes (e.g., habitat fragmentation, increased competition with non-native invaders, and increased exposure to disease) which will complicate or compound the effects (Walther et al. 2002, Pounds et al. 2006).

Possible effects of climate change on birds

Bird populations can be negatively affected by climate change if behavioral responses are impossible (e.g., no local areas of suitable habitat exist) or constrained in some way such that their responses are maladaptive or insufficient to compensate for the degree of climate change. Although behavioral responses to weather are well documented (Elkins 1988, Root et al. 2003), the extent to which plasticity is adaptive or can compensate for climate change is unknown. Additionally, behavioral adjustments to climate change could be maladaptive, e.g., a shift to higher breeding density might lower annual fecundity. It is likely that frequent climatic changes over past millennia have produced highly plastic avian life histories and behaviors. However, anthropogenic changes to global climate and increased variation in both individual responses and habitat quality will unquestionably alter population dynamics for many migratory species and influence the effectiveness of current conservation management strategies.

One of the possible effects of climate change to migratory bird populations is a temporal mismatch in avian reproduction and insect emergence, or the food resources available for insectivorous species. Timing of reproduction is a life-history trait with important fitness consequences for individuals (Klomp 1970, Perrins 1970, Daan et al. 1990, Verhulst et al. 1995).

For many species, there is a short window within the annual cycle where conditions are adequate for successful reproduction. This time period is often dictated by the abundance of food necessary to raise offspring (Lack 1950, Martin 1987). Often the main variable determining reproductive success for a species is the abundance of prey items (Dias and Blondel 1996, Verboven et al. 2001, Durant et al. 2003, Pearce-Higgins and Yalden 2004). Visser et al. (2006) found that Great Tits (*Parus major*) fledged more and heavier offspring from nests timed with the annual peak of caterpillar biomass than individuals who fledged young later. Prior studies of Great Tits have also shown that heavier offspring are more likely to survive and breed in the following year, thus directly influencing individual fitness and population dynamics (Verboven and Visser 1998). Research of other songbird species has corroborated these findings (Maxted 2001, Naef-Daenzer et al. 2001). Overall, these studies, while providing strong evidence for a direct influence of availability and timing of food resources on the productivity of songbirds, are limited in number. In breeding habitats where food is a limiting resource, changes resulting from annual warming or periods of extreme weather have the potential to drastically alter productivity and population dynamics of many bird species.

Phenology and climate change

For many species, the disruption of phenological coordination between life cycles of predators and prey via climate changes is expected (Harrington et al. 1999, Visser and Both 2005, Parmesan 2006). For example, the phenology of insect emergence and nesting of migrant species has been shown to be important to overall reproductive success in multiple systems (Both and Visser 2001, Pearce-Higgins and Yalden 2004). If migratory birds are not able to adjust timing of clutch initiation to the timing of larval insect emergence, then the ability to adapt to changes in food resources will be constrained, with potential consequences to individual reproductive success and population dynamics. This changing relationship has been demonstrated for a number of migratory bird species that breed in Europe (Both and Visser 2001, Pearce-Higgins and Yalden 2004, Visser et al. 2006), but similar information of altered synchrony for migratory species in the Western Hemisphere is sorely needed.

To examine the potential effects of phenological disruptions on species, an understanding of the basic relationships between predators and prey of a system is required. Although many studies of insectivorous songbirds have investigated these relationships with regard to nest productivity (Brown et al. 1999, Both and Visser 2001, Visser et al. 2006, Pearce-Higgins et al. 2010), little research has been conducted to determine the relationship between availability of insects and survival of young following nest departure (Streby et al. 2011). Moreover, to my knowledge, no studies have been conducted on the timing of insect emergence and its influence on songbird fledgling survival.

The post-fledging period, or the period after young have departed the nest, is a critical life stage for birds. During this period, fledglings remain dependent on parental care while they learn to fly, forage on their own, and hide from predators (Yackel Adams et al. 2001, Kershner et al. 2004). Without information on the postfledging period or yearling migration, annual survival probabilities of juvenile passerines have been estimated from 0.31 (Yackel Adams et al. 2006) to half of adult survival (Donovan et al. 1995). Yet, studies that estimated post-fledging survival in songbirds have produced wide-ranging estimates within and among species (Anders et al. 1998, Rush and Stutchbury 2008, Tarwater et al. 2011). The lack of consensus regarding post-fledging survival rates warrant additional studies of the post-fledging period for other passerines. Exploratory studies on the mechanisms that influence survival of juvenile songbirds are even more important to advancing our understanding of the effects of this period on population dynamics.

Despite evidence that the post-fledging period plays an important role in avian conservation (Anders et al. 1997) and has been implicated as one of the most influential periods on population growth (Gaillard et al. 1998, Reid et al. 2003, Streby and Andersen 2011), data on basic population metrics (i.e., survival, immigration and emigration rates) and underlying mechanisms driving these values (e.g., habitat relationships) during this period are completely unknown for most species. For example, fledgling survival could be constrained by habitat quality as related to food availability or protection from predators or poor weather conditions. Habitat preferences of some forest birds change after the young fledge from the nest (Anders et al. 1998, Cohen et al. 2004, Vitz and Rodewald 2011). Multiple reports of high capture rates of forest-breeding songbirds (juveniles and adults) in early successional habitats (e.g., regenerating clearcuts) during the post-fledging period have been recorded, including many forest-interior specialists (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Mitchell et al. 2009). Most of these studies suggested that young move into these areas of increased shrub density for acquisition of food resources or increased cover (Vitz and Rodewald 2007, Rush and Stutchbury 2008), yet few have tested these hypotheses.

Understanding the mechanisms that promote specific habitat preferences of juvenile songbirds is necessary to effectively manage for these birds. If timing or availability of food drives fledgling habitat use, we could expect that changes to the habitat could influence fledgling movements, and potentially survival. With the advent of improved tracking technology, a number of studies have begun to examine habitat use of fledgling songbirds (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Yackel Adams et al. 2006, Davis and Fisher 2009), but few studies have investigated relationships between fledgling survival and habitat selection (King et al. 2006, Eng et al. 2011, Fisher and Davis 2011, Vitz and Rodewald 2011, Streby and Andersen 2013). In conducting habitat selection research, it is important to consider that neither habitat use (Garshelis 2000) nor animal densities (Van Horne 1983) necessarily indicate high-quality habitat, and understanding the consequence of habitat choices on survival is paramount to assessing quality.

In exploring the relationships between birds and their habitats, it is important to remember that individual responses can be varied and that specific behaviors can explain habitat use. Choices made by dependent young are likely influenced by their adult parents. Previous studies have indicated that age, and therefore experience, of adults can play a large role in explaining fledgling survival (Rush and Stutchbury 2008, King et al. 2006). Both individual behaviors and availability of preferred habitat could simultaneously influence juvenile success. For example, adults could employ specific strategies to minimize predation risk and/or maximize food availability to increase survival of their offspring. Thus, it is necessary when examining effects of habitat on offspring survival to consider the influence of adult characteristics and behaviors, as habitat quality and individual responses could work in concert. Analysis of the plasticity of individual responses and intrinsic habitat relationships will improve understanding of how a species may be affected by habitat changes caused by increased climate warming.

Research needs

The Black-throated Blue Warbler (*Setophaga caerulescens*, hereafter BTBW) is an ideal study organism to investigate the influence of climate change on habitat quality and breeding success. This migratory songbird is well-studied, with many of its habitat associations known from previous research (Holway 1991, Holmes et al. 1996, Harris and Reed 2001, Betts et al.

2008). Unfortunately, the majority of these studies have focused on a single study region at the northern end of its breeding range. The southern population of this species has been shown to be quite distinct from the northern population in terms of plumage (Graves 1997) and song characteristics (Colbeck et al. 2010). Moreover, it is likely that climate change will affect species at the margins of their ranges first, particularly evident through recent poleward movements in range distributions (Walther et al. 2002, Anderson et al. 2009). At the limits of species' ranges, isolation, small population size, and restrictions to movement are likely to affect the persistence of populations, and potentially the species (Hanski and Thomas 1994).

The Southern Appalachians is a region that is expected to experience truncation of available habitat for montane species, as suitable habitat is already limited by physiological tolerances of climate conditions (Bernardo and Spotila 2006). The BTBW prefers areas of high leaf density (Holmes et al. 1996) and abundant larval insects to rear their offspring (Nagy and Holmes 2005). As the Southern Appalachians has become increasingly fragmented by exurban development (Gragson and Bolstad 2006) and the hemlock woolly adelgid (*Adelges tsugae*) has decimated Eastern hemlock (*Tsuga canadensis*) stands that previously served as BTBW nesting substrate (Stodola 2011), optimal breeding habitat has likely shrunk in area. Additionally, BTBW populations have been shown to be affected by shifts in climate, as average survival, fecundity, and recruitment decreases during El Niño years (Sillett et al. 2000). As temperatures and precipitation patterns in the Southern Appalachians are altered by global climate change, aspects of habitat on which the BTBW depend are also likely to be altered. The compounding effects of habitat loss and decreased suitability of breeding habitat could contribute to population declines for this species.

Currently, the BTBW is listed as a species of least concern by the International Union for Conservation of Nature (IUCN) based on population estimates from North American Breeding Bird Survey (BBS) data (IUCN 2012). Yet, previous comparisons of abundance information on a local (one intensively studied site) and regional scale (BBS) implied spatial heterogeneity in population trends (Holmes and Sherry 1988). Thus, it is important to consider such heterogeneity across a species range in assessing the vulnerability of a population or species to extinction. In the Southern Appalachians, BBS data indicate that populations across this region are declining faster than 1.5% per year on average, but recent trends show as much as 6.5% decline per year in parts this range (Sauer et al. 2011). Trends of population decline are also evident in other bird species with similar life histories.

Identifying the factors that influence animal population dynamics is essential to accurate modeling of populations and implementation of appropriate management strategies and conservation plans (Sibly and Hone 2002). More specifically, an understanding of the mechanisms associated with the survival and productivity of individuals is integral to the effective management of populations (Saether and Bakke 2000). Although most aspects of BTBW breeding demography have been examined at various locations throughout the breeding range (Bourque and Villard 2001, Stodola et al. 2009, Holmes 2011), there is no information on the post-fledging period for this species. Estimates of juvenile survival and an investigation of the habitat needs of BTBW fledglings will allow for better explanation of declining population trends in the Southern Appalachians and the influence of climate change on population dynamics of this species.

Study Overview

This study was developed as part of a long-term research project on BTBW demography and population dynamics in the Nantahala National Forest, NC with a specific emphasis on understanding the influence of climate change on trophic relationships. The goal of my research was to generate estimates of BTBW fledgling survival and determine how aspects of habitat influence these estimates. Recognized population declines of this species in this region (Sauer et al. 2011) call for increased knowledge of all aspects of the breeding season, particularly the postfledging period for which there is no information. Moreover, by understanding the relationship of demographic parameters and available habitat, we can identify specific habitat qualities that are deemed necessary to maintain reproduction at levels to allow population persistence. Especially in light of major environmental changes to habitats in the southeastern United States, studies that can identify specific habitat requirements for breeding populations will become increasingly valuable to management and conservation of declining species.

Given the paucity of information on BTBW fledgling survival and which factors contribute to their habitat selection, this research provides meaningful insight into the habitat requirements for a population currently in decline.

Study Objectives

In Chapter 2, I discuss objective one: to identify the mechanisms that promote BTBW fledgling survival. I was particularly interested in exploring if timing or abundance of food (in this case, larval insects) influenced survival of BTBW offspring. I employed a mark-resight technique to monitor individual fledglings and account for detectability. I collected measurements of larval insect abundance across space and time in areas where fledglings were tracked. I explored drivers of fledgling survival across multiple scales, including individual characteristics (body condition), nest-level attributes (timing of fledge and brood size), and site-specific attributes (larval insect abundance and weather variables). I expected that BTBW fledglings that fledged early in the season (date) and with greater access to larval insects would have a higher probability of survival. I also expected that competition for available resources from siblings (brood size) and individuals in poorer body condition at fledge (lower mass) could have negative effects on survival. Lastly, I hypothesized that weather conditions (temperature and precipitation), especially during the first week after a fledgling departed the nest, could influence survival outcome. A Bayesian framework was used to determine the most influential covariates on survival and allow for partitioning of variability of random nest-level effects.

In Chapter 3, I focus on the second objective of my research: to determine microsite habitat use of BTBW fledglings and drivers of habitat selection. Previous fledgling habitat selection studies have implied that young use more structurally complex habitat and dense vegetative cover than located near nest sites (Rush and Stutchbury 2008, Mitchell et al. 2010). I hypothesized that in the Southern Appalachians the understory shrub layer serves to buffer fledglings from risk of predation, and that fledglings (or adults guiding those young) would actively seek this protection. I also postulated that a preference for evergreen vegetation would likely be due to a need for cover, as the predominant evergreen vegetation in this region exhibits larger leaf area than most evergreen plants. Finally, I expected that older (and thus more experienced) adults would be better at guiding young to areas of greater cover, and thus their offspring would be in denser habitat than those of younger adults. To meet this second objective, I implemented a frequentist approach to investigate BTBW fledgling habitat selection.

In Chapter 4, I summarize the conclusions for each objective and make suggestions for specific techniques to be employed in future study of fledgling survival and habitat selection. I also make recommendations of the implications of BTBW fledgling survival estimates and habitat use for a species that will likely encounter increased variability in its environment in the near future, resultant from climate change.

Study area

I conducted research from April to August 2011 and 2012 along the Southern Appalachian range in the Nantahala National Forest within the Blue Ridge physiographic province. More specifically, study sites were located in western North Carolina near the Coweeta basin where the US Forest Service Coweeta Hydrologic Laboratory is located. Mean July temperatures average 21.6 °C. Annual precipitation varies significantly in this region, from 178 centimeters at lower elevations to over 250 centimeters at higher elevations (Swank and Crossley 1988).

Two study sites of approximately 35 and 60 hectares in size were established in 2003 in contiguous forest at two elevations, averaging 1100 and 1350 meters respectively (hereafter, low and high sites) (Stodola 2011, see Figure 1.1). The low site was located at approximately 35.02° N, 83.45° E and the high site was located at 35.04°, 83.47° in the WGS 84 datum. These sites include both cove hardwood and northern hardwood forest cover types (Day et al. 1988) with *Rhododendron maximum* and *Kalmia latifolia* as the main evergreen understory components (Day and Monk 1974). Changes to the landscape as a result of climate change are likely to be noticeable in this area before the remainder of the BTBW breeding range, as high-elevation habitat contracts with climatic zone shifts in response to overall warming trends (Karl et al. 2009). The effects of climate change may be more pronounced at lower (warmer) elevations first where species are already at the edge of their physiological tolerances.

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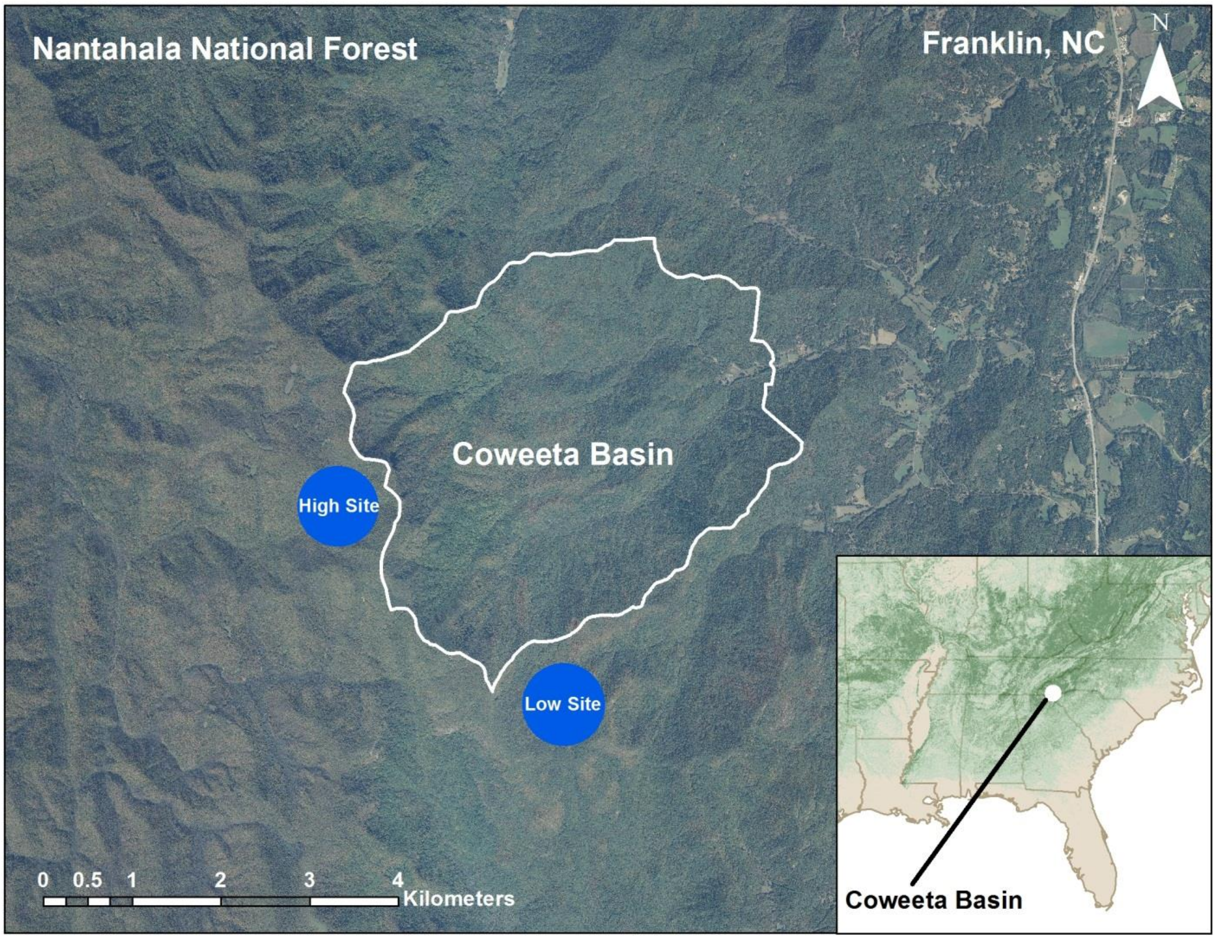

Figure 1.1. Map of BTBW study area sites within the Nantahala National Forest of western North Carolina, adjacent to the Coweeta Basin. Low and high elevation sites are noted separately. Inset map depicts deciduous forest cover for the Southeastern US.

CHAPTER 2

TEMPORAL INFLUENCES OF HABITAT QUALITY ON FLEDGLING SURVIVAL OF BLACK-THROATED BLUE WARBLERS (*SETOPHAGA CAERULESCENS*) IN THE SOUTHERN APPALACHIANS[1]

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[1] Hatt, J. L., J. Hepinstall-Cymerman, M. H. Cline, M. J. Conroy, and R. J. Cooper. To be submitted to *The Auk*.

Abstract

For many birds, the most critical life stage is the period after the bird has departed the nest, or the post-fledging period. However, few studies have examined the factors underlying fledgling survival. The Black-throated Blue Warbler (*Setophaga caerulescens*) is a Neotropical migrant songbird that relies primarily upon larval insects to provision its offspring. Warmer spring temperatures caused by climate change could result in a phenological mismatch between songbird nesting and larval insect emergence. This study focuses on the effects of larval insect availability on Black-throated Blue Warbler fledgling survival in the Nantahala National Forest of North Carolina, USA. For two years, I observed fledglings during the dependency period (15 days) and conducted concurrent larval insect surveys. Survival and detection probabilities of fledglings were calculated using Cormack-Jolly-Seber models in a Bayesian framework using Program R and WinBUGS. I developed models to test the relative importance of food availability, fledge date, brood size, and bird condition on probabilities of fledgling survival. In an interactive model, the fledge date and food availability covariates were most important in explaining fledgling survival. These results indicate that a mismatch between larval insect availability and Black-throated Blue Warbler nesting could have negative consequences for fledgling survival, and similar relationships could be expected for other insectivorous migrant songbird species.

Key words: Black-throated Blue Warbler, fledgling survival, insect availability, climate change

Introduction

Identifying the factors that influence animal population dynamics is essential to accurate population modeling and implementation of appropriate management strategies and conservation plans (Sibly and Hone 2002). Specifically, an understanding of the mechanisms associated with the individual survival and productivity s is integral to effective management of populations (Saether and Bakke 2000). For many vagile species, entire parts of the annual cycle remain unstudied and estimates of survival during different life stages are particularly sparse. Little is known about juvenile songbird survival, despite a number of studies that have indicated this period is critical to some species population growth (Gaillard et al. 1998, Reid et al. 2003, Streby and Andersen 2011).

The post-fledging period, or after young have departed the nest, is a critical life stage for birds. During this period, fledglings remain dependent on parental care while they learn to fly, forage on their own, and hide from predators (Yackel Adams et al. 2001, Kershner et al. 2004). Studies of the post-fledging period in songbirds have produced variable survival estimates both within and among species (Anders et al. 1998, Rush and Stutchbury 2008, Tarwater et al. 2011). These results warrant additional studies of the post-fledging period for other species of passerines, especially for species that require a variety of habitats. Exploratory studies of the mechanisms that influence survival of juvenile songbirds are increasingly relevant to advancing our understanding of the effects of this period on population dynamics.

Habitat quality can strongly influence fledgling survival, as shown by recent research demonstrating links between vegetation characteristics and fledgling dispersal in forest songbirds (King et al. 2006, Moore et al. 2010, Streby et al. 2011, Vitz and Rodewald 2011). Evidence supporting these links suggested that vegetation structure provides protective cover from predators (Vega Rivera et al. 1998) and increased access to fruit (White et al. 2005, Vitz and Rodewald 2007). However, an alternative hypothesis is that vegetation characteristics are an indicator of insect abundance, or that both food and cover are driving forces in fledgling movement and consequent survival. To date, few studies have examined this hypothesis through indirect analyses (Wiens et al. 2006, McDermott and Wood 2010) and even fewer have examined it directly (Streby et al. 2011).

As habitat structure and quality change due to unprecedented anthropogenic influences on natural landscapes (e.g., degradation, urban development, or climate change), resources critical to fledgling survival are likely to be affected. In particular, climate change has the potential to significantly and asymmetrically influence habitat and disrupt delicately evolved relationships within ecosystems. Current climate change projections strongly suggest that the distribution and abundance of many organisms will be altered (Parmesan and Yohe 2003). An understanding of the factors that drive both survival and productivity of organisms is essential to the development of mitigation strategies in the face of such changes.

The implications of a changing climate are still largely unknown because organisms, communities, and ecosystems will likely respond differently and the degree of response is also likely to vary. The disruption of phenological coordination between life cycles of predators and prey via climate changes is an expected consequence (Parmesan 2006). Changes to the predator-prey relationship have been documented for a number of migratory bird species that breed in Europe (Both and Visser 2001, Pearce-Higgins and Yalden 2004, Visser et al. 2006), but similar information of altered synchrony and its influence on productivity of migratory birds in the Western Hemisphere is still needed.

Timing of reproduction is a life-history trait with important fitness consequences for adults (Perrins 1970, Verhulst et al. 1995). For example, the phenology of insect emergence and nesting of migrant species has been shown to be important to overall reproductive success in multiple systems (Both and Visser 2001, Pearce-Higgins and Yalden 2004). Visser and colleagues (2006) found that Great Tits (*Parus major*) fledged more and heavier offspring from nests timed with the annual peak of caterpillar (Lepidoptera) biomass than individuals who fledged young later. Prior studies of Great Tits also have shown that heavier offspring are more likely to survive and breed in the following year, thus directly influencing individual fitness and population dynamics (Verboven and Visser 1998). Research of other songbird species has corroborated these findings (Maxted 2001, Naef-Daenzer et al. 2001) and provided strong evidence for a direct influence of availability and timing of food resources on the productivity of songbirds. In breeding habitats where food is a limiting resource, changes in food availability resulting from annual warming or periods of extreme weather have the potential to drastically alter nestling and fledgling survival and consequently population dynamics of many bird species.

My study explored the mechanisms that promote fledgling survival of Black-throated Blue Warblers (hereafter, BTBW) and specifically, the influences of food availability on BTBW fledgling survival in the Nantahala National Forest of western North Carolina, USA. I hypothesized that BTBW fledglings that fledged early in the season (date) and with greater access to larval insects would have a higher probability of survival. I also posited that competition for available resources from siblings (brood size) and poorer body condition at fledge (lower mass) may have negative effects on survival. Lastly, I conjectured that weather conditions (temperature and precipitation), especially within the first week after a fledgling departed the nest could influence survival outcome. Previous studies have suggested that cooler temperatures and heavy precipitation during the juvenile period can influence to thermoregulation and foraging ability, with negative consequences for survival (Hovick et al. 2011, Jackson et al. 2011). Results from my research will provide the first estimates of BTBW fledgling survival and further elucidate the relationship of fledgling survival of a migratory songbird to potential changing attributes of its breeding habitat. By understanding how timing and abundance of food can influence juvenile survival, we will be able to better predict individual and population responses to environmental changes.

Study Area and Species

Study area

I conducted research from April to August 2011 and 2012 along the Southern Appalachian range in the Nantahala National Forest within the Blue Ridge physiographic province. More specifically, study sites were located in western North Carolina near the Coweeta basin where the US Forest Service Coweeta Hydrologic Laboratory is located. Mean July temperatures average 21.6 °C. Annual precipitation varies significantly in this region, from 178 centimeters at lower elevations to over 250 centimeters at higher elevations (Swank and Crossley 1988).

Two study sites of approximately 35 and 60 hectares in size were established in 2003 in contiguous forest at two elevations, averaging 1100 and 1350 meters respectively (hereafter, low and high sites) (Stodola 2011, see Figure 1.1). The low site was located at approximately 35.02° N, 83.45° E and the high site was located at 35.04°, 83.47° in the WGS 84 datum. These sites include both cove hardwood and northern hardwood forest cover types (Day et al. 1988) with *Rhododendron maximum* and *Kalmia latifolia* as the main evergreen understory components (Day and Monk 1974). Changes to the landscape as a result of climate change are likely to be noticeable in this area before the remainder of the BTBW breeding range, as high-elevation habitat contracts with climatic zone shifts in response to overall warming trends (Karl et al. 2009). The effects of climate change may be more pronounced at lower (warmer) elevations first where species are already at the edge of their physiological tolerances.

Study species

The Black-throated Blue Warbler is a Neotropical migrant songbird that breeds along the Appalachian Mountains northward through New England, New York, and Pennsylvania, and in mountains southward to northern Georgia (Holmes et al. 2005). BTBWs breed in mature deciduous and mixed coniferous-deciduous woodlands, preferably with a thick understory. The primary diet for the BTBW is arthropods, especially caterpillars (Lepidoptera larvae), located on understory and subcanopy foliage (Robinson and Holmes 1982, Goodbred and Holmes 1996). During the breeding season, males defend territories, attract females, and pairs forage and feed young primarily within these areas. Nests are constructed solely by the female and are placed in low shrubs or saplings, usually within 1–1.5 meters of the ground. Both males and females feed the nestlings and feeding rate increases significantly with increased number of young in the nest and as young age (Goodbred and Holmes 1996). Nestlings depart from the nest 9-11 days post-hatch (Holmes et al. 2005). All young typically leave the nest within a short period of time within the same day. Upon leaving the nest, fledglings stay low in the understory for a week or two, usually remaining within the territory, but sometimes moving more than 300 meters away (Davis 2001). The typical duration of the dependency period is about 2–3 weeks post-fledging, although this has not been thoroughly examined (Holmes et al. 2005).

Methods

Field methods

Nest and fledgling monitoring: I located all nests in 2011 and 2012 on both sites by intensive systematic searching throughout the season. Locations of nests were recorded using a Garmin Rino 530HCx. Nests were checked every 1-3 days, depending on nest phenology, to determine fate (success or failure). Nestlings were uniquely marked within each nest with two color bands and a USGS service band. Nestlings were weighed to the nearest tenth of a gram using a digital scale on day 6 (hatching day = day 0) and mass of nestlings were recorded at all nests. Productivity was quantified by the number of young present at the last nest check before fledging. Additionally, date of fledge (expressed as ordinal date) and brood size were summarized for each nest.

For fledged nests, I monitored fledglings every other day until independence from adults (approximately 15 days post-fledge). For each territory, multiple observers searched for fledglings for up to two hours per day or until fledglings were located. All band combinations observed were recorded. These fifteen-day observation periods for individual fledglings were used to develop encounter histories to model individual survival.

Larval insect surveys: I assessed larval insect availability based on previous studies of preferred food during the breeding season and the foraging strategy of the BTBW from previous studies (Holmes and Schultz 1988, Nagy and Holmes 2005). Surveys of larval insects were conducted at points separated by 50-meter intervals along five parallel transects that were systematically located 200 meters apart on both study sites. Larval insects were visually counted, identified to family, and their lengths measured on a maximum of two 50-leaf samples (leaves and supporting petioles) for all common understory saplings within 0.04-ha circular plots. I calculated a mean abundance at each site for each two-week period and then used those values to calculate a weighted mean of larval insect abundance available to the fledgling based on an individual's site location and dates of observation period.

Climatic data: I used daily minimum temperature (°C) and total precipitation (mm) data gathered by the US Forest Service Coweeta Hydrologic Laboratory - Climate Station 1 (Laseter et al. 2012). I then calculated two values for temperature: 1) the minimum temperature experienced by each individual fledgling during the first week post-fledge and 2) minimum temperature for the entire observation period. Two values of total precipitation experienced by a fledgling were also calculated using the same methodology.

Statistical analysis

Probabilities of BTBW fledgling survival (φ) and detection (p) were modeled with a state-space formulation of the Cormack-Jolly-Seber (CJS) model mark-recapture analysis (Lebreton et al. 1992) using individual encounter histories of the 15-day observation period (Gimenez et al. 2007). Only individuals that were resighted at least once following the initial marking period were used in the mark-recapture analyses of survival and data from the two years were pooled. Since individuals are assumed to be independent from each other in CJS model specification, I conducted a hierarchical analysis of survival and detection in a Bayesian framework using Markov chain Monte Carlo (MCMC) techniques (Brooks et al. 2000). By including the natural variation occurring at the nest-level, I could account for non-independence that could lead to overdispersion in my data. Thus, all models considered in the survival analysis contained the random-effects factor of nest, formulated as a random-intercepts model drawn from a normal distribution.

I checked for multicollinearity of all individual covariates using the Pearson Product-Moment Correlation statistic to confirm independence. I retained variables having $r < 0.6$ in the analysis (Green 1979), and standardized these covariates to have mean = 0 and SD = 1 to improve model convergence (Spiegelhalter et al. 2003). In addition to modeling factors that influence fledgling survival, I considered two competing hypotheses to explain variation in detection probabilities (Table 2.1a). Because observer experience may influence detection of a small, cryptic songbird, I classified observers into two categories based on prior field experience. The majority of CJS models of survival were built primarily based on detection varying by observer, but for a subset of top-ranked models, I also tested if detection probabilities were constant over time.

I created a candidate set of 31 models to represent my original hypotheses of factors that influence fledgling survival (Table 2.1b). Models containing individual covariates of body condition (fledgling mass), fledge date, food availability (mean larval insect abundance), brood size, and total precipitation and minimum temperature experienced by a fledgling within the first week were all in the initial set. I considered models that included additive effects between fledge date and food availability, and fledge date and total precipitation. At my study sites, larval insect abundance and precipitation declines as the breeding season progresses, and thus I expected the effects of these covariates on survival to be more pronounced. I also tested an interaction between food availability and fledge date, as nestling provisioning increases as the season progresses and adults place more emphasis on preparation for fall migration (Stodola et al. 2009). Therefore, I expected the influence of food availability to increase for fledglings later in the season. I additionally considered a model allowing survival to vary by year, as previous research on this species has shown high interannual variability in demographic parameters (Holmes 2011). Lastly, I included models that allowed survival to vary by day and week after the young had departed the nest. Previous studies of fledgling survival have shown that weekly age class to be important variable to explain survival, as the first week likely represents a period of increased vulnerability to predation (Vormwald et al. 2011).

All analysis was conducted in Program R version 2.14.0 (R Core Development Team 2011) and WinBUGS (Lunn et al. 2000) using the R2WinBUGS package (Sturtz et al. 2005). Models were constructed as General Linear Mixed Models specifying a logit link to restrict the response variables (survival and detection) to probabilities between 0 and 1. I modeled survival by observation day of individual *i*, as a series of Bernoulli trials with a probability of success φ_{it} = Pr{individual *i* alive at observation *t* | alive at observation *t*-1}. For example, a model allowing detection to vary by observer and survival explained by the individual covariate of food availability and the random effect of nest was calculated by the equations:

$$\text{Logit}(\varphi_{it}) = \mu + \beta_{g(i)} + \beta x_i \qquad \text{(Equation 1)}$$

$$\text{Logit}(p_{it}) = \mu + \beta x_{it} \qquad \text{(Equation 2)}$$

where φ_{it} = survival and p_{it} = detection for a given individual at a given time period, μ mean survival or detection, x_i = food available to an individual, and x_{it} = fixed effect of observer at each observation. I specified uniform flat priors on the log scale for the variance of all individual covariates. For all models, $\beta_{g(i)}$ denoted the random effect for each level of nest described by a hyperprior following a normal distribution with a mean of zero and Jeffrey’s prior on tau of the logit survival between nest groups (Equation 3). The hyperprior for the standard deviation of the nest effect followed a uniform distribution from 0 to 10 (Equation 4).

$$\beta_{g(i)} \sim \text{Normal}(0,\sigma^2) \qquad \text{(Equation 3)}$$

$$\sigma \sim \text{Uniform}(0,10) \qquad \text{(Equation 4)}$$

For each model, I ran three overdispersed parallel MCMC chains to evaluate model convergence (Gelman et al. 1996). The Gelman-Rubin diagnostic and visual inspections of the chains were used to determine if convergence had been reached (Gelman and Rubin 1996)). I implemented 100,000 iterations with 30,000 burned iterations for posterior summarization.

Currently, there is no consensus on evaluation of hierarchical model uncertainty (Link and Barker 2009, Kéry and Schaub 2011). I compared support for the candidate models based on the data by evaluating the Deviance Information Criterion (DIC) computed for each model in R, as it is currently considered the standard tool for hierarchical model selection (Link and Barker 2009, Moore and Barlow 2011). DIC allows for Bayesian hierarchical model selection when the number of parameters derived from random factors is not easily estimable (as is needed for Akaike's Information Criterion, or AIC) (Akaike 1974, Spiegelhalter et al. 2002). Models were ranked based on smallest DIC score, which represented the model that was best at predicting a replicate dataset with the same structure as the model observed (Spiegelhalter et al. 2002). Estimates of survival and detection from the posterior distribution of the top-ranked model were produced, and the 95% Bayesian credible intervals (CRI) of the beta coefficients from this model were examined to ensure that they were informative (i.e., exhibited change from the priors). I calculated odds-ratios and the lower and upper 95% credible limits of the parameter estimates from the top model to determine the influence of each variable on survival and detection.

Results

Data summary

Overall, estimates of BTBW fledgling survival were similar for 2011 and 2012 and relatively constant throughout the observation period (Figure 2.1), with a slight decrease 2-3 days after young had departed the nest. In 2011, of the 113 monitored Black-throated Blue

Warbler nests, 27 fledged at least one offspring. I banded 87 nestlings from nests that survived to fledge and resighted 34 individuals on multiple occasions ($\bar{x}$ =4, STD=1.12, range=3-8) throughout the dependence period (15 days). Given this information, I calculated raw estimates of fledgling survival for 2011 to be 39.1% (34 out of 87 fledglings). In 2012, I monitored 98 nests, of which 45 fledged at least one offspring. I banded 135 nestlings from nests that survived to fledge and resighted 47 individuals on multiple occasions ($\bar{x}$ =4, STD=0.8, range=3-6). Based on this information, I estimated that 47 of the 135 (34.8%) fledglings survived the dependence period. Raw estimates seemed to be more realistic than those produced in the model selection. In examination of the data, survival seemed most variable on the first few days of fledge, however, limited sample size prohibited an exploration of time varying throughout the observation period. Thus, estimates of mean survival from the posterior distribution are likely inflated, as they are conditioned on resighting a fledgling after the marking event and many individuals were not resighted after initial capture.

Variable multicollinearity

Examination of the Pearson's correlation coefficients revealed that minimum temperature for the observation period was highly correlated with a few variables of interest (Table 2.2). Therefore, it was discarded from the initial candidate set. Models were then built with all remaining variables of interest. I only considered reduced models (i.e., fewer than five parameters), as credible intervals from parameter estimates of more complex models were wide, and some parameters were not identifiable likely due to significant overdispersion in the data or insufficient data on individuals. As expected, precipitation variables were highly correlated with each other ($r = 0.63$). Of these two variables, total precipitation in the first week was selected to remain in the analysis, since fledglings are likely more vulnerable to rain events before they have developed the ability to fly.

Model selection

I found that a model with weekly age variation in survival and the interaction between fledge date and food availability (with detection varying by observer group) best predicted the data (Table 2.3). Although the credible intervals for these variables overlapped zero, the posterior estimates and intervals shifted considerably from the priors. This finding was consistent with my initial hypotheses that the availability of food and timing of fledge (date) would be influential on BTBW fledgling survival. Beta coefficients from the top model indicated that the date-food interaction effect was positive (Table 2.4). In other words, the effect of food availability on fledgling survival was more pronounced later in the breeding season (Figure 2.2). Observer experience had a strong influence on detection probability, with the majority of the variability in detection explained by observer group (Table 2.4). Odds-ratio calculations showed that experienced observers were 2.3 times more likely to detect fledglings than inexperienced observers (Table 2.5a). Parameter estimates from this model indicated that fledglings that survived to the second week post-fledge were 4.9 times more likely to survive to dependence from adults (Table 2.5b).

My model selection did provide evidence for my hypothesis of the influence of food availability and timing of fledge on BTBW fledgling survival. Examination of the beta coefficients of the top model showed directional influence congruent with the original hypotheses that young fledging early in the season and with more available food should have higher survival probabilities (Table 2.4). The model that included the interaction between these two parameters was better supported than models that included additive effects of food and fledge date (Table 2.3). However, low mean detection probabilities ($p<0.25$) likely limited the ability to model survival by all individual covariates. Additionally, the 95% Bayesian CRI did overlap zero for these covariates making it difficult to conclude their relative importance in explaining fledgling survival variability. It is possible that with additional years of data and higher detection probabilities, this model would be more informative.

Discussion

This study was one of the first to investigate the influence of weather and food availability on postfledgling survival. Although low detectability influenced the ability to model survival based on individual covariates, results from my research do support the hypothesis that BTBW fledgling survival could be negatively affected by a potential mistiming of available food resources. As shown by the importance of a model including the interaction of food availability and timing of fledge, late-season fledglings may have reduced survival if larval insect emergence occurs earlier (Visser et al. 2006). According to the top model in my analysis, the effect of food availability magnifies as the season progresses, with the consequences exacerbated by the naturally-occurring seasonal declines of larval insects at my sites. Thus, BTBW fledglings are at a distinct disadvantage when still dependent on their parents during the latter end of the breeding period.

My model selection showed strong support for survival varying with week since fledge. While this finding agrees with results of other studies that investigated survival of young songbirds (Anders et al. 1997, Sankamethawee et al. 2009, Vormwald et al. 2011, Cox and Kesler 2012), it also argues the importance of incorporating all relevant variables when modeling. Susceptibility to certain predator guilds could influence survival, e.g., if rodent predators are more likely to depredate young before they are mobile (Sankamethawee et al. 2009, Cox and Kesler 2012). Moreover, fledglings may be in greater competition with their siblings for parental care during the first week after fledge (Gottlander 1987).). I did not find support for the effects of year, brood size, or body condition on fledgling survival during the dependence period. Although the analysis did not support a year effect, fledging rate for Black-throated Blue Warblers was much higher in 2012 than 2011. However, since we followed only 34 individuals in 2011 versus 47 in 2012, it is difficult to compare fledgling survival between years. Anecdotal evidence from both years of data collection suggests that differences in rodent predator abundances between the two years may explain the differences in fledging rates. More specifically, the rodent predator guild may play a significant role in influencing BTBW fledgling survival, but not detected with the available data.

Information on fledgling survival before young undergo migration is becoming more available (Streby and Andersen 2011, Vitz and Rodewald 2011, Vormwald et al. 2011). However, few studies have considered such a large suite of factors that influence survival. My estimates of fledgling survival are higher than most other studies, yet most of those studies employed radio telemetry methods in order to increase detection and increase precision of survival estimates. Mattsson et al. (2006) showed that fledgling survival can be negatively influenced by radio transmitter attachment. The period after young have dispersed from the nest and are learning to fly is an energetically expensive and vulnerable transition that could be negatively affected by additional weight or reduced movement caused by a transmitter (Mattsson et al. 2006, Schmidt et al. 2008). Other studies of fledglings that have employed capture-recapture methods to investigate survival have estimated higher probabilities (Vormwald et al. 2011). Although detection was greatly reduced in my sampling, I believe that models to explain natural variability in survival for this species are likely more accurate than those conducted with radio telemetry. Furthermore, future studies employing this capture-recapture technique should include consideration of observer effects on detection probabilities, especially when designing the study.

Conclusion

To my knowledge, my study is the first to estimate fledgling survival for this migratory songbird, and one of the first studies in the Southern Appalachian ecoregion to investigate fledgling survival for any bird species. Since many migrant songbirds are declining in this area, more emphasis should be placed on determining where in the life cycle most mortality occurs. Furthermore, these results indicate that mistiming of breeding and peak larval insect availability could have negative effects on BTBW fledgling survival, and consequently, the population. Lacking a better understanding of postfledgling survival, the picture of breeding success for this and many other species is incomplete. However, effects of observer on detection and yearly variability on survival should be foremost considered when calculating estimates of survival to be used in population demographic models. Although it is promising that we found fledgling survival higher than reported in many other studies, these estimates should not discredit that this is a critically vulnerable life stage for passerines. My results should serve to highlight the importance of this time period encourage researchers to consider the postfledging period in population estimates, especially for species with declining populations.

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Table 2.1. Model names and corresponding hypotheses for BTBW fledgling **a)** detection and **b)** survival probabilities in the Nantahala National Forest, North Carolina, 2011-2012.

a).

Model Name	**Hypothesis**
Observer	Experienced observers are more likely to detect fledglings than inexperienced observers
Constant	No influence of observer on detection

b).

Model Name	**Hypothesis**
Time Trend Models	
Daily age	Fledgling survival varies by age group
Constant	Survival is constant throughout the fledgling dependency period
Weekly age	Fledgling survival varies by weekly age group
Year	Fledgling survival varies annually
Individual Covariate Models	
Food availability	Fledglings are more likely to survive when they fledge with peak food availability
Fledge date	Fledglings are more likely to survive if they fledge early in the season
Min temperature (1st week)	Fledgling survival decreases with cooler temperatures (increased thermoregulatory needs)
Min temperature (both weeks)	Fledgling survival decreases with cooler temperatures (increased thermoregulatory needs)
Precipitation (1st week)	Fledgling survival decreases with increasing precipitation
Precipitation (both weeks)	Fledgling survival decreases with increasing precipitation
Brood	Fledglings are less likely to survive if they have more siblings
Body condition	Fledglings are more likely to survive if they are heavier at fledging

Table 2.2. Pearson's correlation coefficient matrix showing the relationship between individual covariates in model selection. Values of *r* greater than 0.6 indicated that the variables were highly correlated.

Variable	Fledge date	Food availability	Brood	Body condition	Min temperature (1st week)	Min temperature (both weeks)	Precipitation (both weeks)	Precipitation (1st week)
Fledge date	**1.00**	-0.59	-0.59	-0.02	0.50	0.60	0.42	0.41
Food availability	-0.59	**1.00**	0.34	0.29	0.02	-0.09	-0.28	-0.22
Brood	-0.59	0.34	**1.00**	-0.06	-0.37	-0.33	-0.23	-0.32
Body condition	-0.02	0.29	-0.06	**1.00**	0.15	0.08	0.03	0.07
Min temperature (1st week)	0.50	0.02	-0.37	0.15	**1.00**	0.89	0.35	0.48
Min temperature (both weeks)	0.60	-0.09	-0.33	0.08	0.89	**1.00**	0.53	0.65
Precipitation (both weeks)	0.42	-0.28	-0.23	0.03	0.35	0.53	**1.00**	0.63
Precipitation (1st week)	0.41	-0.22	-0.32	0.07	0.48	0.65	0.63	**1.00**

Table 2.3. Candidate set used in model selection of natural variability in survival (φ) and detection (*p*) of BTBW fledglings, Nantahala National Forest, North Carolina, 2011-2012. Dev is mean model deviance and pD is the effective number of parameters. Weights are DIC model weights, scaled to sum to 1 across models.

Models	**Dev**	**pD**	**DIC**	**ΔDIC**	**Weight**
φ (Fledge date*Food availability + Weekly age), *p* (Observer)	722.426	114.4	836.8	0	0.9895
φ (Fledge date + Weekly age), *p* (Observer)	722.201	124	846.2	9.4	0.0090
φ (Precipitation (1st week) + Weekly age), *p* (Observer)	721.751	128.5	850.2	13.4	0.0012
φ (Weekly age), *p* (Observer)	721.581	132.1	853.7	16.9	0.0002
φ (Fledge date + Food availability + Weekly age), *p* (Observer)	723.441	133.8	857.3	20.5	0.0000
φ (Fledge date + Precipitation (1st week) + Weekly age), *p* (Observer)	723.103	134.4	857.5	20.7	0.0000
φ (Daily age), *p* (Observer)	725.098	132.6	857.7	20.9	0.0000
φ (Food availability + Weekly age), *p* (Observer)	722.600	137.3	859.9	23.1	0.0000
φ (Fledge date + Daily age), *p* (Observer)	727.212	133.4	860.6	23.8	0.0000
φ (Weekly age), *p* (Constant)	737.17	125.2	862.4	25.6	0.0000
φ (Fledge date*Food availability), *p* (Observer)	728.432	134.9	863.3	26.5	0.0000
φ (Fledge date), *p* (Observer)	728.762	137.6	866.4	29.6	0.0000
φ (Precipitation (1st week) + Daily age), *p* (Observer)	724.982	142.1	867.1	30.3	0.0000
φ (Precipitation (1st week)), *p* (Observer)	728.539	143.6	872.1	35.3	0.0000
φ (Fledge date*Food availability + Daily age), *p* (Observer)	729.129	144.1	873.2	36.4	0.0000
φ (Constant), *p* (Observer)	727.306	146.7	874	37.2	0.0000
φ (Food availability), *p* (Observer)	728.212	148.1	876.4	39.6	0.0000
φ (Year), *p* (Observer)	728.237	149.7	878	41.2	0.0000
φ (Food availability + Daily age), *p* (Observer)	727.415	150.8	878.3	41.5	0.0000
φ (Fledge date + Precipitation (1st week)), *p* (Observer)	730.325	149.6	879.9	43.1	0.0000
φ (Brood), *p* (Observer)	728.765	151.8	880.5	43.7	0.0000

φ (Min temperature (1st week)), *p* (Observer)	730.181	151	881.2	44.4	0.0000
φ (Constant), *p* (Constant)	743.154	139.8	883	46.2	0.0000
φ (Fledge date), *p* (Constant)	744.573	142.6	887.2	50.4	0.0000
φ (Fledge date + Food availability), *p* (Observer)	730.911	157.1	888	51.2	0.0000
φ (Body condition), *p* (Observer)	728.621	160.1	888.7	51.9	0.0000
φ (Brood), *p* (Constant)	744.297	145.6	889.9	53.1	0.0000
φ (Fledge date + Food availability + Daily age), *p* (Observer)	730.140	160.4	890.5	53.7	0.0000
φ (Food availability), *p* (Constant)	745.206	146.4	891.6	54.8	0.0000
φ (Year), *p* (Constant)	744.010	148.4	892.5	55.7	0.0000
φ (Fledge date + Precipitation (1st week) + Daily age), *p* (Observer)	730.432	172.3	902.8	66.0	0.0000

Table 2.4. Mean estimates, standard deviations, and 95% Bayesian credible intervals (CRI) of beta coefficients for parameters in the top-ranked CJS model (Table 3) on the natural log scale. Deviance is a measure of the predictability of the model, or (-2*log(likelihood) + C), where the likelihood = Pr(data|model) and C = unknown constant. For each parameter, effective N is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (Rhat<1.1 is considered a sufficient convergence measure (Gelman and Rubin 1996).

CJS model components	Parameters	mean	SD	2.50% CRI	97.50% CRI	Rhat	effective N
Survival	Weekly age	1.591	1.049	-0.177	3.925	1.002	3200
	Fledge date	-0.218	0.366	-0.937	0.510	1.003	1300
	Food availability	0.373	0.410	-0.395	1.227	1.003	830
	Fledge date*food availability	0.760	0.422	-0.033	1.645	1.001	16000
	Intercept (φ)	2.902	0.496	2.082	4.03	1.001	16000
	Random effect (nest)	0.691	0.439	0.061	1.719	1.014	500
Detection	Intercept (p)	-2.221	0.343	-2.894	-1.552	1.001	57000
	Observer	0.816	0.202	0.421	1.214	1.001	18000
Deviance		722.426	15.124	693.6	752.8	1.001	14000

Table 2.5. Parameter estimates (standard deviations), odds-ratios, lower and upper 95% credible intervals (LCI, UCI) for the best supported model of BTBW fledgling **a)** detection and **b)** survival. Estimated odds-ratios with an asterisk (*) denote a credible interval not including 1.

a).

Parameter	**Estimate (sd)**	**Estimated odds-ratio**	**Odds-ratio 95% LCI**	**Odds-ratio 95% UCI**
Intercept (*p*)	-2.221 (0.343)	0.109	0.055	0.212
Observer	0.816 (.202)	2.261*	1.523	3.367

b).

Parameter	**Estimate (sd)**	**Estimated odds-ratio**	**Odds-ratio 95% LCI**	**Odds-ratio 95% UCI**
Intercept (φ)	2.902 (0.496)	18.211	8.020	56.261
Weekly age	1.591 (1.049)	4.909	0.838	50.653
Fledge date	-0.218 (0.366)	0.804	0.392	1.665
Food availability	0.373 (0.41)	1.452	0.674	3.411
Fledge date*Food availability	0.760 (0.760)	2.138	0.968	5.181
Random effect (nest)	0.691 (0.439)	1.996*	1.063	5.579

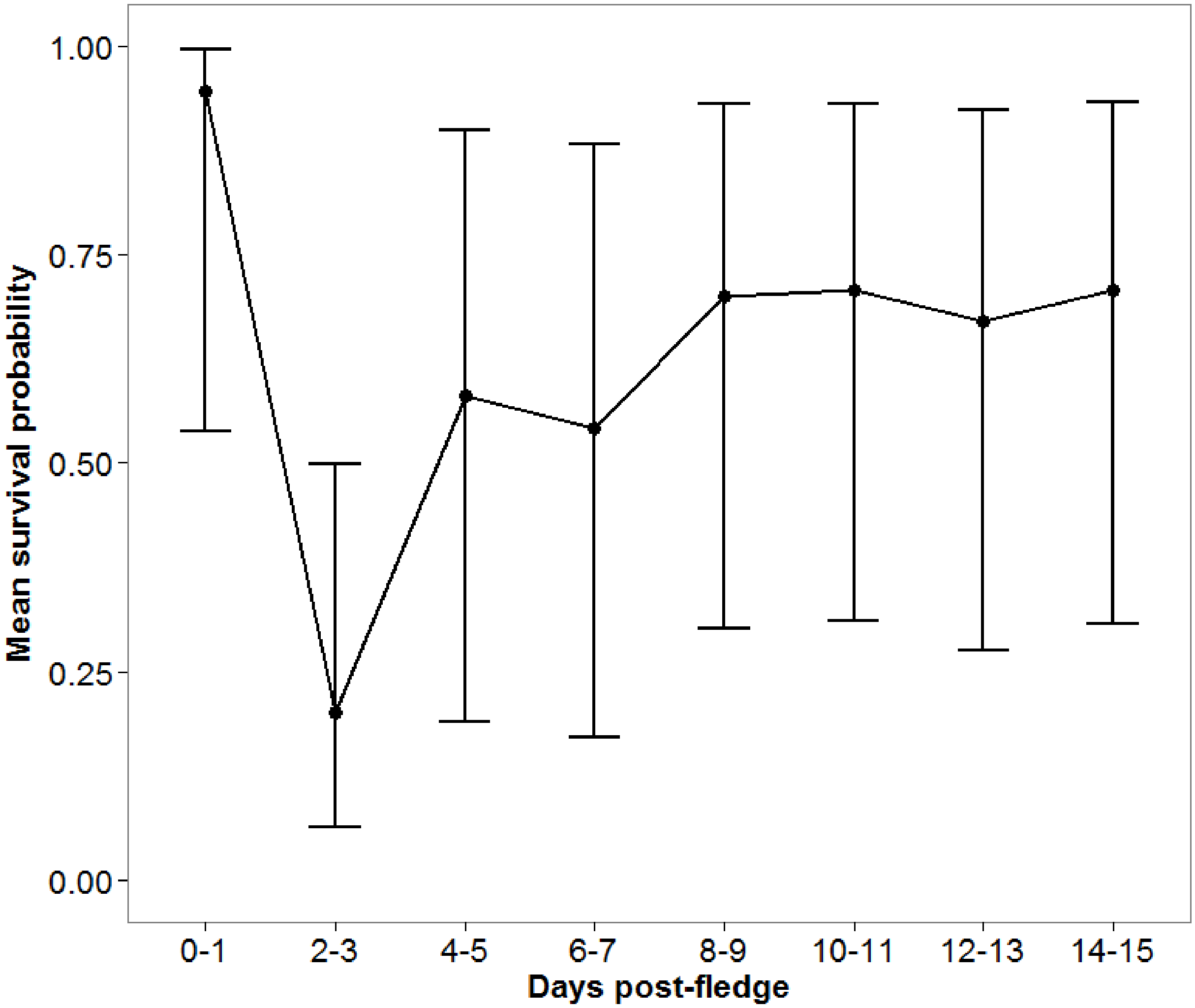

Figure 2.1. Age-specific survival probabilities for individual fledgling BTBWs during 15-day observation period in the Nantahala National Forest, North Carolina, 2011-2012. Days post-fledge represent time since the fledglings have departed the nest (with 0 starting from the day of fledge until the end of the observation period). Bars represent 80% Bayesian credible intervals.

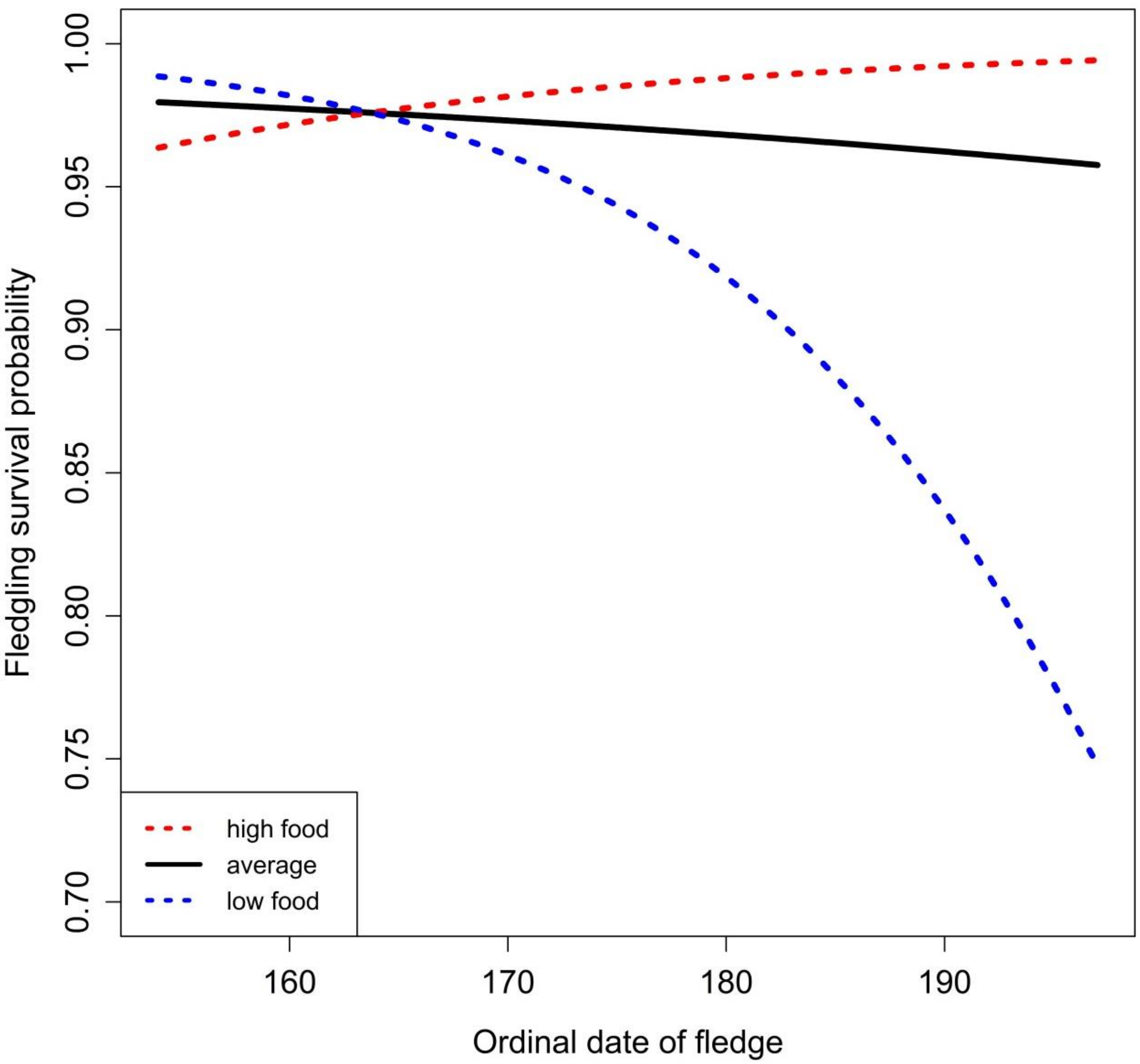

Figure 2.2. Influence of interaction of fledge date and food availability on mean survival estimates of BTBW fledglings in the Nantahala National Forest, North Carolina, 2011-2012. Dashed lines indicate ± 1 SD from mean food availability and consequent effect on survival probabilities with increasing fledge date.

CHAPTER 3

THE IMPORTANCE OF ADULT EXPERIENCE ON HABITAT USE OF FLEDGLING BLACK-THROATED BLUE WARBLERS (*SETOPHAGA CAERULESCENS*) IN THE SOUTHERN APPALACHIANS[2]

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Abstract

An understanding of species breeding habitat requirements is important in efforts to conserve bird populations. Until recently, information on habitat use and selection of fledgling birds and effects on survival have been largely missing. The Black-throated Blue Warbler (*Setophaga caerulescens*) is a migratory songbird that breeds in the Appalachians for which there is copious information on habitat associations, but only pertaining to the nesting period at the northern extent of its breeding range. In this study, I evaluated habitat selection of juvenile Black-throated Blue Warblers at the southern end of the breeding range during the postfledging period. Specifically, I compared microsite characteristics of the understory shrub layer for used and potentially available habitat. In 2011 and 2012, I observed fledglings during the dependency period (15 days) and collected data on vegetation structure in the study area. Estimates of shrub density were calculated at fledgling and random locations within territories from a Kriged surface raster. Fledglings did not show a preference for evergreen or deciduous shrub types ($t_{48} = 0.7773$, $P = 0.22$) or areas of higher shrub densities (evergreen: $t_{48} = -0.5705$, $P = 0.57$, deciduous: $t_{48} = 1.2835$, $P = 0.21$). Yet, age class of parents influenced the selection of evergreen shrub density among fledglings ($F_{3,43} = 2.9673$, $P = 0.04$). These results indicate that managing habitat for Black-throated Blue Warbler fledglings may require additional information about the age distribution (and experience) of the breeding population.

Key words: Black-throated Blue Warbler, habitat selection, fledgling, adult age

Introduction

The postfledging period is one of the least understood phases of the avian life cycle largely because it is difficult to observe young birds after they leave the nest (Ogden and Stutchbury 1997). The juvenile songbird dependency period may be as long as or longer than the nesting period (With and Balda 1990, Langen 2000) and survivorship of juvenile birds through the entire period of dependence is a more accurate assessment of reproductive output than is nesting data alone (Anders et al. 1997). Since Lack (1954) noted that mortality of altricial young is understudied, but likely great, there has been increased emphasis on investigating this life stage. Studies of numerous types of birds indicate that mortality of young is high, especially during the postfledging period (Woolfenden 1978, Dhondt 1979, Naef-Daenzer et al. 2001, Rush and Stutchbury 2008, Sankamethawee et al. 2009).

Qualitative and quantitative assessments of species habitat needs are important in efforts to conserve bird populations. Until recently, most breeding site studies have lacked information on habitat use and selection of fledgling birds and how habitat characteristics can influence survival (King et al. 2006, Vitz and Rodewald 2011, Streby and Andersen 2013). Within a given landscape, a species may require several habitat types for different stages of the life cycle (Law and Dickman 1998). Patterns of habitat selection by nesting adults of many bird species are relatively well understood (Block and Brennan 1993); however, recent studies indicate that the habitat preferences of some forest birds change after the young fledge from the nest (Anders et al. 1998, Cohen et al. 2004, Vitz and Rodewald 2011). Dissimilarities in habitat use throughout the annual cycle are perhaps an unsurprising phenomenon, given that breeding birds have numerous requirements (i.e., nest-site selection, mate acquisition, courtship, nestling provisioning), whereas nonbreeding birds, including fledglings, should be focused primarily on survival. For example, multiple studies indicate that Wood Thrush fledglings move from nest sites in mature forest into stands of dense vegetation in which they stay for extended periods of time until they migrate (Anders et al. 1998, Vega Rivera et al. 1998). Cohen et al. (2004) found that White-throated Robins nested successfully in agricultural habitats, but required forested areas for increased survival during the postfledging dependent period. The extent to which most other forest-breeding migratory birds follow this pattern remains unknown.

Recently, multiple reports of high capture rates of forest-breeding songbirds (juveniles and adults) in early successional habitats (e.g., regenerating clearcuts) during the post-fledging period have been recorded, including many forest-interior specialists (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Mitchell et al. 2009). Nevertheless, the effects of different habitats on fledgling songbird survival are still largely untested. In conducting habitat selection research, it is important to consider that neither habitat use (Garshelis 2000) nor animal densities (Van Horne 1983) necessarily indicate high-quality habitat, and likely the consequence of habitat choices on survival is paramount to proper assessments of quality.

Our poor understanding of post-fledging ecology results primarily from the difficulty associated with collecting data on birds during a phase when they are furtive and do not broadcast their presence through song (Vitz and Rodewald 2011). The use of light-weight transmitters is primarily responsible for recent expansion of research on the post-fledging period, and several recent studies have investigated habitat use of fledgling songbirds (Yackel Adams et al. 2001, King et al. 2006, Rush and Stutchbury 2008, Moore et al. 2010, Streby and Andersen 2011, Vitz and Rodewald 2011, Rivers et al. 2012). However, these results should be taken with caution, as the effects of transmitters on survival and habitat choice should not be overlooked (Mattsson et al. 2006). King et al. (2006) argued that transmitters have opened up avenues to studying post-fledging habitat use, but it is likely that the additional weight of these units did influence juvenile mobility and survival. Until further testing is done to investigate the direct impacts of transmitters on young songbird movements and survival, mark-resight methods may be more appropriate to study fledgling habitat use.

In exploring the relationships between birds and their habitats, it is important to remember that individual responses can be varied and that specific behaviors can explain habitat use. Choices made by dependent young are likely influenced by their adult parents. Previous studies have indicated that age, and therefore experience, of adults can play a large role in explaining fledgling survival (Rush and Stutchbury 2008, Moore et al. 2010). Both individual behaviors and quality of habitat could simultaneously influence juvenile success. For example, strategies to minimize predation of offspring or maximize food availability could be employed by adults to increase survival of their offspring.

Thus, the role of habitat selection on fledgling survival is central to our understanding of the system. By examining the influence of habitat on survival, we can better manage for species threatened by increasingly fragmented habitats. The Black-throated Blue Warbler (*Setophaga caerulescens*, hereafter BTBW) is one forest-interior songbird species that is exposed to threats of increasing fragmentation of its breeding habitat, particularly at the southern end of its range. Additionally, the southern breeding BTBW population has recently experienced a loss of a major nesting substrate (*Tsuga canadensis*) (Ford et al. 2012). Recent Breeding Bird Survey trends show as much as a 6.5% decline per year of BTBWs in this region (Sauer et al. 2011), which could be resultant from poleward shifts due to contraction of suitable habitat by climate change (Parmesan et al. 1999). Furthermore, no information currently exists on the post-fledging period for this species, largely because sufficiently small transmitters are not currently available. Events during the post-fledging period could be responsible for declines in the southern BTBW breeding population. Therefore, there is a great need to estimate these vital rates (see Chapter 2) and examine the relationship of habitat characteristics and survival to predict the influence of the changing landscape on continued persistence of this species in this region. To investigate these basic relationships, I implemented a mark-resight study of BTBW fledglings in high-quality breeding habitat at the southern end of the species' breeding range. Individual movement may play a large role in survival and identifying specific habitat preferences that increase survival probabilities could improve conservation efforts.

My objectives were to: 1) compare habitat use of BTBW fledglings with available habitat at the territory level; 2) investigate if young preferentially selected denser shrub habitat or specific shrub types; and 3) determine if adult age influences habitat use of the young. Previous studies of habitat comparisons between nest and fledgling sites of forest interior species have indicated that fledglings use more structurally complex habitat and dense vegetative cover than at nest sites (Rush and Stutchbury 2008, Mitchell et al. 2010). This suggests that fledglings may seek habitat with high cover to avoid predation. For insectivorous bird species, selection of dense shrubby habitat could also indicate a preference for sources of higher food availability (Streby et al. 2011). However, I hypothesized that in the Southern Appalachians the understory shrub layer serves to buffer fledglings from risk of predation, and that fledglings (or adults guiding those young) would actively seek this protection. I also postulated that a preference for evergreen vegetation would likely be due to a need for cover, as the predominant evergreen vegetation (*Rhododendron maximum*) in this region exhibits larger leaf area than most evergreen plants and anecdotally has fewer larval insects than deciduous vegetation. Lastly, I expected that older (and thus more experienced) adults would be better at guiding young to areas of greater cover, and thus their offspring would be in denser habitat than those of younger adults. Holmes et al. (1996) showed that older BTBWs bred in higher densities in areas with greater shrub density, and that these individuals also had higher nest productivity. Thus, all of these studies suggest that dense shrubby habitat would be an important predictor of BTBW fledgling locations, and that habitat selection could have possible consequences for juvenile survival.

Study Area and Species

Study area

I conducted research from April to August 2010 and 2012 along the Southern Appalachian range in the Nantahala National Forest within the Blue Ridge physiographic province. More specifically, study sites were located in western North Carolina near the Coweeta basin where the US Forest Service Coweeta Hydrologic Laboratory is located. Mean July temperatures average 21.6 °C. Annual precipitation varies significantly in this region, from 178 centimeters at lower elevations to over 250 centimeters at higher elevations (Swank and Crossley 1988).

Two study sites of approximately 35 and 60 hectares in size were established in 2003 in contiguous forest at two elevations, averaging 1100 and 1350 meters respectively (hereafter, low and high sites) (Stodola 2011, see Figure 1.1). The low site was located at approximately 35.02° N, 83.45° E and the high site was located at 35.04°, 83.47° (WGS 84). These sites include both cove hardwood and northern hardwood forest cover types (Day et al. 1988) with *Rhododendron maximum* and *Kalmia latifolia* as the main evergreen understory components (Day and Monk 1974). Changes to the landscape as a result of climate change are likely to be noticeable in this area before the remainder of the BTBW breeding range, as high-elevation habitat contracts with climatic zone shifts in response to overall warming trends (Karl et al. 2009). The effects of climate change may be more pronounced at lower (warmer) elevations first where species are already at the edge of their physiological tolerances.

Study species

The Black-throated Blue Warbler is a Neotropical migrant songbird that breeds along the Appalachian Mountains northward through New England, New York, and Pennsylvania, and in mountains southward to northern Georgia (Holmes et al. 2005). BTBWs breed in mature deciduous and mixed coniferous-deciduous woodlands, preferably with a thick understory. The primary diet for the BTBW is arthropods, especially caterpillars (Lepidoptera larvae), on understory and subcanopy foliage (Robinson and Holmes 1982, Goodbred and Holmes 1996).

During the breeding season, males defend territories, attract females, and pairs forage and feed young primarily within these areas. Nests are constructed solely by the female and are placed in low shrubs or saplings, usually within 1–1.5 meters of the ground. Both males and females feed the nestlings, and feeding rate increases significantly with increased number of young in the nest and as young age (Goodbred and Holmes 1996). Nestlings depart from the nest at 9-11 days post-hatch (Holmes et al. 2005). Usually, all young leave the nest within a short period of time within the same day. Upon leaving the nest, fledglings stay low in the understory for a week or two, remaining within the territory while males are still maintaining the boundaries, but sometimes move more than 300 meters away (Davis 2001). Both adults continue to provision the young while they remain in the territory and will either divide the brood or forage together. The typical period of dependency is about 2–3 weeks post-fledging, although this has not been thoroughly examined (Holmes et al. 2005).

Methods

Field methods

Territory mapping:

To assess spatial distribution of breeding BTBWs, I attempted to capture and uniquely mark all BTBW adults. Mist-nests were used for capture of both sexes, and con-specific playback recordings and decoys were used to lure males to nets. Adult females were captured at previously located nests during the incubation stage, as likelihood of nest abandonment is lower during this period of nesting. Adults were given unique color band combinations to facilitate identification of individuals and placed in age classes via specific plumage characteristics (Pyle 1997). Since BTBW adults can only be aged to "second year" (SY) or "after second year" (ASY), all ASY adults were considered to be "experienced", having previously experienced at least one complete breeding season. For both years, territories were minimally visited every other day to determine movements of adult male warblers. Individual adults were followed closely without disturbing them for 15-20 minute periods from early May to late June each year (the period that males maintain territories). Male locations were recorded on a map according to their position on the alphanumeric grid system on the sites. These positions were transcribed onto a digital map of the study sites. In 2012, GPS locations were additionally recorded using a Garmin Rino 530HCx.

Nest and fledgling monitoring:

I located nests in 2011 and 2012 on both sites by intensive systematic searching throughout the season. Locations of nests were recorded using a Garmin Rino 530HCx. Nests were checked every 1-3 days, depending on nest phenology, to determine fate (success or failure). Nestlings were uniquely marked within each nest with two color bands and a USGS service band. Nestlings were weighed to the nearest tenth of a gram using a digital scale on day 6 (hatching day = day 0) and mass of nestlings were recorded at all nests. Nest success was quantified by the number of young present at the last nest check before fledging.

For fledged nests, I monitored fledglings every other day until independence from adults (approximately 15 days after nest departure). For each territory, multiple observers searched for fledglings for up to two hours per day or until fledglings were located. All band combinations observed were recorded. I monitored fledgling movements every other day, and recorded GPS points when a visual observation was made of an individual. Available habitat was defined as the parental territory space where a fledgling was located, as movement of fledglings was largely constrained to this area while males defended territories.

Vegetation:

As my research continued from a long-term demography study, I was able to use vegetation data from years prior to the fledgling study. From 2010-12, data was collected on stem density of all understory shrubs in 3-meter circular radius plots, a modification of the standard James and Shugart (1970) quantitative analysis of bird habitat. All understory shrub and tree species were counted and identified within the circular plots. Stem density was measured at additional 3-meter circular radius plots interspersed along transects throughout my two sites (Figures 3.1 and 3.2). GPS locations were recorded for all vegetation plots. From these data I calculated an estimate of average stem density for evergreen and deciduous shrub types at each of the plots for both years.

Larval insect surveys:

I assessed larval insect availability based on an understanding of preferred food during the breeding season and the foraging strategy of the BTBW from previous studies (Holmes and Schultz 1988, Nagy and Holmes 2005). I was primarily interested in estimating abundance of types of Lepidopteran larvae preferred by this species (Holmes et al. 2005). Surveys of larval insects were conducted at points separated by 50-meter intervals along five parallel transects that were systematically located 200 meters apart on each study site. Larval insects were visually counted, identified to family, and their lengths measured on a maximum of two 50-leaf samples (leaves and supporting petioles) for all common understory saplings within 0.04-ha circular plots. In order to examine the differences in larval insect loads between deciduous and evergreen shrubs, I calculated a mean abundance estimate for each 50-leaf sample by shrub type.

Data analysis

GIS analysis:

To estimate territory boundaries, I implemented a heads-up digitizing technique using the points from male locations to delineate the extent of each territory. I restricted the analyses to when breeding BTBW males defend territories and therefore fledgling movements were largely restricted to specific areas. All points uploaded from GPS units to be used in the analysis were registered in NAD83 UTM Zone17N coordinates using ArcGIS version 10. I conducted a spatial interpolation using plot estimates of stem density of evergreen and deciduous shrubs at both study sites. Specifically, I used Ordinary Kriging to predict stem densities at unsampled locations. The Ordinary Kriging method has been shown to be robust to a number of assumptions concerning the distribution of variance of the data (Kleijnen and van Beers 2005) and allows for incorporation of spatial autocorrelation (Oliver 1990). Kriged shrub density maps were produced independently for both study sites, with a spatial resolution of 5 meters (Figures 3.1 and 3.2). GPS points for fledgling locations at each study site were overlaid on the corresponding Kriged shrub density layer.

I conducted a habitat selection analysis for BTBW broods to examine the effects of microsite characteristics on fledgling locations. I summarized fledgling movements by brood to account for potential non-independence in movements for young from the same nest. For a given brood, I specified all areas within the territory as “available” habitat and fledgling locations as “used” habitat. I generated random points within territory boundaries for each fledgling group, matching the number of random points generated per territory to the number of fledgling points collected for each brood for each site in each year (Figures 3.3 and 3.4). I then extracted stem density estimates of both evergreen and deciduous shrubs for both the fledgling and random points. For each fledgling group, I compared habitat use for the entire post-fledging period using mean estimates of evergreen and deciduous shrub densities of the fledgling locations. I estimated mean shrub density for each fledgling group at random points in each territory as a measure of available habitat to compare against habitat used by fledglings. Finally, I estimated a mean ratio of evergreen to deciduous shrub availability for each fledgling group to assess preference for deciduous versus evergreen shrubs. To evaluate if fledglings were selecting for evergreen shrubs, I compared the ratio of evergreen to deciduous shrubs for fledgling locations to similar ratios for random points.

Statistical analysis:

All statistical analyses were conducted in Program R version 2.14.0 (R Development Core Team 2011). To determine if shrub type influenced larval insect loads, I conducted a negative binomial regression of larval insect abundance on evergreen and deciduous shrubs separately. I selected a negative binomial regression to investigate these differences, as it has been proposed as a superior technique for zero-inflated data where extra-Poisson variation occurs (Lawless 1987).

I analyzed BTBW fledgling habitat selection in a frequentist framework with a series of hypothesis tests. I used a paired Student's t-test to determine if the mean shrub density of fledgling locations was equal to the mean at the random points. All evergreen to deciduous shrub ratios were log transformed to better conform to the Student's t-test assumption of normally-distributed residuals. I then conducted a one-tailed Student's t-test on these data to investigate if fledgling points had higher ratios of evergreen to deciduous shrubs than the random points.

To test if adult age influenced habitat selection by fledglings, I categorized fledglings based on four categories of age of parents: two inexperienced parents; one experienced and one inexperienced parent for each gender; or two experienced parents. I conducted a one-way ANOVA to test the effect of adult age on density of shrub types for fledgling locations. I performed Tukey multiple comparisons tests when an ANOVA was significant. Adult age effects on shrub density of fledgling locations were also analyzed separately by sex. To examine if territory quality naturally varied by age class, I conducted an additional one-way ANOVA of mean shrub density values at the random points for both evergreen and deciduous shrubs.

Results

Data summary

In 2011, of the 113 monitored Black-throated Blue Warbler nests, 27 fledged at least one offspring. I banded 87 nestlings from nests that survived to fledge and resighted 34 fledglings on multiple occasions ($\bar{x} = 4$, SD = 1.12, range = 3-8) throughout the dependence period (15 days after departure from the nest). I followed fledglings for 10 territories at the high site and 10 territories at the low site. For both sites in 2011, I retrieved 146 GPS locations of these 20 different family groups ($\bar{x} = 8.75$, SD = 3.39, range = 2-9). In 2012, I monitored 98 nests, of which 45 fledged at least one offspring. I banded 135 nestlings from nests that survived to fledge and resighted 47 individuals on multiple occasions ($\bar{x}$ = 4, SD = 3.39, range = 3-6). I followed fledglings for 15 territories at the high site and 13 territories at the low site. In total, I retrieved 162 GPS locations of these 28 different family groups ($\bar{x}$ = 7.25, SD = 3.52, range = 2-9).

Average evergreen and deciduous shrub densities were estimated for 346 vegetation plots on the two study sites (168 points for high site, 178 for low site). Estimates from these plots were used to create the interpolated map surface of shrub density (Figures 3.1 and 3.2). Mean estimates of evergreen shrub densities were similar between sites and deciduous shrub density was higher at the low site based on the Kriged data (Table 3.1). Results from the Kriging interpolation revealed that vegetation data collected at additional locations could improve prediction errors, particularly for the high elevation site (Table 3.2). However, I believe that estimates from the surfaces generated by this analysis are adequate to assess relevant differences in shrub density across the sites.

Differences in larval insect availability on shrub types

Larval insect loads on evergreen shrubs were significantly smaller than on deciduous shrubs (odds ratio = 0.12, SE = 0.43017, $P<0.001$). In other words, larval insect loads on evergreen shrubs were 0.12 times smaller than that of deciduous shrubs. Therefore, any preference for evergreen shrubs could likely be attributed to strategies to avoid predation or find cover from bad weather.

Differences in fledgling habitat use versus availability

Analysis of BTBW fledgling habitat selection indicated that fledglings do not seek out denser shrubs in the territory. Densities of evergreen shrubs at fledgling locations were not statistically different than from random locations (t_{48} = -0.5705, P = 0.57, see Figure 3.5). Similarly, fledglings did not select areas in the territory with more deciduous shrubs (t_{48} =

1.2835, $P = 0.21$, see Figure 3.6). Lastly, counter to my hypothesis, fledglings did not prefer evergreen to deciduous shrubs ($t_{48} = 0.7773$, $P = 0.22$, see Figure 3.7).

Adult influence on fledgling habitat use

Age of adults seemed most influential in explaining differences in evergreen shrub stem density of fledgling locations. When at least one adult of the breeding pair was an older, experienced adult, their fledglings were more likely to be found in denser evergreen shrubs ($F_{3,43} = 2.9673$, $P = 0.04$, see Figure 3.8). This pattern did not hold up for deciduous shrubs, however ($F_{3,44} = 0.8486$, $P = 0.47$, see Figure 3.9). Tukey HSD contrasts showed that differences in adult age effects on evergreen shrub density of fledgling locations were only significant for pairs with an experienced male (ASY) and inexperienced female (SY) versus pairs with two inexperienced adults (both SY) (Tukey HSD, $P = 0.02$, see Figure 3.8). Overall, estimates of evergreen shrub density were higher for older adults (Figure 3.10) for fledgling locations, although the confidence intervals overlapped zero in the majority of the Tukey HSD tests. However, neither male nor female age separately explained this pattern of higher evergreen shrub densities for fledgling locations (Figure 3.11). Furthermore, analysis of the random point data indicated that age class of adults did not explain mean evergreen shrub densities of the territories ($F_{3,44} = 1.2835$, $P = 0.13$), although there is a similar pattern (Figure 3.12).

Discussion

Habitat use by BTBW fledglings, as explained by evergreen shrub density, seems to be largely driven by adult age in this region. Fledglings of older adults were found in areas of denser evergreen shrubs, but deciduous shrub density of fledgling locations did not differ by adult age class. As older BTBWs have been shown to predominate in territories with higher shrub density (Holmes et al. 1996), territory quality could explain differences in fledgling habitat use. However, my results suggest that territory quality in terms of shrub density is relatively similar at these study sites. An alternative hypothesis for the effect of adult age class on fledgling habitat selection is that older adults selectively move their fledglings to areas of higher evergreen shrub density. Since my results indicate that evergreen shrubs have fewer larval insects than deciduous shrubs, it seems likely that adult selection of denser evergreen shrubs is motivated by a need to provide increased cover for their young.

Behavioral observations indicated that BTBW offspring position in the shrub layer does not limit foraging range of adults (JLH observation). Comparison of larval insect loads on different shrub types indicated that there was a significant difference in food availability between the two types of shrubs. However, the magnitude of difference was not great and confidence intervals were wide. Although it is possible that fledglings could also seek deciduous shrubs for cover in addition to evergreen shrubs, this analysis would benefit from information on the predator population dynamics of this area. Similar studies to investigate fledgling habitat use should attempt to collect such data.

Additional results of this research suggest that BTBW fledglings do not select habitats with denser shrubs or show a preference for evergreen over deciduous shrub types, contrary to my original predictions. There are a couple of possible explanations for these results. First, breeding adult BTBWs may be actively seeking areas of higher shrub density when settling territories or variability of shrub density within a territory may be small. Holmes et al. (2006) indicated that older, experienced males tend to occupy territories with higher shrub density than younger, inexperienced individuals. If more experienced adults were settling territories with greater shrub density, I would expect to see a difference between shrub density of fledgling locations for younger versus older males, but this pattern was not evident in my analysis. Second, if sufficient data were available to investigate these landscape-level differences in vegetative structure of unoccupied areas versus territories, fledgling use of shrubbier habitats might be more apparent. While this shrub density hypothesis is incongruent with previous studies of habitat selection by breeding BTBWs (Steele 1992), studies like this likely have not evaluated habitat use at a large enough spatial scale to assess a spectrum of suitable BTBW breeding habitat and are potentially not capturing sufficient variability in sampling.

Multiple studies of fledgling use of habitat have indicated that fledglings tend to be in areas of dense shrubs (Thompson III and Dessecker 1997, Rush and Stutchbury 2008, Mitchell et al. 2010, Moore et al. 2010). At my study sites, a number of shrub species predominate in the understory, including mountain laurel (*Kalmia latifolia*), rosebay Rhododendron (*Rhododendron maximum*) and huckleberry (*Gaylussacia sp*.) and all three species are ubiquitous across both sites. These shrubs are the primary nesting substrates for BTBWs in this region and are quite likely occupied by fledglings throughout the dependency period. It is important to note that vegetative structure at higher elevations in the study area is fairly homogeneous and likely represents some of the best quality breeding habitat available for songbirds in the Southern Appalachian region. The older age structure of breeding BTBWs and relatively high territory densities are indicative of high quality habitat for this species (Holmes et al. 2005). Although it is possible that BTBW fledglings have different habitat needs than other songbirds, particularly during the dependency period, it is more likely that my data were insufficient to capture fine-scale variability in vegetative structure at the sites. Incorporation of additional BTBW breeding sites with greater variability in shrub density would likely improve characterization of fledgling use of microsites.

Previous studies of this species have shown that higher leaf density is an important predictor of settlement and consequently influences breeding productivity (Steele 1992, Holmes et al. 1996). Insectivorous migratory birds might directly associate leaf area with food availability when selecting suitable habitat. It is possible that leaf density would be a good predictor of fledgling habitat selection as well, particularly for evergreen shrubs. Moreover, leaf density metrics could provide a sufficiently fine scale to distinguish of patterns in fledgling habitat selection between shrub types. Unfortunately, data on leaf density are not currently available to test fledgling preference, although I would expect that patterns of shrub density could be correlated with leaf density. Future studies on songbird fledgling habitat selection should consider a suite of vegetation measures.

Conclusion

This is one of the first studies to document the influence of adult characteristics on fledgling habitat selection. Although a couple of studies have noted that adult age is positively related to fledgling survival (King et al. 2006, Rush and Stutchbury 2008), none of these studies have investigated the influence of adult age on fledgling habitat use. Reports of fledgling preference for dense habitat may very well be dictated by adult preference. Previous research of the influence of adult age on songbird nesting success has shown that experience can play an important role, with more experienced adults being able to locate more or better-quality prey or lower the risk of predation of their young (Porneluzi and Faaborg 2001, Zanette 2001). This study is the first to indicate that breeding experience of older BTBW adults likely contributes to success of fledglings, with experienced individuals more able to provide food and protection for their offspring during this vulnerable dependency period. Future research on habitat selection of dependent offspring should consider parental influence.

For songbirds in the Southern Appalachians, densities of evergreen shrubs may play a vital role in juvenile survival. High densities of evergreen shrubs seem preferred by fledglings of older, more experienced BTBW. For dependent songbirds, this habitat selection is likely driven by adult decisions to minimize predation or exposure. This study does not seek to downplay the role of adequate food availability in BTBW fledgling survival. In fact, model selection analyses from Chapter 2 reflect the importance on survival of appropriate timing of fledging to peak insect availability. Rather, multiple strategies may be employed to maximize juvenile survival probabilities that operate on different temporal and spatial scales. Thus, in managing habitat for fledgling survival it is important to bear in mind that both aspects of adult behavior and species-specific habitat associations could influence this life stage. If BTBW populations in this region trend towards younger age classes, managing for shrub density alone may not be sufficient to maintain relatively high rates of fledgling survival.

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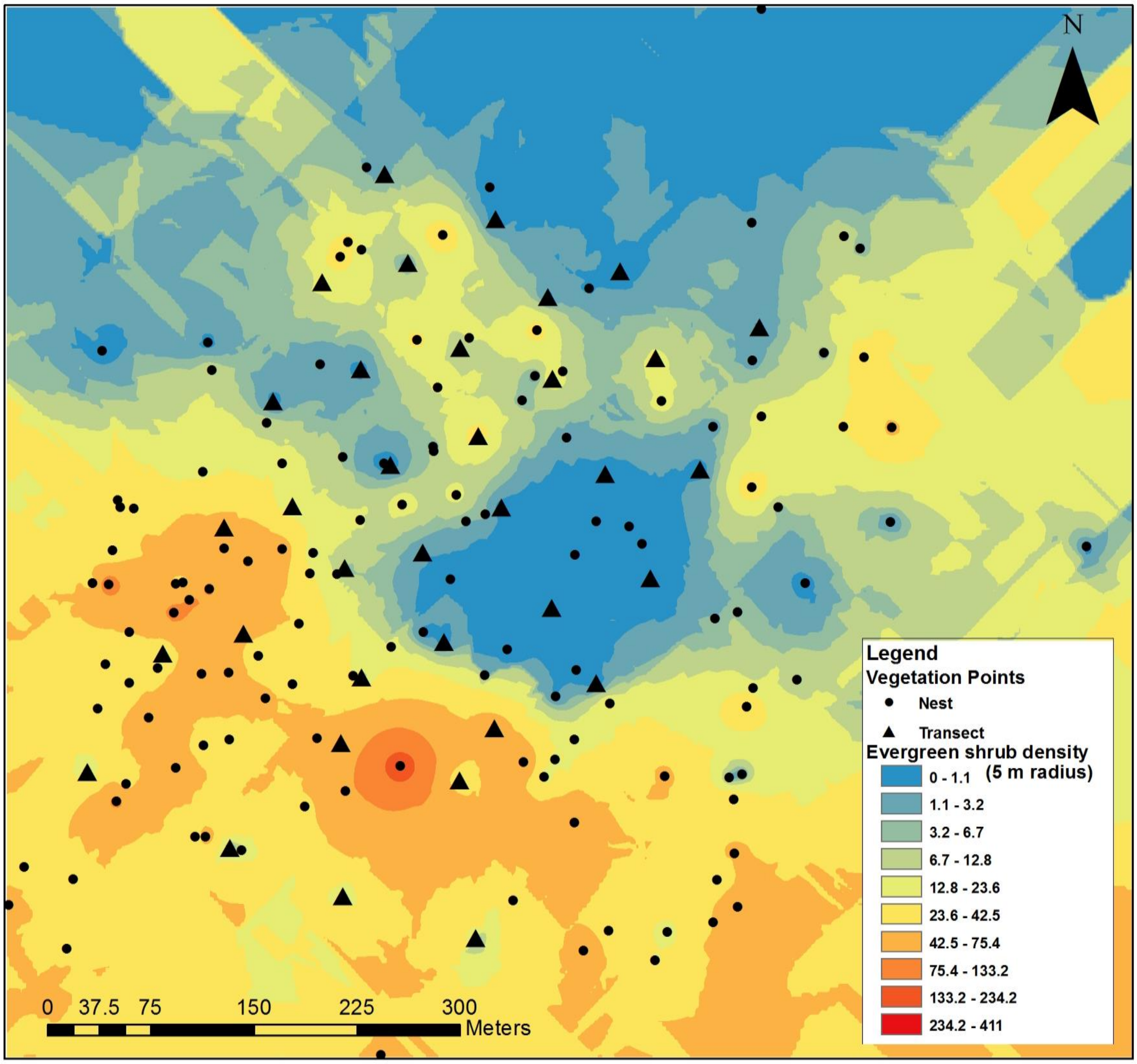
Table 3.1. Mean estimates, standard errors, and ranges of shrub density for both evergreen and deciduous shrub types from Kriged surfaces at the low and high sites. Stem density counts in 3-meter circular radius plots were conducted at nest locations and transect locations (displayed in Figure 3.1-3.2 as vegetation points) from 2010-2012 in the Nantahala National Forest, NC.

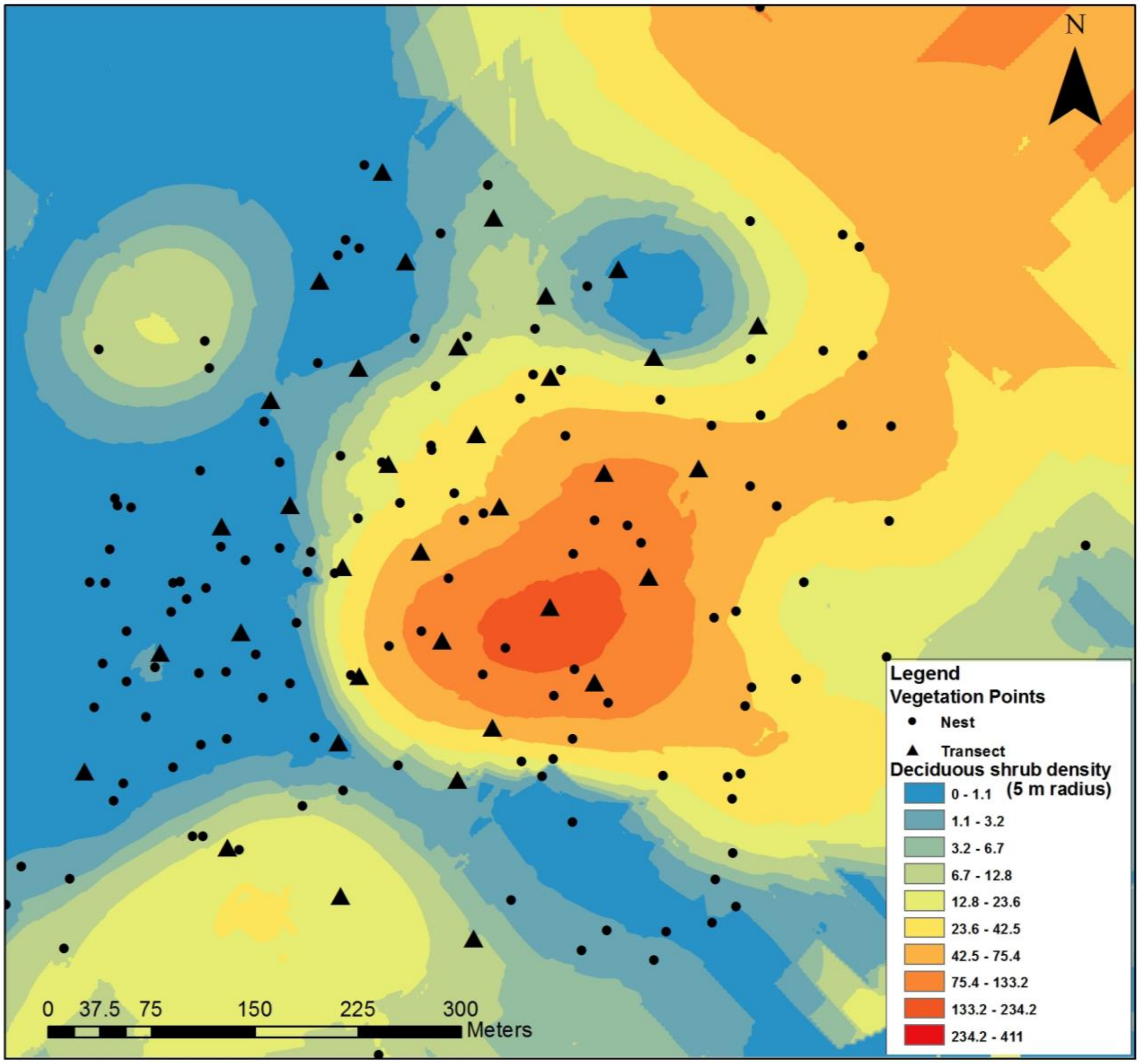
	Mean	**SE**	**Range**
Evergreen			
Low site	27.4	0.05	0 - 99.6
High site	30.0	0.09	0 - 194.3
Deciduous			
Low site	49.1	0.17	0 - 318.2
High site	30.8	0.06	0 - 137.6

Table 3.2. Prediction errors of ordinary Kriging interpolation methods conducted for evergreen and deciduous shrub density at two study sites in the Nantahala National Forest, North Carolina. For unbiased estimates, root-mean-square prediction errors (calculated as the square root of the average of the squared distances between predicted and measured values) should be as small as possible. Moreover, mean standard errors of estimates (variability of the predictions estimated from measurement values) should be close to the RMS prediction errors.

	Deciduous shrubs		Evergreen shrubs	
Site	low	high	low	high
Mean	-0.20	-0.35	-0.41	-0.34
Root-mean-square (RMS)	52.43	44.35	30.59	35.38
Average standard error	47.65	45.62	30.31	32.98
RMS standardized	1.09	0.99	1.01	1.07

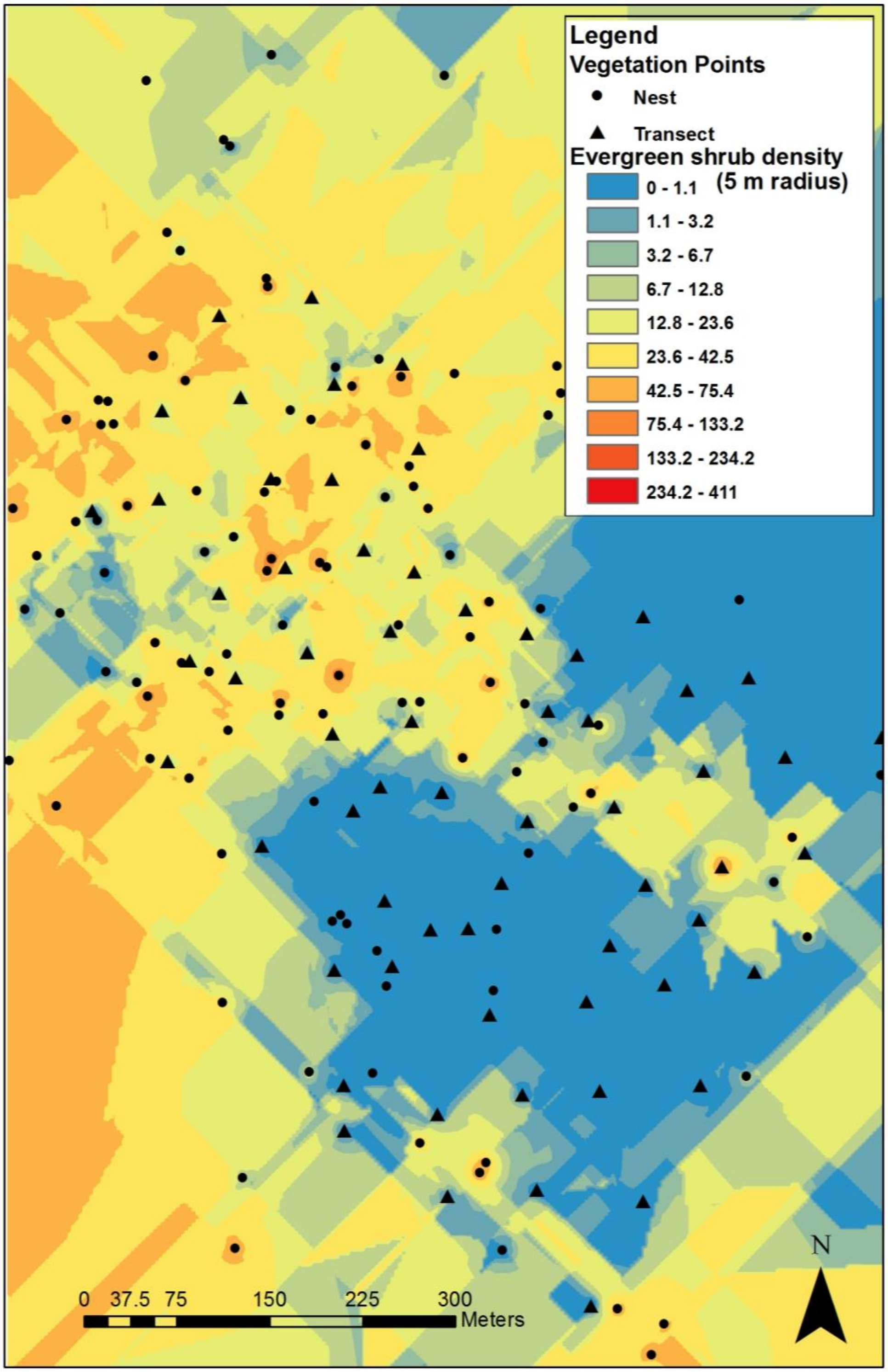

N
Legend
Vegetation Points
Nest
Transect
Evergreen shrub density
(5 m radius)
0 - 1.1
1.1 - 3.2
3.2 - 6.7
6.7 - 12.8
12.8 - 23.6
23.6 - 42.5
42.5 - 75.4
75.4 - 133.2
133.2 - 234.2
234.2 - 411
0
37.5
75
150
225
300
Meters

a).

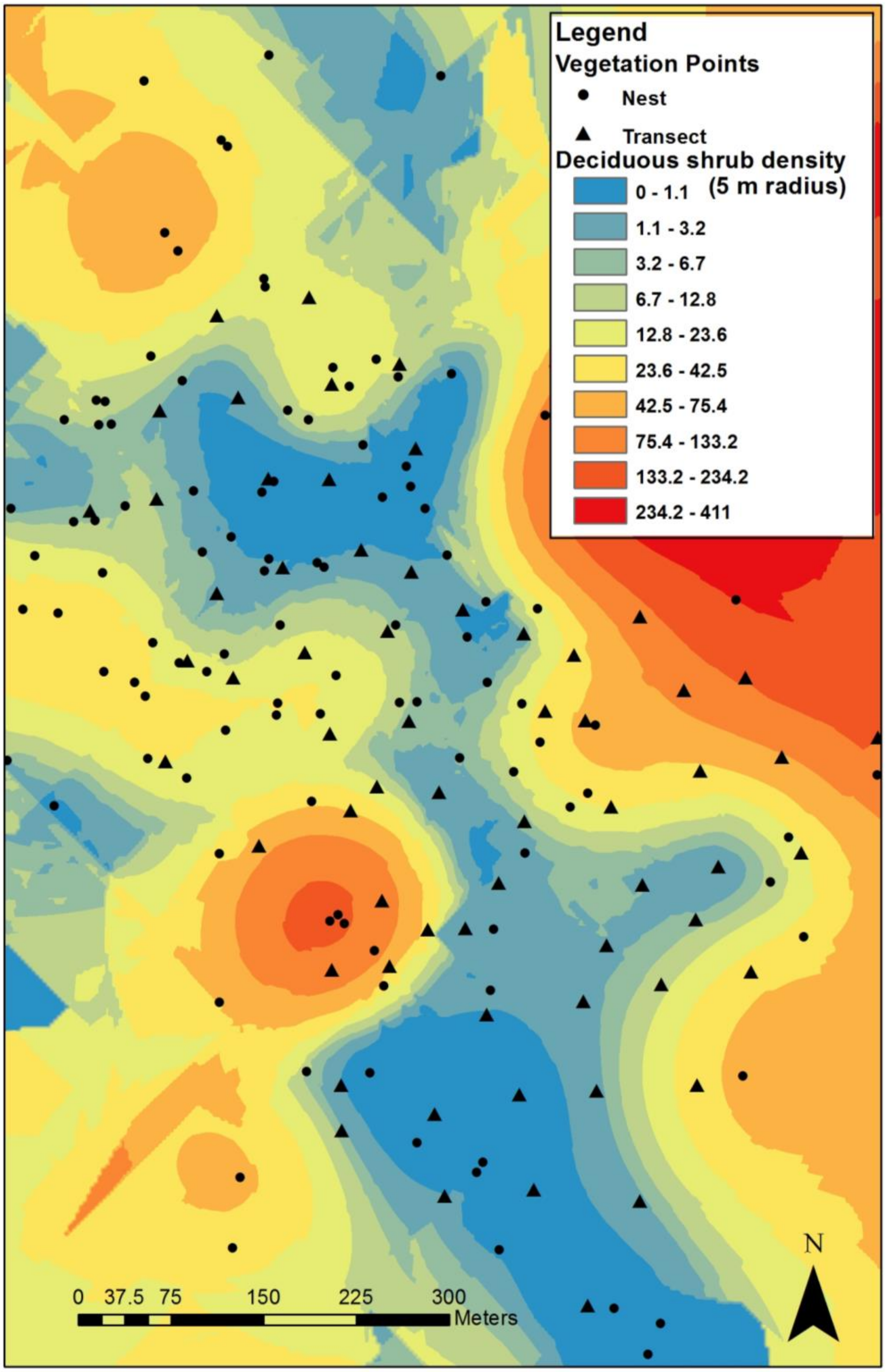


b).

Figure 3.1. Ordinary Kriging interpolations of **a)** evergreen and **b)** deciduous shrub density (within 5-meter radius) from vegetation points collected at the high site. Stem density counts in 3-meter circular radius plots were conducted at nest locations and transect locations (displayed below as vegetation points) from 2010-2012 in the Nantahala National Forest, North Carolina.

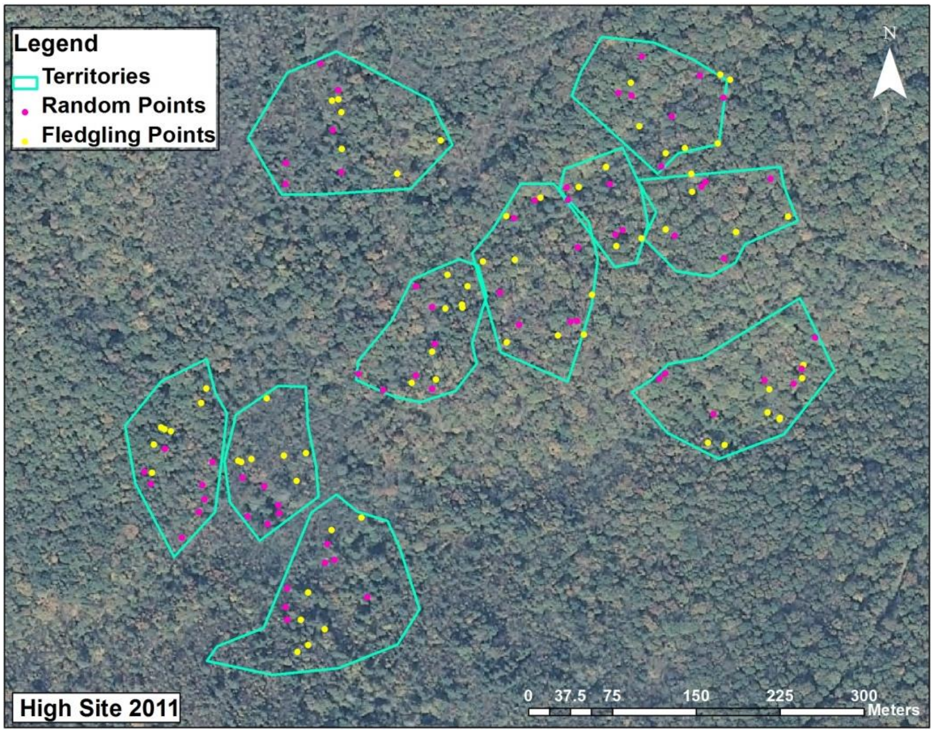

Legend
Vegetation Points
● Nest
▲ Transect
Evergreen shrub density (5 m radius)
0 - 1.1
1.1 - 3.2
3.2 - 6.7
6.7 - 12.8
12.8 - 23.6
23.6 - 42.5
42.5 - 75.4
75.4 - 133.2
133.2 - 234.2
234.2 - 411
N
0
37.5
75
150
225
300
Meters

a).

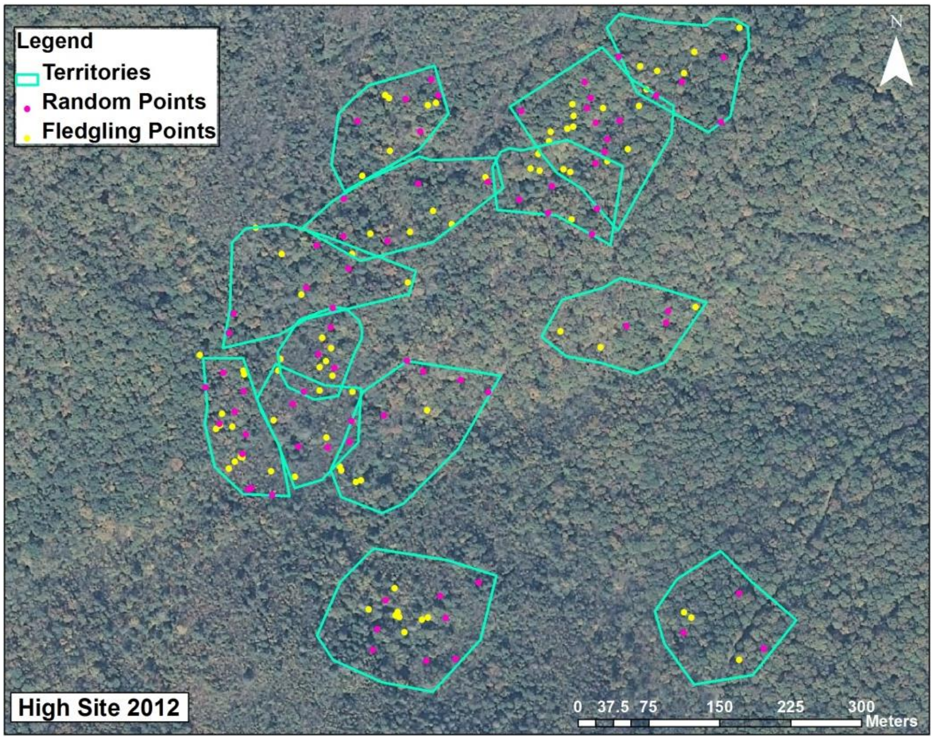


b).

Figure 3.2. Ordinary Kriging interpolations of **a)** evergreen and **b)** deciduous shrub density (within 5-meter radius) from vegetation points collected at the low site. Stem density counts in 3-meter circular radius plots were conducted at nest locations and transect locations (displayed below as vegetation points) from 2010-2012 in the Nantahala National Forest, North Carolina.

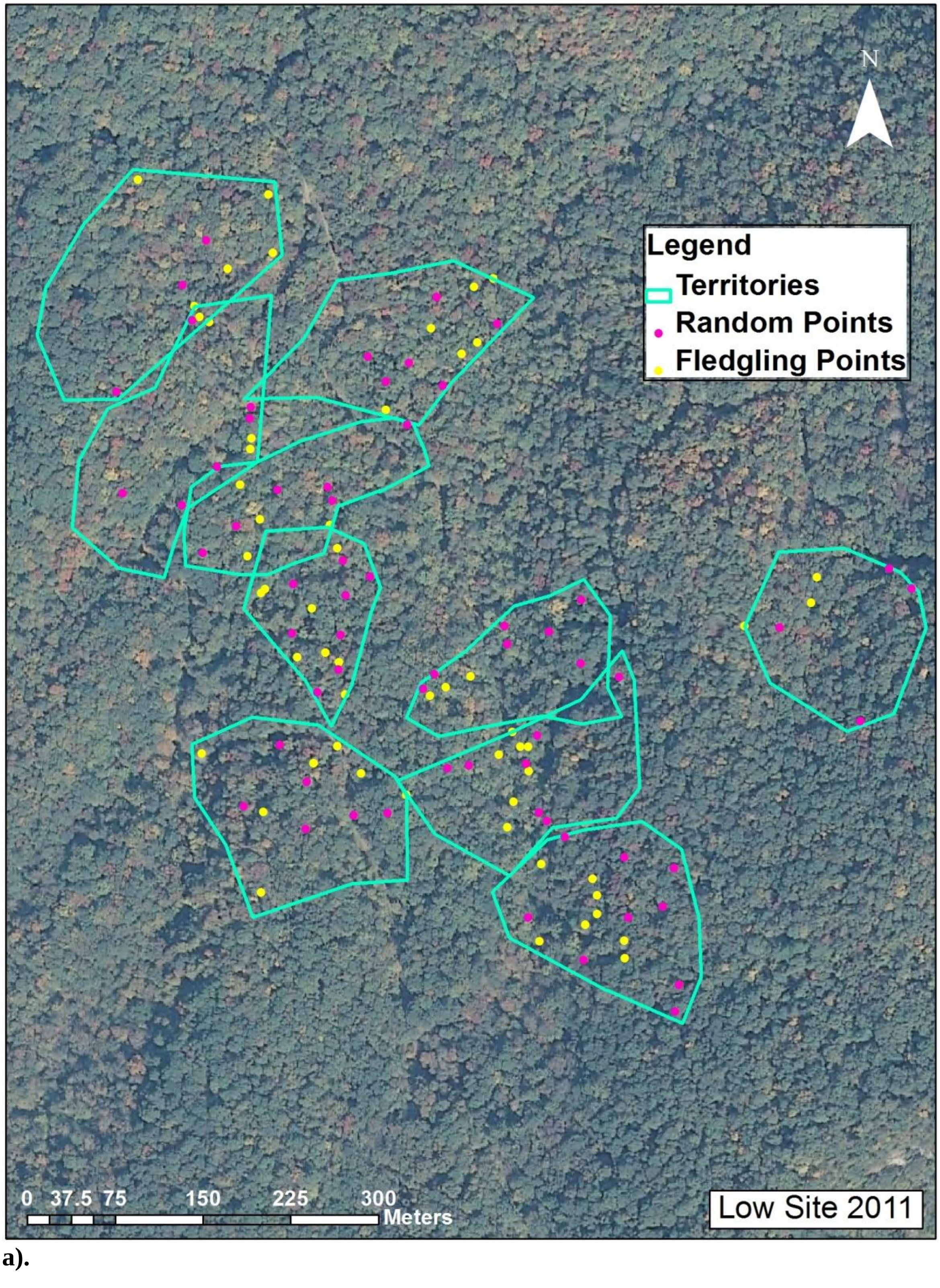


a).

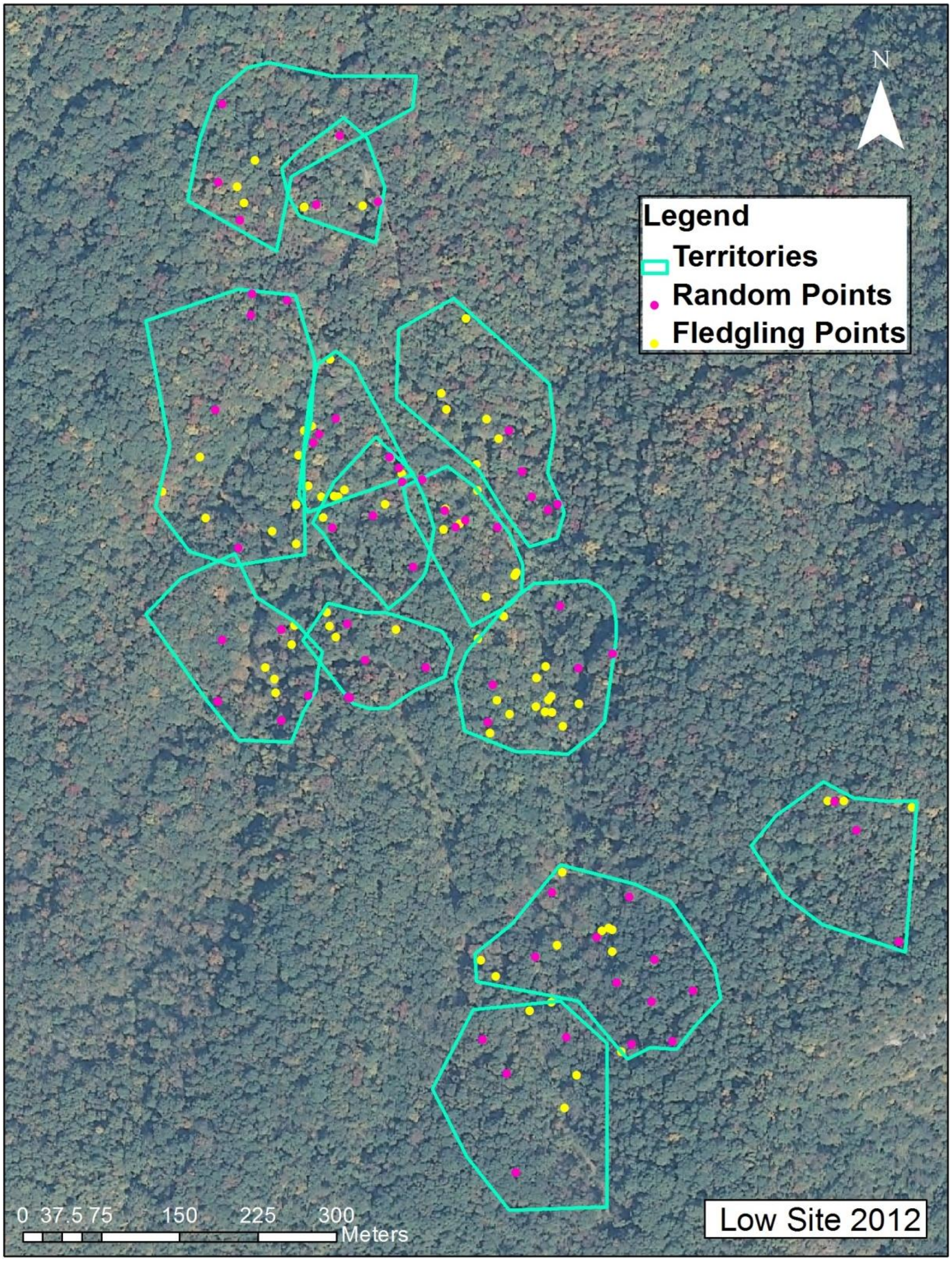


b).

Figure 3.3. Fledgling locations and randomly generated points within BTBW territory boundaries for high site in **a)** 2011 and **b)** 2012 in the Nantahala National Forest, North Carolina overlaid on true color leaf-on 2009 National Agricultural Imagery Program Digital Orthophotos.


N
Legend
Territories
Random Points
Fledgling Points
0
37.5
75
150
225
300
Meters
Low Site 2011

a).



b).

Figure 3.4. Fledgling locations and randomly generated points within BTBW territory boundaries for low site in **a)** 2011 and **b)** 2012 in the Nantahala National Forest, North Carolina overlaid on true color leaf-on 2009 National Agricultural Imagery Program Digital Orthophotos.

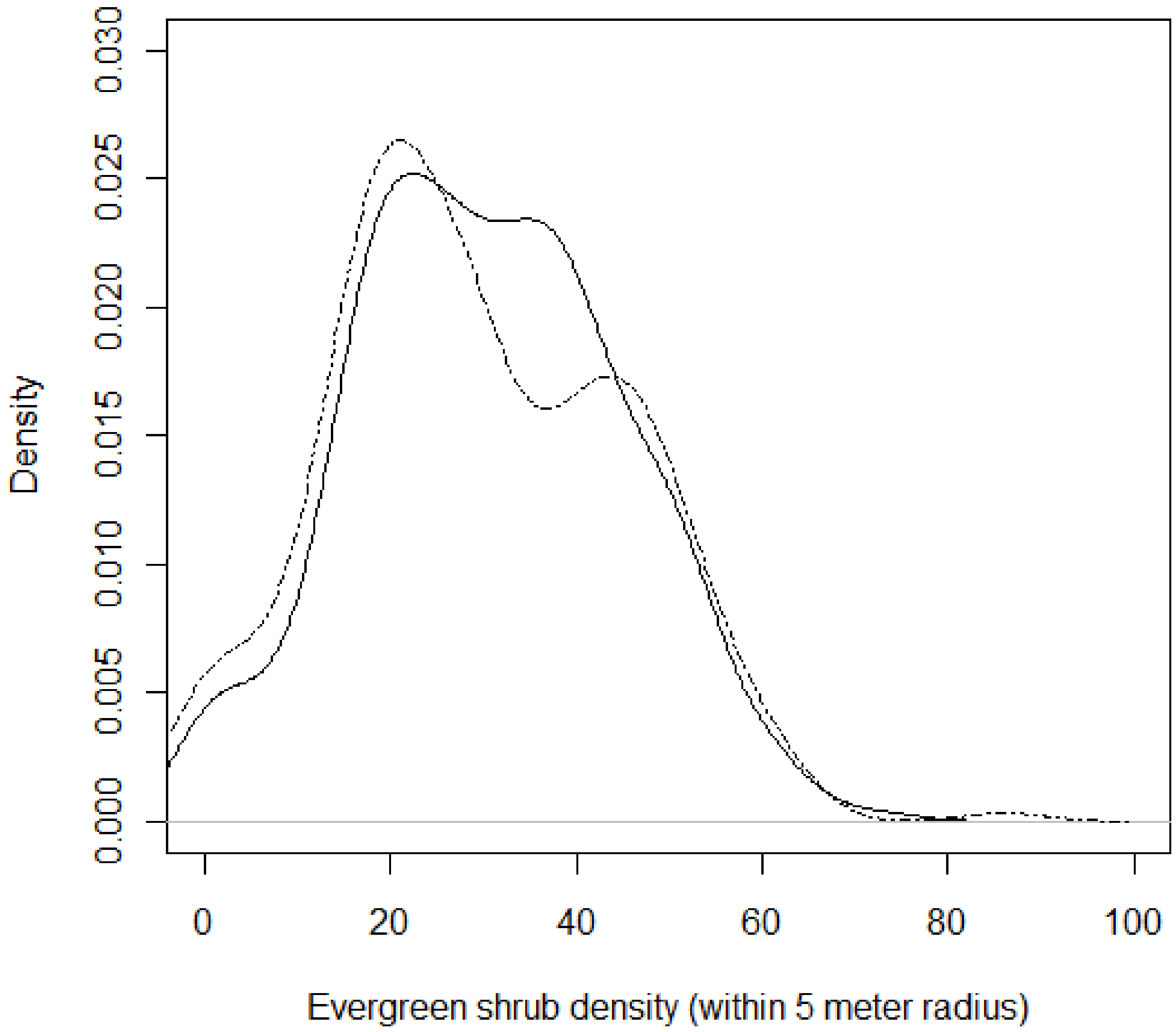


Figure 3.5. Kernel density plot of evergreen shrub density estimates from Kriging interpolation of fledgling locations compared to random locations for 2011-2012 in the Nantahala National Forest, North Carolina.

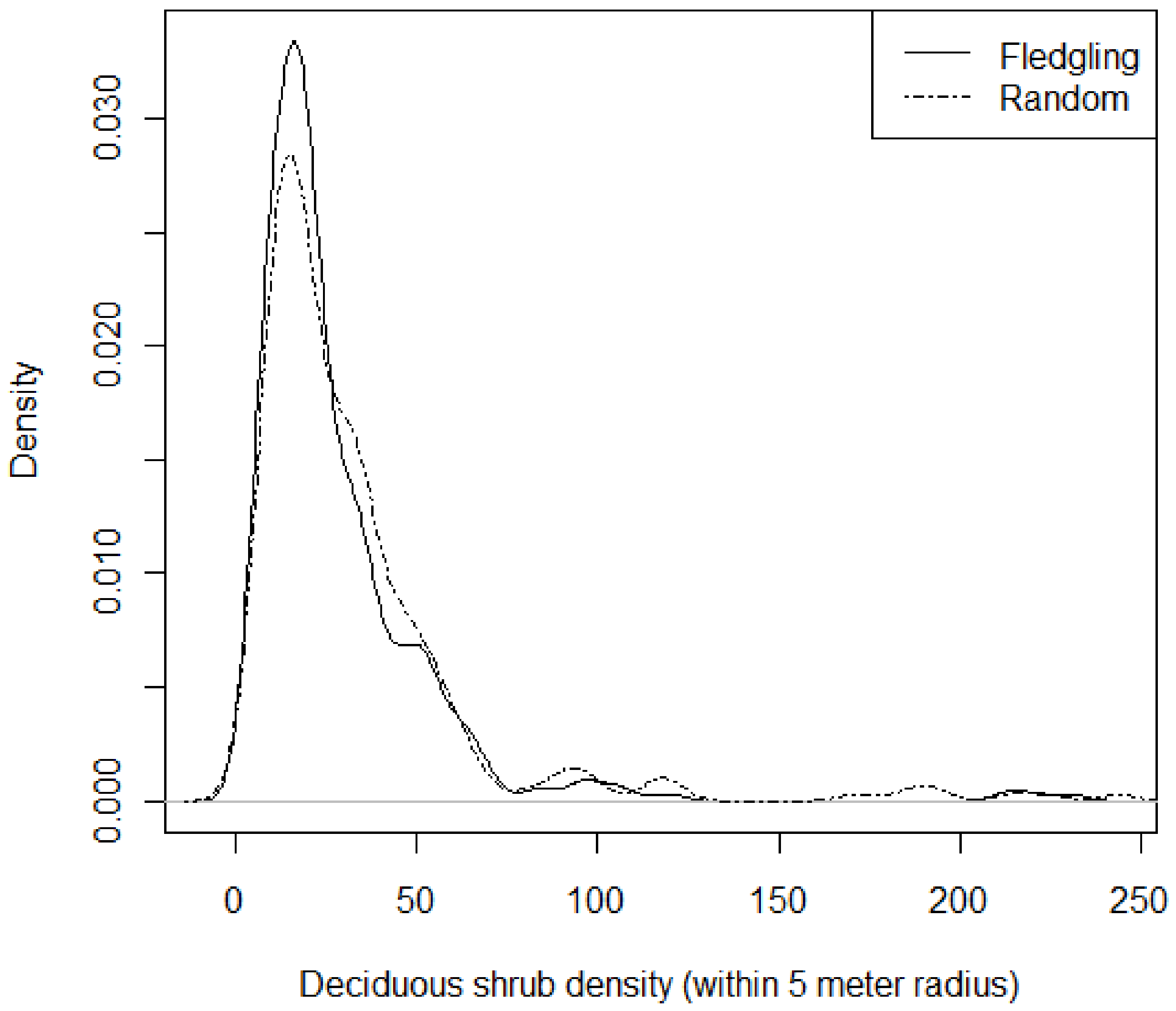


Figure 3.6. Kernel density plot of deciduous shrub density estimates from Kriging interpolation of fledgling locations compared to random locations for 2011-2012 in the Nantahala National Forest, North Carolina.

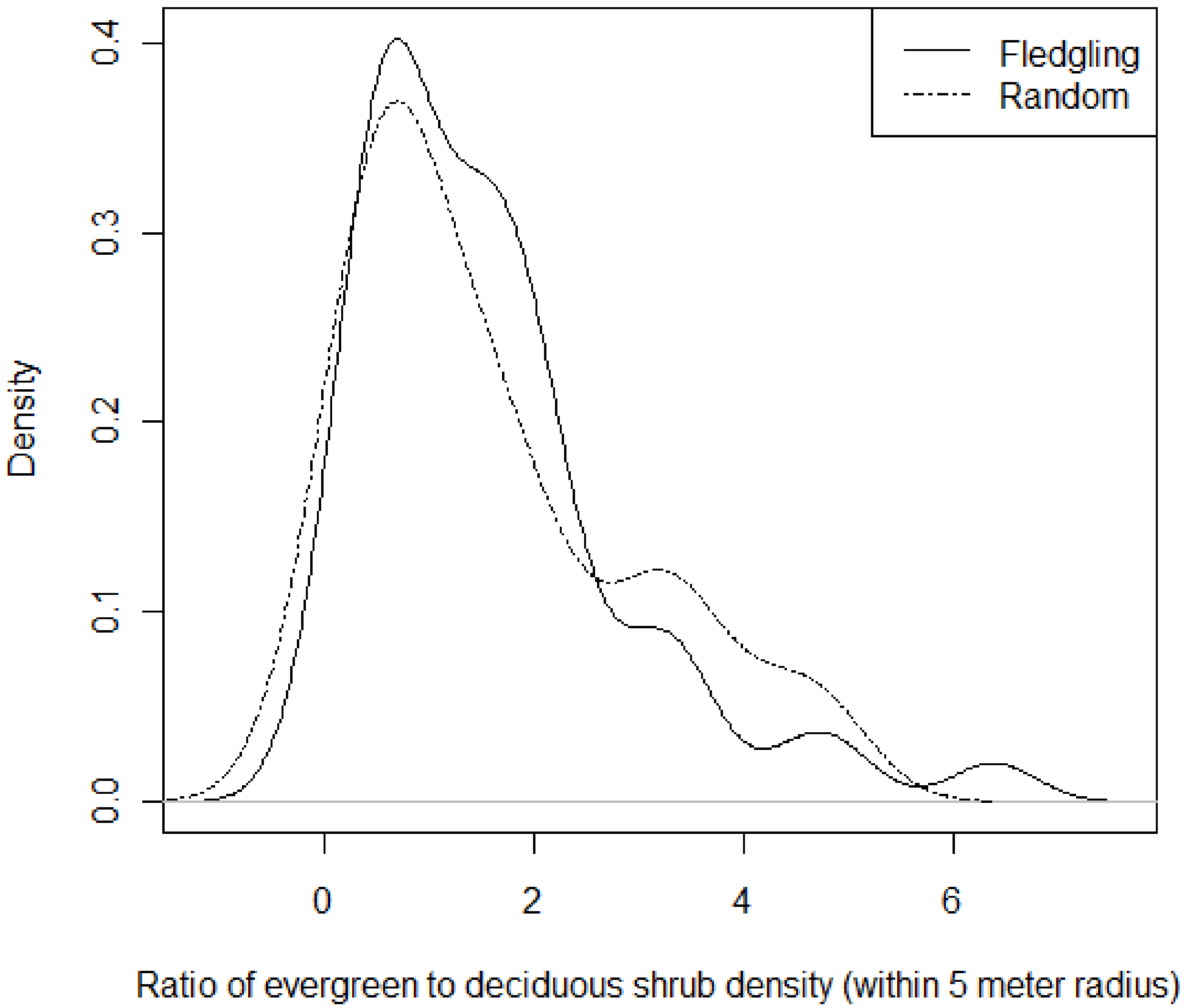


Figure 3.7. Kernel density plot of ratios of evergreen to deciduous shrub density for fledgling locations compared to random locations for 2011-2012 in the Nantahala National Forest, North Carolina.

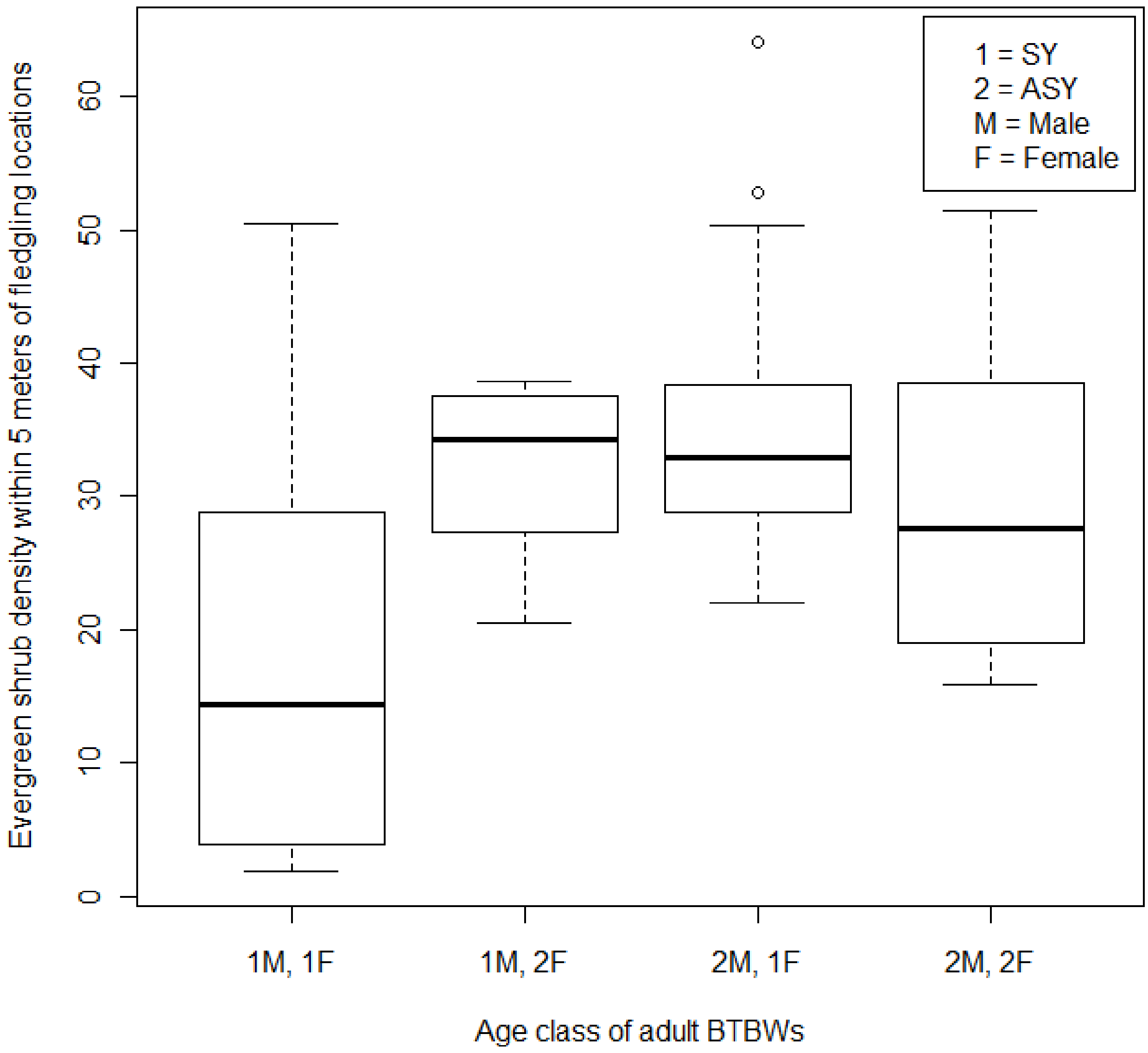


Figure 3.8. Variability in evergreen stem density for fledgling locations summarized by age of BTBW adult pairs in the Nantahala National Forest, North Carolina, 2011-2012, pooled for both sites. Possible combinations of adult pairs on x-axis is indicated in legend. Boxes represent the 25th to 75th quartiles and lines within boxes denote median shrub density. Whiskers extend to data points within 1.5 times the interquartile range and dots indicate outliers beyond 1.5 times the interquartile range.

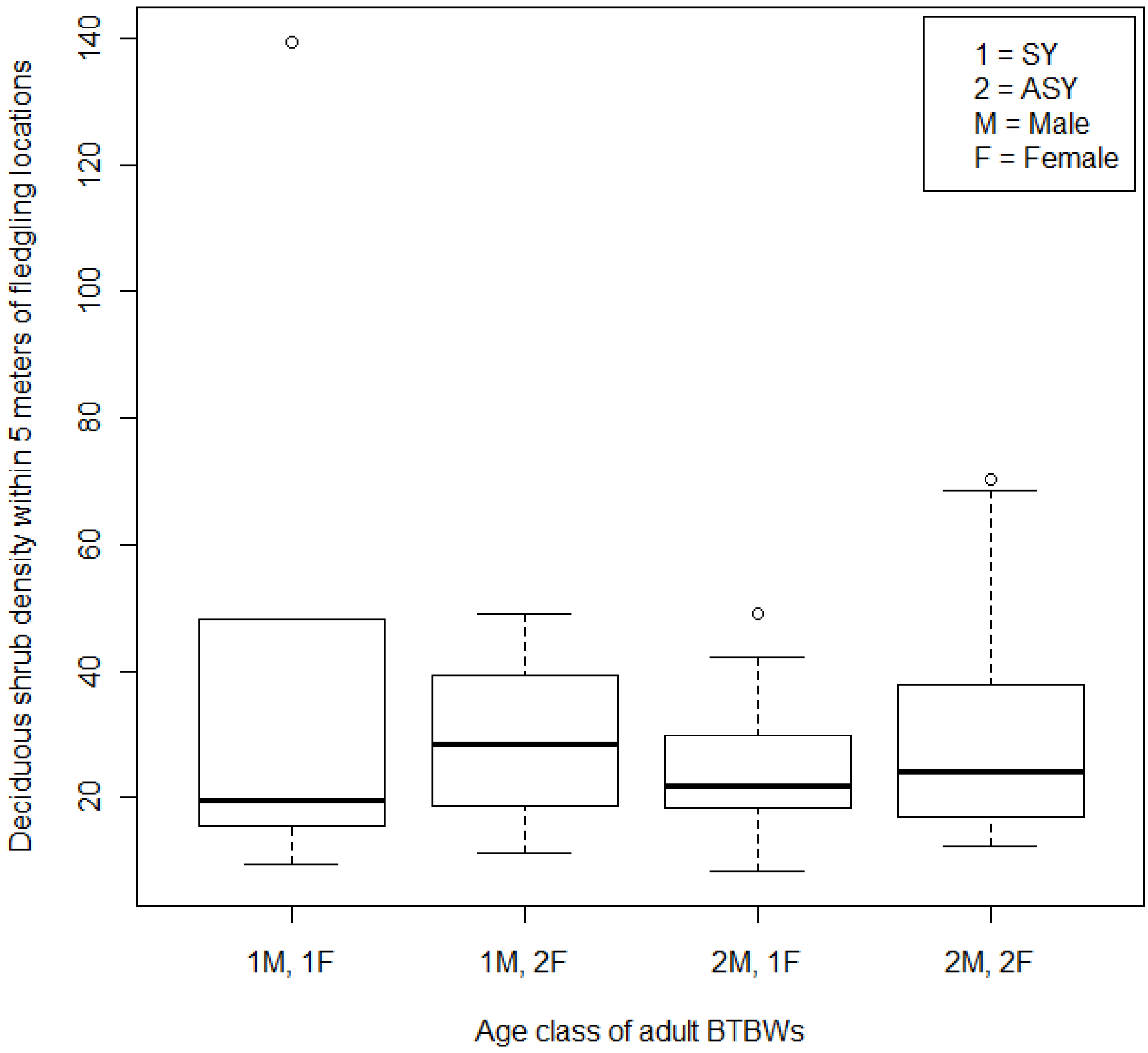


Figure 3.9. Variability in deciduous stem density for fledgling locations summarized by age of BTBW adult pairs in the Nantahala National Forest, North Carolina, 2011-2012, pooled for both sites. Possible combinations of adult pairs on x-axis is indicated in legend. Boxes represent the 25th to 75th quartiles and lines within boxes denote median shrub density. Whiskers extend to data points within 1.5 times the interquartile range and dots indicate outliers beyond 1.5 times the interquartile range.

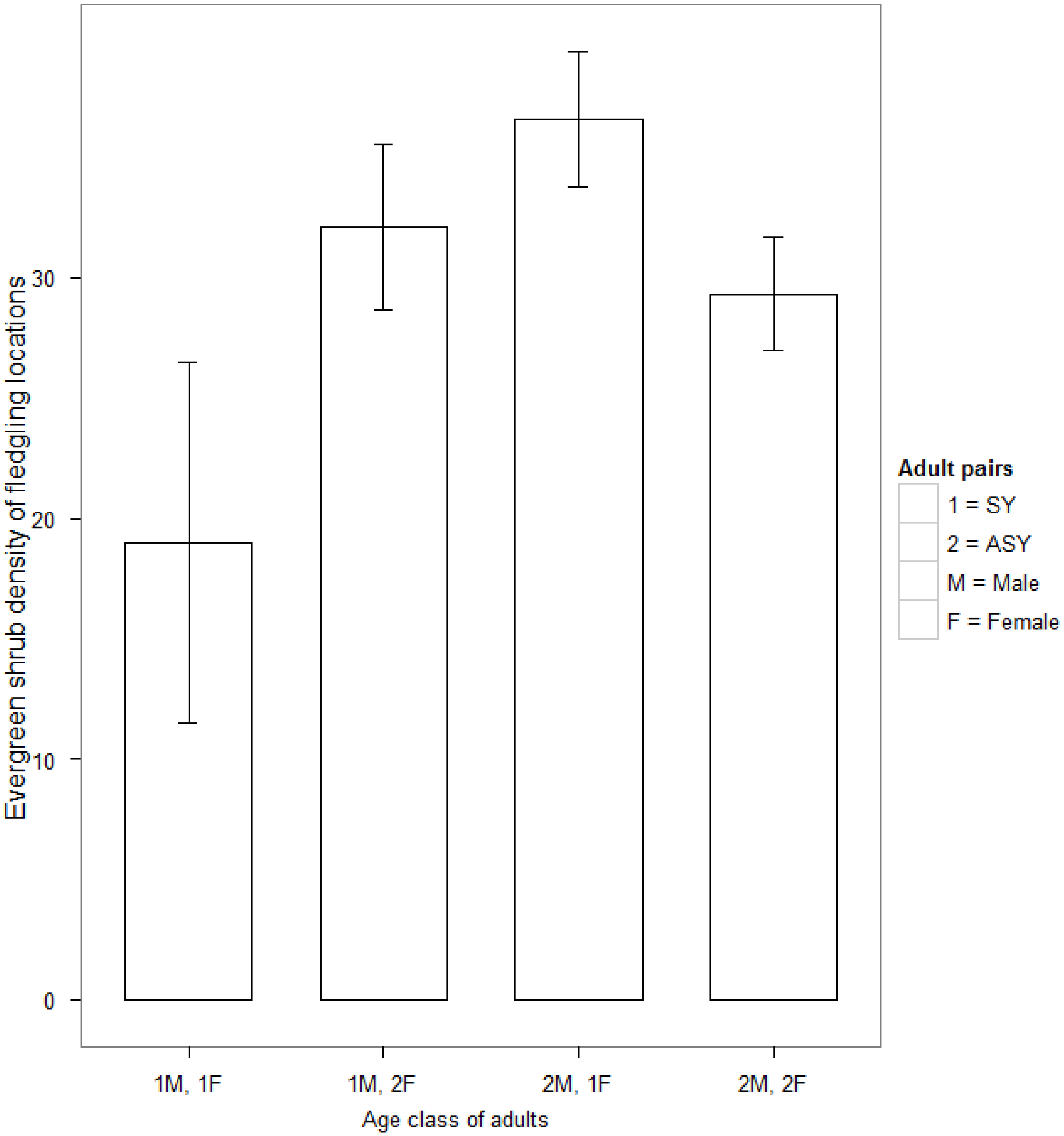
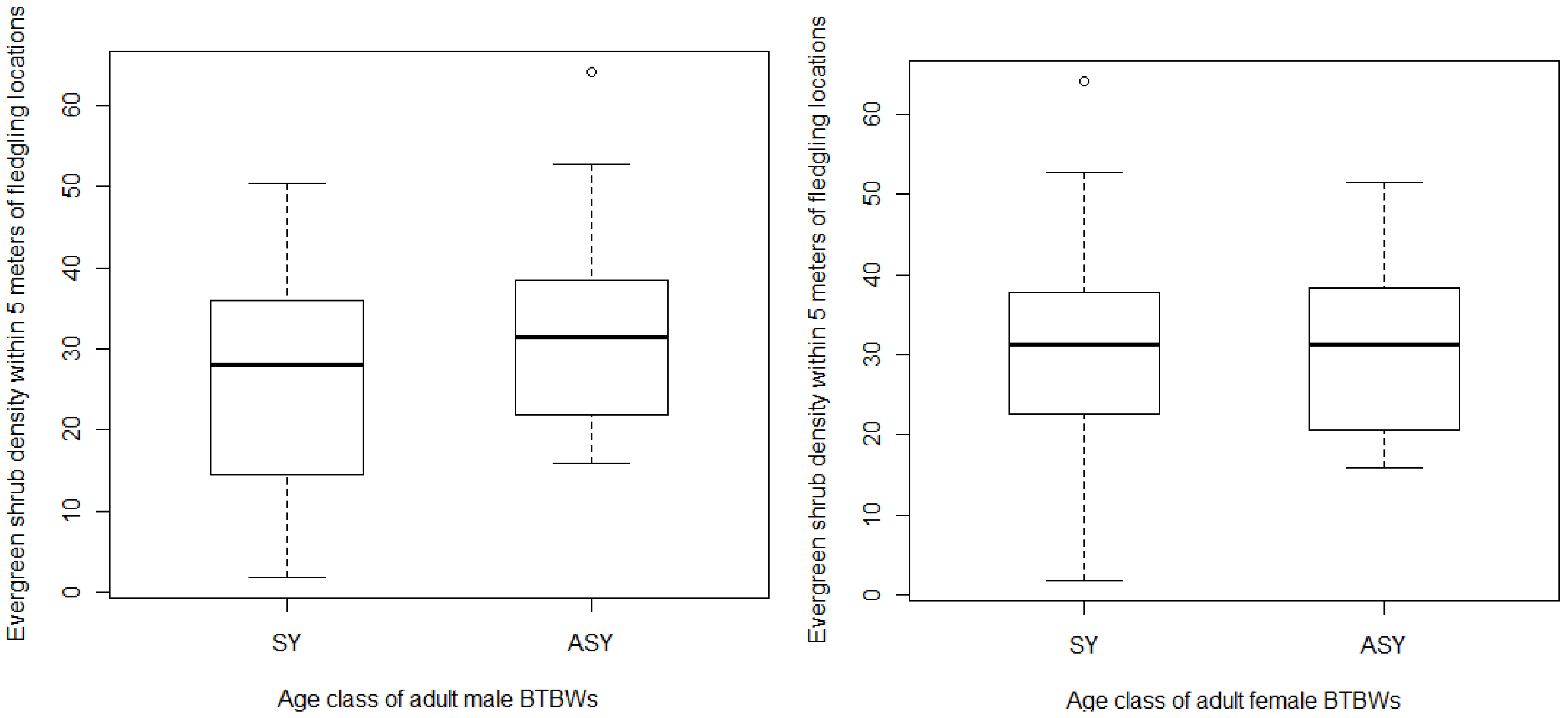


Figure 3.10. Mean estimates and standard errors of evergreen shrub stem density for fledgling locations summarized by age of adult pairs in the Nantahala National Forest, North Carolina, 2011-2012 for both sites.



a). **b).**

Figure 3.11. Variability in evergreen stem density for fledgling locations summarized by age of BTBW adult **a)** males and **b)** females in the Nantahala National Forest, North Carolina, 2011-2012, pooled for both sites. Boxes represent the 25th to 75th quartiles and lines within boxes denote median shrub density. Whiskers extend to data points within 1.5 times the interquartile range and dots indicate outliers beyond 1.5 times the interquartile range.

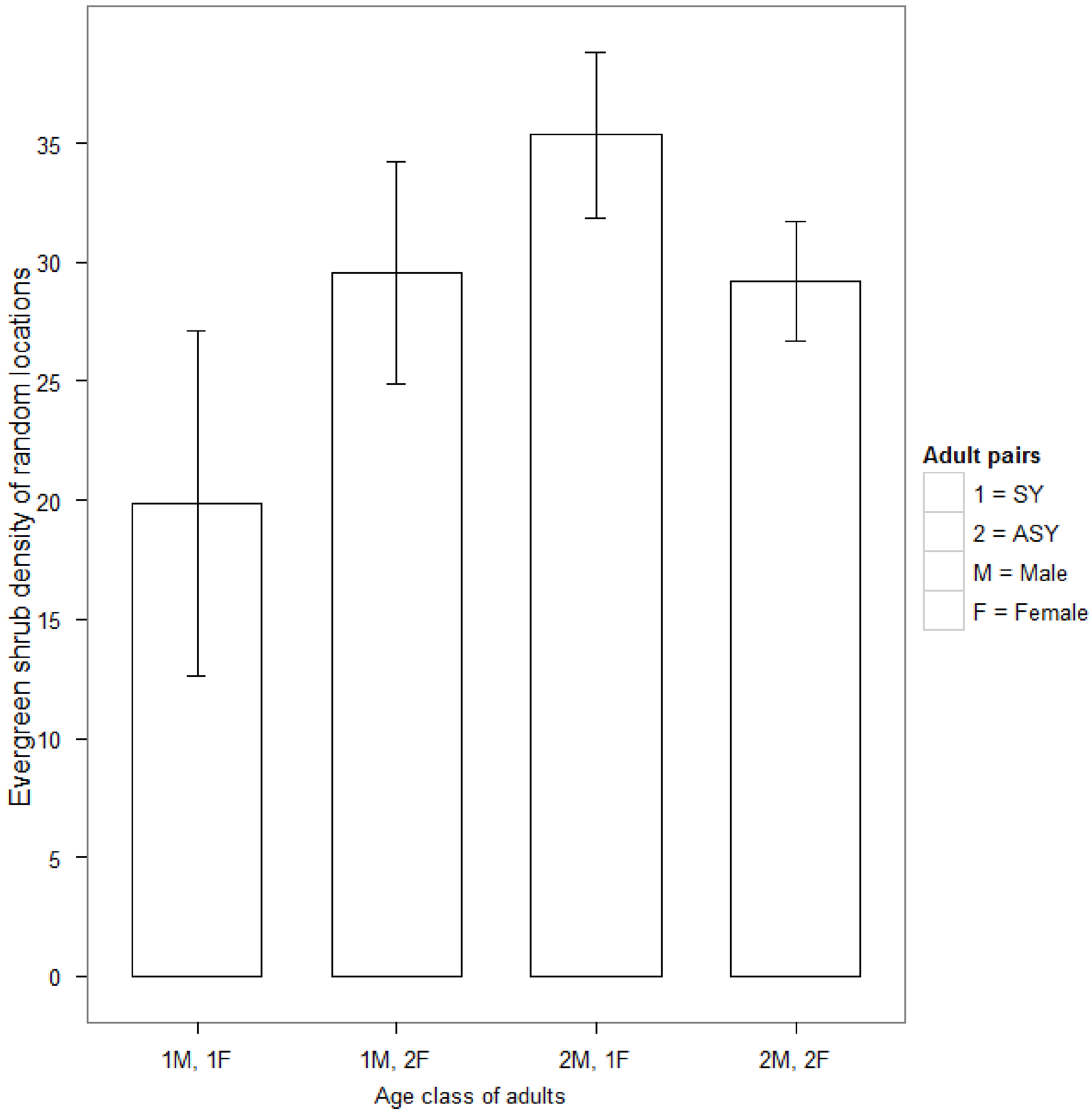


Figure 3.12. Mean estimates and standard errors of evergreen shrub stem density for random locations summarized by age of adult pairs in the Nantahala National Forest, North Carolina, 2011-2012 for both sites.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Summary

The primary goals of this research project were to: 1) produce reliable estimates of fledgling survival for BTBW populations in the Southern Appalachians; and 2) advance the understanding of how young select habitat and make inferences about the potential consequences of their decisions. I was particularly interested in knowing if asynchrony in the timing of breeding and peak food availability could have negative ramifications on fledgling survival. Phenological mismatches, possibly spurred by climate change, are often cited as potential factors contributing to decreased songbird productivity (Parmesan and Yohe 2003), yet few studies have investigated such mismatches (Both and Visser 2001, Visser et al. 2006, Both et al. 2009, Pearce-Higgins et al. 2010). My research demonstrated that variability in food resources can have negative consequences for fledgling survival, as the effect of food availability on survival was greater for young that fledged much later than the initial larval insect peak. Additionally, I provided the first estimates of BTBW fledgling survival which will aid in a more holistic understanding of population dynamics for this species. Lastly, I presented evidence that adults may play a major role in habitat selection for young, which had not been previously considered in other fledgling studies. This information provides a cautionary reminder of the importance of considering both extrinsic and intrinsic factors when attempting to understand the survival and movements of young birds.

In Chapter 2, I tested hypotheses of the major contributing factors to BTBW fledgling survival using a model selection approach. I compared competing hypotheses of factors that could influence fledgling survival probabilities. Variables considered in the analysis included spatially and temporally varying aspects of habitat and individual bird characteristics. I found an interactive effect between fledge date and food availability (i.e., larval insects) best explained BTBW fledgling survival. In fact, juvenile BTBWs that departed the nest at the end of the breeding season and with access to fewer insects had a 10% reduction in survival from those that had access to greater insect loads. Although a few studies have demonstrated that breeding success can be affected by phenological mismatches of food resources and nesting, my research suggests that mismatches in peak larval insects and timing of breeding could have protracted consequences into the postfledging period. Future studies of the effects of climate change on songbirds should collect data to include the postfledging period to examine effects of fledging survival on total reproduction.

Fledgling survival was best explained by a model that included an interaction between food availability and timing of fledge, thus, more research should be conducted to determine the mechanisms driving this interaction. It is likely that food quality declines as the breeding season progresses at these study sites (Verboven et al. 2001) and such information would be valuable to explain discrepancies in survival probabilities at different times of the season. Additionally, the top model of survival also included an effect of fledgling age. Since mobility of BTBW young increases with time from nest departure, this result is consistent with an understanding of fledgling mortality risk.

I modeled fledgling survival of color-banded birds using mark-resight techniques with CJS models in a Bayesian framework. The design of my analysis permitted me to accomplish two things that have largely been absent in other fledgling survival studies. First, I could generate reasonable estimates of juvenile survival without potentially impeding mobility of individuals. BTBW fledgling survival estimates were high (35-39%) compared to other songbird estimates (King et al. 2006, Rush and Stutchbury 2008, Moore et al. 2010, Vitz and Rodewald 2011). The difference in survival estimates of my study from prior fledgling research is possibly attributable to negative effects of transmitters (Mattsson et al. 2006) and future work should attempt to make use of widely-accepted survival models to avoid this confounding factor. Second, issues of non-independence arise in the study of individual birds from the same brood. Using a Bayesian analysis, I was able to incorporate natural stochasticity and account for overdispersion in my limited dataset, likely improving survival estimates.

In Chapter 3, I evaluated microsite habitat selection by BTBW fledglings. I expected that BTBW fledglings would prefer areas of greater shrub density and would more likely be found in evergreen shrubs than deciduous shrubs, given the high availability of both on my study sites. Other research conducted on habitat use has indicated that songbirds require dense shrubby habitat during the postfledging period. However, my results showed that fledglings did not favor either evergreen or deciduous shrubs or areas of greater shrub density. However, adult age seemed to contribute to habitat selection, with fledglings of older adults more likely to be located in areas of greater evergreen shrub density. This selection could influence BTBW fledgling survival, as older adults are more experienced breeders. These experienced adults may preferentially seek areas of greater evergreen shrub density. Evergreen shrubs surveyed at the study sites had significantly smaller larval insect loads than deciduous shrubs and thus preference for evergreen shrubs is likely based on a need for cover rather than food. BTBW fledglings are susceptible to a host of potential predators including Blue Jays (*Cyanocitta* *cristata*), Broad-Winged Hawks (*Buteo platypterus*), Eastern Chipmunks (*Tamias striatus*), Red Squirrels (*Tamiasciurus hudsonicus*) and a variety of snake species. Adults may seek out areas in their territories to minimize predation risk and future studies should examine in greater detail the influence of predators on fledgling habitat selection.

Conclusion

My project was developed from an interest in gaining more knowledge of the influence of food on songbird fledgling survival. Many avian studies have demonstrated the importance of synchronization of breeding with key food resources, but have solely focused on timing of nesting (Dunn and Winkler 1999) or nest success (Both et al. 2006) and have largely been conducted in Europe (Gordo et al. 2005, Visser et al. 2006, Pearce-Higgins et al. 2010). Results of my research indicate that changes to the timing of peak emergence of larval insects would likely modify BTBW fledgling survival. On the other hand, fledgling movements seem largely shaped by parental decisions, at least during the dependency period. Thus, adult experience with predator avoidance and food acquisition may directly affect offspring survival. Future studies should directly investigate whether age-varying abilities in providing care for young or age segregation in territory quality explains these differences in fledgling habitat selection.

The findings of this study contribute valuable information to the management and conservation of Black-throated Blue Warblers, under the likely scenario of a changing climate and consequent effects on the ecosystem where this species breeds. Although climate change will potentially alter the timing of peak food abundance for this breeding bird, adult behaviors may be able to compensate for reductions in offspring survival due to declining food resources. Plastic responses of individuals to a changing environment could contribute to this species’ ability to cope with changes to the phenology or abundance of habitat resources, and such plasticity and resulting productivity has recently been demonstrated in a northerly breeding BTBW population (Lany et al. 2013). However, adaptive responses of migratory species will likely be constrained by life-history tradeoffs or other components of the annual cycle. An individual's potential for adaptation to climate change is likely affected by how climate variables interact with the species and its habitat throughout the year. Three recent studies of migratory warblers have found strong indications of carry-over effects of winter habitat conditions on breeding success (Drake et al. 2013, Rockwell et al. 2012, McKellar et al. 2012). Conservation efforts that attempt to mitigate the effects of climate change on migratory birds should consider the influence of individual traits and behavioral responses on habitat relationships and constraints of the annual cycle on adaptation and plasticity. A more holistic approach is necessary when studying the relationship of a species with its environment in order to make accurate predictions of how individuals and populations will respond to a changing climate.

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