COMMUNICATION, REPRODUCTION, AND SURVIVAL OF A LONG-DISTANCE MIGRATORY SONGBIRD, THE BLACK-THROATED BLUE WARBLER (*SETOPHAGA CAERULESCENS*)

by

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(Under the Direction of ROBERT J. COOPER and MICHAEL J. CONROY)

ABSTRACT

Many bird species display elaborate plumage characteristics. The evolution of these traits, and their associated functions, is a central area of study in avian biology. Conspicuous plumage characteristics can be important in many different contexts and may have multiple functions, both between and within bird species. Additionally, these traits often incur various costs to their bearer. To better understand such conspicuous plumage traits, I studied a prominently displayed plumage characteristic of male Black-throated Blue Warblers (*Setophaga caerulescens*), the wing spot. I examined this trait in the contexts of social communication, reproduction, and survival. With regard to communication, I found that the male Black-throated Blue Warbler wing spot was important in intraspecific male-male communication even in situations where males were familiar with one another. However, regarding the wing spot's potential importance in a reproductive context, I did not find a relationship between male wing spot length and extra-pair paternity in this species. Instead, I found that extra-pair paternity increased with male age and size. Thus, any function of the male wing spot in communication with conspecific females remains unclear. Female warblers may still use the male wing spot as a cue or signal, but not in the context of extra-pair paternity. Moreover, I found that male wing spot length was not important in explaining annual survival, thus it is unlikely that displaying a wing spot carries an obvious survival cost. Other associated costs with displaying a long wing spot are possible and should be investigated. Taken together, the Black-throated Blue Warbler male wing spot appears to function, during the breeding period, primarily as a signal in male-male communication.

INDEX WORDS: Black-throated blue warbler, *Setophaga caerulescens*, social communication, extra-pair paternity, survival, movement, Coweeta

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Many bird species display elaborate plumage characteristics. The evolution of such traits, and any associated function, is a central question in avian biology (Tibbetts and Safran 2009). Some plumage traits have obvious functions, while others do not (Savalli 1995). Often, plumage characteristics have been found to be important in social signaling contexts (Hawkins et al. 2012, Sheehan et al. 2015). As social signals, plumage traits can be used for intraspecific communication in both non-reproductive and reproductive contexts (e.g., Guindre-Parker et al 2013). Costs are frequently associated with elaborate plumage characteristics and can be incurred in their display or production. Moreover, some elaborate plumage characteristics may carry a survival cost (Hill and McGraw 2006). The functions and costs surrounding the display of prominent plumage characteristics can vary within and among species. Thus it is important to identify the circumstances in which plumage conveys information and any costs to the signaler. To date, very little is known about how variation in plumage traits is generated or how it evolves in birds (Hill and McGraw 2006).

In birds, conspicuous and distinctive coloration is often used for communication purposes (Butcher & Rohwer 1989). Traits such as bill color (Karubian et al. 2011, Murphy et al. 2014), skin color (Velando et al. 2006), and various plumage characteristics can communicate an individual’s condition or social status (Rohwer 1975). Empirical evidence indicates support for a wide range of plumage traits used as status badges in numerous species, e.g., bib color (Senar and Camerino 1998), flank spots (Crowhurst et al. 2012), cheek patch (Galván and Sanz 2008), forehead patch (Järvistö et al. 2013, Pärt and Qvarnström 1997), wing bars (Moreno-Rueda and Hoi 2011), epaulet (Pryke and Andersson, 2003), and tail spots (McGlothlin et al. 2007). However, while conspicuous and distinctive plumage characteristics function as status signals in many bird species, not all phenotypic traits investigated are reliable indicators of social dominance (Dale 2000, Korsten et al. 2007, Vedder et al. 2008). Additionally, although many studies have examined social status signals in birds, a minority have looked at achromatic plumage signaling (Mennill et al. 2003, Svensson and Wong 2011) despite the potential for achromatic signals to be effective (Guindre-Parker et al. 2013).

Plumage signaling can also be important in a reproductive context (e.g., Doucet et al. 2005, Webster et al. 2008) and could influence mating success. Determining the drivers of variation in male mating success is key to understanding reproductive behaviors. While the predominant avian mating system is social monogamy, within this system many studies have discovered prevalent extra-pair paternity (Griffith et al. 2002). In birds, increased frequency of extra-pair paternity can be related to certain male traits or characteristics including showier plumage (Yezerinac and Weatherhead 1997), increased age (Richardson and Burke 1999), and larger body size (Kempenaers et al. 1997). Further, extra-pair paternity can be important for sexual selection in situations where it provides variation in male mating success upon which sexual selection can act (Schlicht and Kempenaers 2011, Cleasby and Nakagawa 2012).

Showy plumage can be costly to produce and maintain (Walther and Clayton 2005), for instance influencing survival (Hill and McGraw 2006). In some cases, plumage characteristics may be related to individual quality. That is, individuals with elaborate plumage may also be individuals that have high survival (Delhey and Kempenaers 2006, Galván and Møller 2013). Related to individual quality, some individual characteristics are correlated with avian survival.

A possible mechanism for increased survival corresponding with showier plumage could be energetic benefits conferred from reduced agonistic interactions with conspecifics (Cline et al. 2015). Alternatively, plumage coloration may be unrelated to adult survival (Delhey and Kempenaers 2006) or birds expressing more elaborate plumage coloration may have decreased survival (Griffith et al. 2003). The subject of avian survival is complex and many factors can influence adult annual survival in birds (Aebischer and Coulson 1990, Karr et al. 1990, García-Pérez et al. 2014). For example, many researchers have found that age class can influence annual survival (reviewed in Martin 1995, Tavecchia et al. 2001). For short-lived migratory birds, annual survival often increases from the youngest age class to an older age class, but decreases in the oldest age class as a result of senescence (Møller and De Lope 1999). Additionally, empirical evidence has shown increased investment in reproduction is related to lowered survival for some birds (Santos and Nakagawa 2012).

Understanding the functions and costs associated with conspicuous plumage traits will provide valuable information about avian behavior and communication systems. Such information can help us to better comprehend how these traits and systems evolved. Conspicuous plumage is important in many different contexts and may have multiple functions. To better understand the function of conspicuous plumage traits, I studied a prominently displayed plumage characteristic of male Black-throated Blue Warblers (*Setophaga caerulescens*), the wing spot.

DISSERTATION OBJECTIVES AND STRUCTURE

In Chapter Two, I examine how the male Black-throated Blue Warbler wing spot functions in social communication during the breeding season. Many bird species display a conspicuous achromatic wing spot at the base of the primary feathers and some studies have found this plumage patch to be important for communication purposes (Justice 2000), as a sexual ornament (Heij et al. 2011), and as a condition-dependent indicator of viability (Török et al. 2003). The Black-throated Blue Warbler displays this prominent achromatic wing spot at the base of the primary feathers and it may be used as an intraspecific signal in certain social situations. To date, this wing spot has received little empirical attention, but is generally known to increase in length with age. Currently, the only evidence indicating that male Black-throated Blue Warblers use the wing spot for communication is wing-drooping behavior observed mainly during interactions with conspecific females (Holmes et al. 2005). Consistent with theory and prior observation, I hypothesize the male Black-throated Blue Warbler wing spot functions as a status signal, but with limited function during the breeding season when animals are familiar with each other. I test this hypothesis via a manipulative experiment in free-living animals, post breeding territory establishment, and after birds were familiar with their neighbors.

In Chapter Three, I investigate predictors of extra-pair paternity in the Black-throated Blue Warbler. Females often use male characteristics to assess male quality, particularly with regard to male quality as a mate, including as an extra-pair mate. Thus, I sought to better understand what male characteristics explain extra-pair paternity in Black-throated Blue Warblers. I hypothesize that wing spot length, male age class, and male size were important in explaining extra-pair paternity in this species. For this analysis, I use data collected during the warblers' breeding period at two spatially distinct study sites.

In Chapter Four, I estimate annual survival for Black-throated Blue Warblers breeding in the southern Appalachians using a robust design framework. Additionally, I determine if individual characteristics, including wing spot length, affected year-to-year survival of adult Black-throated Blue Warblers using Cormack-Jolly-Seber methods. Populations of Black-throated Blue Warblers have recently declined in the southernmost part of their breeding range (Sauer et al. 2014), but the cause of decline remains elusive. I use mark-resight data collected from 2010–2015 in the Nantahala National Forest, North Carolina, USA to estimate survival. Finally, Chapter Five is a summary of my findings regarding the importance of the Black-throated Blue Warbler wing spot.

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CHAPTER 2

EXPERIMENTAL EVIDENCE FOR A PHENOTYPIC TRAIT AS AN AGE-DEPENDENT INTRASEXUAL SOCIAL SIGNAL BETWEEN FAMILIAR INDIVIDUALS[1]

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[1] Cline, M. H., J. L. Hatt, M. J. Conroy, and R. J. Cooper. Accepted to Animal Behaviour

ABSTRACT

Signals of social status can function to alert conspecifics of an individual’s dominance, social rank, and fighting ability. Such signals are beneficial in resource-limited systems because they can act to reduce conflict between competitors, especially when individuals are unfamiliar with each other. Here, I investigate the social communication function of a conspicuous plumage characteristic of a Neotropical migrant songbird, the Black-throated Blue Warbler (*Setophaga caerulescens*), after breeding territory establishment when individuals are familiar with neighbors. To do this, I experimentally manipulated males’ white wing spots, a putative signaling trait, and subsequently observed their behavior. I found that males with experimentally eliminated wing spots had more frequent close-range interactions within and at their territory boundaries with conspecific males and had more agonistic interactions involving aggressive vocalizations compared to control males, though the effects differed according to age class. However, frequency of close-range interactions with female conspecifics was not influenced by wing spot manipulation. Finally, wing spot manipulation did not influence males’ territorial song rates or responses to a simulated intruder, indicating no change in individual self-perception. My study provides evidence that, even when individuals are familiar with each other and on established territories, social status signals continue to convey important information.

Resource limitation drives competition in many animal systems and often is a source of conflict between individuals. Physical conflict and resolution of competition over resources is costly because of associated energetic expenditure and the potential risk of physical injury. Thus, it is expected that selection should favor ways of resolving conflicts without resorting to physical confrontations and conflicts (Maynard Smith & Harper, 2003). In some cases, phenotypic traits may be used as signals to settle these conflicts. The status-signaling hypothesis posits that traits, often referred to as status signals or badges of status (Dawkins & Krebs, 1978; Roper, 1986), may evolve to communicate information about an individual's resource-holding potential (Senar, 2006) or abilities to win agonistic interactions (Rohwer 1975, 1977; Searcy & Nowicki, 2005). Using this signal allows a dominant individual to maintain its rank in the social hierarchy while avoiding costly physical agonistic interactions. Status signals occur in many taxa including mammals (Setchell & Jean Wickings, 2005), herpetofauna (Carpenter, 1995; Crothers & Cummings, 2015), fish (Morris, Mussel, & Ryan, 1995), insects (Baracchi et al., 2013), and birds (reviewed in Santos, Scheck, & Nakagawa 2011; Senar, 2006).

A key assumption of the status-signaling hypothesis is that competitors are unfamiliar with each other (Quesada, Chávez-Zichinelli, Senar, & Schondube, 2013; Senar, 2006; Vedder, Schut, Magrath, & Komdeur, 2010). Many studies have investigated status signals in systems where individuals commonly encounter unfamiliar conspecific competitors. In these situations, status signals are assumed to be most important (Maynard Smith & Harper, 2003; Rohwer, 1975, 1982; Senar, Burton, & Metcalfe, 1992) and, in the case of experimental investigation, detection of an effect is expected. In fact, the original status-signaling hypothesis was proposed as a way for animals to reduce agonistic confrontations between individuals unaware of the resource-holding potential of unfamiliar opponents (Rohwer, 1975). Thus, status signaling should be especially relevant for nomadic group-living species, since these individuals will frequently interact with numerous unfamiliar conspecifics (Senar et al., 1992). The assumption that status signals should have little impact on the outcome of agonistic interactions between individuals with prior experience with each other (Lemel & Wallin, 1993; Senar, 1999; Senar, 2006) has been rarely tested.

In species where territories are established for resource defense, theory suggests that status signals, or badges, may not be particularly important post territory establishment (Brotons, 1998; Lemel & Wallin, 1993; Senar, 2006). In such cases, after territories are established, prior ownership advantage (Austad, 1989; Hammerstein, 1981; Leimar & Enquist, 1984) may override any advantage conferred by a badge of status (Rohwer, 1982; Senar, 1999). Therefore, badges of status may only be efficiently used during periods before territory settling (Lemel & Wallin, 1993; Wilson, 1992), after which adjacent territory holders are familiar and their social status known. For migratory species, status signals should be most important immediately after arrival on the wintering or breeding quarters and just prior to territory establishment (Pärt & Qvarnström, 1997). However, any continued utility of status signals post territory establishment has been rarely investigated in migratory animals.

Phenotypic traits have evolved to communicate status in a variety of animal taxa; signals can be seismic, chemical, tactile, auditory, or visual (Walter & Elgar, 2012). In particular, birds have evolved conspicuous and distinctive coloration for communication purposes (Butcher & Rohwer, 1989). Traits such as bill color (Karubian, Lindsay, Schwabl, & Webster, 2011; Murphy et al., 2014), skin color (Velando, Beamonte-Barrientos, & Torres, 2006) and various plumage characteristics can communicate an individual’s condition or social status (Rohwer, 1975). Empirical evidence indicates support for a wide range of plumage traits used as status badges in numerous species, e.g., bib colour (Senar & Camerino, 1998), flank spots (Crowhurst, Zanollo, Griggio, Robertson, & Kleindorfer, 2012), cheek patch (Galván & Sanz, 2008), forehead patch (Järvistö, Laaksonen, & Calhim, 2013; Pärt & Qvarnström, 1997), wing bars (Moreno-Rueda & Hoi, 2011), epaulet (Pryke & Andersson, 2003), and tail spots (McGlothlin, Duffy, Henry-Freeman, & Ketterson, 2007). However, although conspicuous and distinctive plumage characteristics function as status signals in many bird species, not all phenotypic traits investigated are reliable indicators of social dominance (Dale, 2000; Korsten, Vedder, Szentirmai, & Komdeur, 2007; Vedder, Korsten, Magrath, & Komdeur, 2008).

Although many studies have examined social status signals in birds, a minority have looked at achromatic plumage signaling (Guindre-Parker, Gilchrist, Baldo, & Love, 2013; Mennill, Doucet, Montgomerie, & Ratcliffe, 2003; Svensson & Wong 2011), despite the potential for achromatic signals to be very effective (Guindre-Parker et al., 2013). Many bird species display a conspicuous achromatic wing spot at the base of the primary feathers and some studies have found this plumage patch to be important for communication purposes (Justice, 2000), as a sexual ornament (Heij, Gustafsson, & Brommer, 2011), and as a condition-dependent indicator of viability (Török, Hegyi, & Garamszegi, 2003). The Black-throated Blue Warbler (*Setophaga caerulescens*) displays this prominent achromatic wing spot at the base of the primary feathers and it may be used as an intraspecific signal in certain social situations. To date, this wing spot has received little empirical attention, but is generally known to increase in length with age. Currently, the only evidence indicating that male Black-throated Blue Warblers use the wing spot for communication is wing-drooping behavior observed mainly during interactions with conspecific females (Holmes, Rodenhouse, & Sillett, 2005). Consistent with theory and prior observation, I hypothesized the male Black-throated Blue Warbler wing spot functions as a status signal, but with limited function during the breeding season when animals are familiar with each other. I tested this hypothesis via a manipulative experiment in free-living animals, post breeding territory establishment, and after birds were familiar with their neighbors.

Related to my hypothesis, I made three predictions. First, the male Black-throated Blue Warbler wing spot is not used to communicate social rank to conspecific males when individuals are familiar with each other. Thus, I predicted, post-territory establishment, the frequency of close-range interactions (when males are observed near each other acknowledging each other's presence) and escalated agonistic interactions (as indicated by chatter sounds and soft songs) would be equal for experimental males with darkened wing spots compared to control males because territory ownership and social hierarchies were established, so any signaling function would be diminished. Second, based on previous observations of males putatively signaling to females with wing-drooping behavior, I predicted the frequency of close-range interactions with conspecific females would be lower for experimental, darkened-wing spot males compared to controls. Third, I predicted no difference in territorial behavior between experimental and control males, especially in the absence of a visual signal receiver, because there should be no change in self-perception (i.e., feedback on the signaler) resulting from manipulation. Specifically, I expected neither territorial-type song rates nor male responses to simulated territorial intrusions would change according to manipulation.

METHODS

Study Site and Species Description

This study was conducted during three consecutive Black-throated Blue Warbler breeding seasons in Macon County, North Carolina, USA (35°02' N, 83°28' W) at three 35-ha study sites at respectively 1150, 1300, and 1400 m above sea level (hereafter low, mid, and high) within the Nantahala National Forest. The forest is comprised of a diverse assemblage of mainly hardwood trees with very dense shrub and understory layers composed of great laurel (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) thickets. The Black-throated Blue Warbler breeds in this area from mid-April to mid-July. This research was performed as part of a long-term warbler demography study initiated in 2002. During this study, all breeding warbler pairs were monitored through direct observation.

The Black-throated Blue Warbler is a Nearctic-Neotropical migrant songbird that breeds in forested areas of eastern North America and winters mainly in the Greater Antilles. Female Black-throated blue warblers build nests in the shrub layer of the forest. Male warblers are territorial and longer-range communication between conspecific males in this dense habitat is through frequent song vocalizations. Males and females are easily distinguished by plumage differences, with males showing multiple bright white plumage characteristics (Holmes et al., 2005). Male and most female Black-throated Blue Warblers display a white wing spot, produced by white coloration at the base of the primary feathers, although male wing spots are generally longer and much more pronounced.

Bird Capture and Measurement

Males were captured in their territories using a mist net, playback of a conspecific song recording, and a decoy. Females were captured with a mist net near the nest during. All adults were assigned a unique combination of a numbered U.S. Geological Survey band and three colored plastic leg bands. During banding, all warblers had measurements of the right wing spot taken with calibrated Mitutoyo Absolute Digimatic CD-6”CS digital calipers (Mitutoyo Corporation, Aurora, Illinois, USA) to the nearest tenth of a millimeter along the seventh primary feather where the longest extent of white coloration is visible. These measurements were collected with the bird in-hand with the wing folded in a natural position. For consistency, all measurements were performed by a single observer, MHC. All birds were aged in-hand using plumage characteristics (Pyle, 1997).

Following banding, every male’s territory was mapped via direct observation at least every third day using a Garmin Rino 530HCx GPS unit (Garmin Corporation, Olathe, Kansas, USA). These systematically collected spatial data were uploaded daily to ArcGIS 10 (Environmental Systems Research Institute, Redlands, California, USA; ESRI, 2011) to produce territory maps for estimating male warbler densities and to focus behavioral observations. Additionally, nearly all neighboring males (> 90%) adjacent to each focal male were banded and their territories mapped to determine the number of neighbors surrounding focal males.

Study Design and Plumage Manipulation

My experiment was conducted from late April to late June 2012–2014, during the Black-throated Blue Warbler’s breeding season. Plumages of adult male warblers were manipulated throughout this period according to their *a priori* assignment to two experimental groups. Because wing spot length is known to increase with age, I controlled for any effect of warbler age using a balanced design with an equal number of yearlings in their first breeding season (i.e., second-year [SY]) and older (i.e., after-second-year [ASY]) males in each experimental group. Specifically, before capture and marking, males were assigned to either the experimental or control groups by randomly selecting the first treatment (experimental or control) for each age group and alternating treatment for every following capture.

Regarding plumage manipulation, males in the experimental group had their white wing spot (the base of the primary feathers on both the upper wing and underwing) colored completely black with a Staedtler Lumocolor 350 permanent marker (Staedtler, Nuremberg, Germany). Males in the control group were handled identically, but had the already-black ends of the primary feathers (upper wing and underwing) sham-colored black with the same marker to control for the effect of marking the birds. All birds were given at least 48 hours to recover from any effects of capture and handling before subsequent observations were conducted.

Behavioral Observations

I conducted all behavioral observations within focal males' territories between 0645 and 1100 hours during clement weather conditions throughout the breeding season to record behaviors as related to my predictions. Within two weeks following manipulation, three 30-minute behavioral observations were conducted on different days for each experimental and control male. At the start of each observation, the individual's identifying marks (i.e., leg band combination) were verified using Zeiss Victory 10X42 binoculars (Carl Zeiss Inc., Jena, Germany) to ensure that the correct male was being observed and, in the case of males assigned to the experimental group, that the marker was still visibly covering the wing spot. Following this verification, the male was followed on foot and kept in sight as much as possible during the observation period. Care was taken to move swiftly to not lose sight of the male but also silently to ensure that observer movements did not influence the bird's behavior.

During behavioral observations of focal males, count data were collected on the frequency of focal males' close-range interactions with both conspecific males and females.

Specifically, a close-range interaction was recorded when the focal male was seen near a conspecific and both birds were clearly acknowledging each other's presence. Typical behaviors accompanying close-range interactions included individuals perching and hopping along branches near each other, close-range song at territory boundaries (male only), low-intensity chases, and following behavior (generally male following female). When possible, the conspecific interacting with the focal male was individually identified.

Counts of song types were recorded using a handheld tally counter and a field notebook. Data on four vocalization types produced by male Black-throated Blue Warblers were collected and used in analyses. Two of these vocalization types are mainly used in close-range communication between conspecifics, (1) aggressive chatter (aggressive trill; Holmes et al., 2005) and (2) soft, low-volume song. The other two vocalization types are used primarily in long-range communication, (3) broadcast songs (type 1 and 2; Holmes et al., 2005) and (4) counter songs produced in response to a neighboring males' song. Aggressive chatter is emitted during fighting between conspecific males and is an indicator of an escalated agonistic interaction. Soft song is primarily a courtship song produced to females constructing a nest, although occasionally used as a prelude to an agonistic interaction with a conspecific male (Hof & Podos, 2013). Broadcast songs is the most common, general-purpose, territorial song used for longer-distance (between-territory) communication. Lastly, counter song is songs produced directly in response to a neighboring conspecific males' song.

Response to Simulated Intruder

To test whether males' responses to a conspecific male intruder differed according to treatment group (and thus, whether self-perception was altered by treatment), playback was broadcast following each final behavioral observation and the focal male's response was recorded. I simulated territorial intrusion by playing a recording of unfamiliar conspecific song within 15 m of the male's territory center (as mapped via GPS, see Methods). Playback was three minutes in duration and composed of a compilation of five different songs repeated in a predetermined, fixed order. Songs were played at a rate of six per minute on an iPod nano digital audio player (Apple Inc., Cupertino, California, USA) and an Altec Lansing iM-237 portable speaker (Altec Lansing, San Diego, California, USA) placed on the ground and loosely covered with leaves. Playback setup was conducted when the focal male was not nearby. Following playback setup, the camouflage-clad observer (MHC) moved approximately 20 m away and hid to avoid disturbing the focal male during the simulation. Intensity of the focal male's response to the simulated territory intrusion was categorized according to the aggressiveness of the response using an ordinal, Likert-type scale. Specifically, the five levels used to categorize male response were: (1) none, (2) weak (counter-sang from a distance of > 75 m), (3) medium-weak (counter-sang from a distance of approximately 25–75 m), (4) medium-strong (counter-sang from a distance of approximately 10–25 m, with some searching for the intruder), and (5) strongly aggressive response (approached speaker within 10 m, actively searched for an intruder, and produced either aggressive chatter or soft song).

Statistical Analyses

All statistical analyses were performed using Program R version 3.2.1 (R Development Core Team, 2015). To determine whether treatment groups differed in original wing spot size, a Student's *t* test was conducted. Additionally, because conspecific density can affect warbler behavior and vocalization rates, a *t* test was used to determine whether the number of neighbors adjacent to males involved in this experiment was different according to treatment group. A correlation matrix was constructed to investigate the degree of correlation between explanatory variables. All Pearson’s coefficients were <0.6, indicating low correlation. Models were constructed after initial graphical examination of the data.

To investigate my three predictions, I parameterized null and alternative Poisson generalized linear mixed models (GLMMs) and used likelihood ratio tests (LRT) to compare model pairs. A random effect of individual was included in every model to account for the inclusion of multiple observations of the same individuals. All LRT were conducted using R package “lme4” (Bates, Maechler, Bolker, & Walker, 2014).

I investigated my predictions that (1) frequency of close-range male-male interactions and (2) frequency of escalated agonistic interactions (as indicated by chatter sounds or soft songs) were equal for experimental males with darkened wing spots compared to controls by comparing null and alternative models via LRT. Based on my findings, I further examined whether the frequency of close-range interactions and escalated agonistic interactions (as indicated by chatter sounds) could be predicted by an interactive effect of male age class and treatment group. I also investigated whether time of season (Julian date) influenced the frequency of close-range male-male interactions and chatter sounds. Similarly, I used an LRT to investigate my second prediction that the frequency of close-range interactions with females would differ for experimental versus control groups. I also tested whether time of season influenced male-female close-range interaction frequency.

To investigate my third prediction of no difference in territorial behavior between experimental and control males, I tested whether males’ responses to simulated conspecific territorial intrusion differed by treatment group with ordinal regression via R package “ordinal” (Christensen, 2015). Playback response scale was used as the dependent variable while treatment group was used as the independent variable. To further investigate any feedback effects on the signaler, I examined whether the frequency of territorial song types (i.e., number of broadcast songs, counter songs, and total songs) differed according to treatment group via an LRT. My total song rate variable was calculated by summing soft and broadcast songs.

Ethical Note

I conducted banding and marking under permit number 22587 from the U.S. Geological Survey. My experiment was approved by the University of Georgia’s Office of Animal Care and Use and conducted in accordance with IACUC polices (Permit # A2012 02-017-Y3-A1). Care was taken to ensure that all birds involved in my study were handled as briefly as possible (< 4 minutes) for banding, measurement, and coloring. Birds were removed from mist nets immediately after capture and released immediately following banding at the precise location where they were captured. The marker I used for plumage manipulation has been used in previous studies of warblers with no noticeable negative effects on the birds to which it was applied (Mumme, 2014; Mumme & Prum, 2002). My observations indicated that darkening the wing spot with marker did not have lasting effects on the appearance of males’ plumage. The marker was noticeably faded at two weeks and unnoticeable at four weeks post application.

RESULTS

A total of 42 Black-throated Blue Warbler males was involved in this experiment; of this, 21 had wing spots experimentally darkened (ASY $N = 9$, SY $N = 12$) while the remaining 21 control males had outer primaries sham-darkened (ASY $N = 9$, SY $N = 12$). However, behavioral observations could not be conducted after treatment in five cases because either the terrain was too steep or vegetation too dense to complete a meaningful observation. Thus, the original sample size was reduced to a realized total of 37 males (experimental: ASY $N = 7$, SY $N = 12$; control: ASY $N = 7$, SY $N = 11$).

Initial wing spot length prior to treatment did not differ between the two treatment groups (two-sample *t* test: $t_{34} = 0.28$, $P = 0.78$). The control group had a mean ± SE wing spot length of 9.35 ± 0.36 mm while the experimental group had a mean of 9.58 ± 0.33 mm. Number of neighbors directly adjacent to the focal males' territories did not differ between treatment groups (two-sample *t* test: $t_{31} = 0.85$, $P = 0.40$) with the control group having a mean of 3.9 ± 0.1 neighbors and the experimental group having 3.7 ± 0.1 neighbors.

Contrary to my prediction, the interactive effect of male age class and treatment group explained the frequency of close-range interactions between conspecific males, with younger experimental males experiencing more close-range interactions within or near their territory boundaries (Table 2-1 and Fig. 2-1). Additionally, Julian date was not statistically significant in explaining frequency of close-range interactions with conspecific males (Table 2-1).

Also counter to my predictions, the interactive effect of male age class and treatment group had a significant effect on the number of chatter sounds emitted (Table 2-1 and Fig. 2-2), with more chatter sounds heard on younger, experimental males' territories. Julian date was not statistically significant in explaining frequency of chatter sounds heard on-territory (Table 2-1). The interactive effect of male age class and treatment group was important in explaining soft song frequency (Table 2-1 and Fig. 2-3) with a pronounced effect of manipulation for younger males. Also, Julian date was significant with more soft songs observed earlier in the breeding season (Table 2-1).

Treatment group was unrelated to frequency of close-range interactions with females (experimental: 0.33 ± 0.08, control: 0.26 ± 0.08 close-range interactions per 30 minutes; Table 2-2). The interactive effect of age and treatment group was also not important to explaining close-range interactions with females (Table 2-2). However, for both treatment groups, frequency of close-range interactions with females was related to Julian date with more close-range interactions occurring earlier in the breeding season (Table 2-2).

In line with my predictions, treatment group did not influence number of broadcast songs (experimental: 42.2 ± 4.7, control: 42.4 ± 4.8 songs per 30 minutes), counter songs (experimental: 15.9 ± 2.7, control: 16.0 ± 2.7 songs per 30 minutes), or total songs (experimental: 59.5 ± 4.8, control: 55.5 ± 4.5 songs per 30 minutes) observed (Table 2-3). Also as expected, results from the ordinal logistic regression investigating the influence of experimental treatment on males' responses to simulated territorial intrusion indicated no statistically significant difference between treatment groups (ordinal logistic regression: $\chi^2_1 = 0.29$, $P = 0.77$; Fig. 2-4).

DISCUSSION

My results provide new evidence that an achromatic plumage patch, the wing spot, is an important social status signal in a system where interacting individuals are familiar with each other. This social signal remains important for male-male communication after territory establishment and prior ownership advantage does not ensure that a territory owner lacking this plumage signal will remain unchallenged by conspecific males. Furthermore, the wing spot's importance for intrasexual communication of status differs between age classes with apparent importance being greater for younger males. My findings that increased close-range interactions with conspecific males coupled with increased frequency of chatter sounds and soft songs (i.e., escalated agonistic interactions) indicate that the male Black-throated Blue Warbler wing spot is used as a signal to communicate social rank to conspecific males. Thus, I provide the first evidence that this achromatic phenotypic characteristic is a reliable intraspecific signal of social status.

Wing spot and Close-range Male-male Communication

Counter to my prediction, wing spot is used to communicate social rank to conspecific males even when individuals are familiar with each other. The frequencies of close-range male-male interactions and escalated agonistic interactions (indicated by chatter sounds and soft songs) were greater for experimental males with darkened wing spots compared to sham-treated control males. However, with regard to both types of interactions, wing spot had a more important signalling function for younger males compared to older males, as indicated by significant interactive effects. I interpreted the increased frequency of close-range male-male interactions to mean that, especially for younger birds, conspecific males were more likely to approach a male without a wing spot, possibly to further assess the individual using other visual cues or because the non-focal male was less wary of a bird lacking a wing spot. Additionally, my findings related to escalated agonistic interactions suggest non-focal males were more likely to challenge a younger, manipulated male due to its perception as lower rank, less threatening, and unlikely to dominate potential resulting physical encounters.

The importance of the interactive effect of age class and treatment group for all male-male interaction types suggests that the function of this social status signal is not static and can change over time for individuals. Older males likely possess additional phenotypic traits that can effectively communicate dominant status to other males in the absence of the wing spot. In this way, older males are able to both discourage close-range interactions with conspecific males and, additionally, lessen the probability of an escalated physical fight. Although some research has indicated that age class can have a strong influence on dominance behavior (Lukianchuk & Doucet, 2013), male dominance can also be positively associated with badge size, irrespective of age (Senar, Camerino, Copete, & Metcalf, 1993). For male Black-throated Blue Warblers the importance of the wing spot as a signal to other males appears to change with age.

In addition to my finding that the effect of plumage manipulation on soft song frequency was restricted to younger males, soft song frequency decreased as the breeding season progressed. Soft song has flexibility in its use and is not exclusively used during agonistic interactions (Hof & Podos, 2013). Males often produce soft songs near fertile females, especially during the nest-building stage. This flexibility in soft song function, especially regarding its role in male-female communication, is consistent with my finding that soft song frequency was greater earlier in the breeding season when females are most synchronously fertile.

I propose the results from my first prediction as general support for the skeptical recipient hypothesis (Caryl, 1982), which suggests that it is better for the receiver to believe the least impressive information from opponent because no animal should lie to devalue its social status. Thus, conspecific males perceived younger, manipulated males as inferior (wearing an inferior badge) and easier to defeat in combat, while manipulated males still perceived themselves as having a wing spot of appropriate size relative to their social status. Hence, this perceptional mismatch led to a greater frequency of escalated agonistic interactions within and near the borders of manipulated males' territories. Unfortunately, it was not possible to assign with confidence a victor of these fights. Escalated agonistic interactions were generally brief, averaging approximately 45 seconds, and warblers were swift-moving during these times. However, because territories were not substantially disrupted and I never observed any males being supplanted from their territory, it is likely that the true social status of manipulated individuals was communicated via these contests.

I was unable to definitively identify the non-focal male interactor or aggressor frequently enough to make meaningful statistical inference. However, the non-focal male was positively identified by band combination in 76% of all male-male interactions. In all of these cases the interacting male was a neighbor from a directly adjacent territory. Identified, non-focal males were evenly distributed between the two age classes. Males were identified as unbanded in 16% of all interactions and 8% of interactions involved males that could not be confidently identified as banded or unbanded. It is impossible to know if the unbanded or unidentifiable males were neighbors, but based on the males that were identified, territorial intrusions appear to be happening at a local scale. Further evidence that male-male interactions occur at a local scale includes the absence of floaters in this particular breeding area (MHC, personal observation) and in more northerly breeding areas (Holmes et al. 2005). The local nature of male-male interactions is relevant because this provides further evidence that the wing spot is a social signal that remains important even for familiar individuals on neighboring territories—thus, wing spot continually communicates social rank.

Wing spot and Close-range Male-female Communication

There was no difference in the frequency of close-range interactions with females between groups of males with or without wing spots. Thus, my prediction did not hold. This suggests females did not perceive manipulated males as different from control males, but my metric may not have been sufficient to detect a difference in female perception of males. All observations were completed after territory establishment and pairing had occurred and there were no instances in which a male was manipulated and subsequently lost his mate. Thus, my results are mostly inconclusive regarding how females may or may not use male wing spot as a signal. While the way in which females perceived manipulated males is unclear, this result is a useful contrast to my findings regarding male-male interaction frequencies. This contrast suggests that the patterns I found for males are based in male-like reproductive roles, especially territoriality.

Julian date was an important predictor of close-range male-female interactions, with more interactions occurring earlier in the season. Thus, my evidence suggests that nesting stage (i.e., females are more synchronously fertile earlier in the breeding season) was driving these male-female interactions irrespective of wing spot presence. My findings are seemingly incongruent with the previously observed male wing-drooping behavior, which is ostensibly used as a display to females during courtship (Holmes et al., 2005). More investigation is needed regarding if and how females assess males’ plumage.

Wing spot and Male Territorial-type Behaviors

In line with my predictions, altering male wing spot did not appear to affect how frequently a manipulated male produced territorial-type song (broadcast, counter, or total songs) or the intensity at which males responded to a simulated intruder. I believe these results indicate that eliminating a male's wing spot does not alter its territorial behavior or self-perception (i.e., there is no feedback on the signaler). Taken together, males with manipulated wing spots did not recognize a change in their social status or quality, but were perceived as lower rank by conspecific males. This suggests support for the incongruence hypothesis (Rohwer, 1977; Rohwer & Rohwer, 1978) modified according to Caryl (1982) to be the skeptical recipient hypothesis. Similar support has been found in other studies (González-Santoyo, 2014; Järvi, Røskaft, Bakken, & Zumsteg, 1987). My work provides evidence that experimentally manipulated Black-throated Blue Warbler males experienced a mismatch between self-perception and perception by other conspecifics, and in disputes, non-focal conspecific males escalated agonistic interactions.

My finding of no difference in total song rate between treatment groups is contrary the hypothesis that elimination of the wing spot could make males less apparent to conspecifics and, thus, more close-range interactions could occur via males accidentally intruding into manipulated birds' territories. All males had similar total song rates of approximately two per minute—too frequent for their neighbors to forget their presence. This hypothesis is more firmly refuted when considering the habitat in which my study occurred. My experiment was conducted in extremely dense temperate rainforest comprised of expansive Rhododendron thickets (see Methods) where males must have been within close range to see one another, thus long-range communication between conspecifics was through vocalization. Furthermore, I intentionally left other bright plumage patches (e.g., white spots on outer rectrices and white belly plumage) unaltered thereby manipulated males remained visually obvious.

Future Directions for Research

Given my findings, future research should examine the possibility of context dependence in wing spot communication and how it may interact with other signals. Burtt (1986) found that in some birds certain aspects of plumage coloration can serve different functions depending on the type of social situation. Further, research has demonstrated that status signaling occurs and is important at disparate periods of the annual cycle, including both the nonbreeding (Chaine, Roth, Shizuka, & Lyon, 2013; Rohwer & Ewald, 1981; Rohwer & Rohwer, 1978; Shields, 1977) and breeding season (Griggio, Valera, Casas-Crivillé, Hoi, & Barbosa, 2011; Laubach, Blumstein, Romero, Sampson, Foufopoulos, 2013). Age, reproductive effort, and individual condition can also influence the expression of social signals (e.g., Gustafsson, Nordling, Andersson, Sheldon, & Qvarnström, 1994; Hussell, 1983; Inouye, Hill, Stradi, Montgomerie, & Bosque, 2001; McDonald, 2003; Siefferman, Hill, & Dobson, 2005). Additionally, multiple distinct plumage characteristics can be used simultaneously to signal social status (Balph, Balph, & Romesburg, 1979; Chaine & Lyon, 2008; Chaine et al., 2013). In my study species, the wing spot may be working in concert with other phenotypic characteristics to communicate to receivers, as was suggested by the interaction of treatment group and age; this possibility should be explored.

Increased agonistic interactions do not appear to be a cost of displaying a prominent wing spot, contrary to some previous signaling research. For example, through experimental manipulation of forehead patch size, Qvarnström (1997) showed that a larger white forehead patch in collared flycatchers provoked more intrasexual agonistic interactions. Further research into potential costs associated with achromatic plumage production would aid my understanding of the honesty of this signal (Rohwer, 1975; Senar, 1999; Zahavi, 1975) in the Black-throated Blue Warbler and in animal communication systems generally. Finally, while both sexes of Black-throated Blue Warbler display the wing spot, females' wing spots are comparatively dull and sometimes completely absent. The evolution of female ornaments is a growing field of study (Garciá-Navas, Valera, & Griggio, 2015; Tobias, Montgomerie, & Lyon, 2013) and more research is needed to understand the role of the wing spot in female warblers.

Conclusions

My results provide evidence that the male Black-throated Blue Warbler wing spot is used as a signal to communicate social rank to conspecific males. This plumage characteristic is used as a close-range visual signal that helps to mediate aggressive escalation of interactions between males. Notably, the role of the wing spot in this intrasexual communication varied depending on male age class. However, despite previous observations of male warblers courting females with displays that enhance their wing spot appearance, male-female interaction frequency was not influenced by the wing spot absence. Furthermore, my study demonstrated that the wing spot serves as a signal of social status in Black-throated Blue Warblers, as shown by a mismatch in their self-perception versus their perception by a receiver. In summary, I have shown that animal status signals are used for intraspecific communication, irrespective of familiarity, during periods of the life cycle when they are not predicted to be particularly important.

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Table 2-1. Likelihood ratio test comparisons of the interactive effect of male age class and treatment group, as well as Julian date, on the frequency of close-range interactions with conspecific males, chatter sounds, and soft songs. All comparisons are with a null model. An "X" indicates an interaction between variables. A "*" indicates statistical significance.

Model	Explaining	χ^2	*df*	*P*
Age class X treatment	Close-range interactions with conspecific males	11.21	2	0.02*
Julian date	Close-range interactions with conspecific males	3.58	1	0.06
Age class X treatment	Chatter sound frequency	16.34	2	<0.001*
Julian date	Chatter sound frequency	3.10	1	0.08
Age class X treatment	Soft song frequency	8.08	1	0.04*
Julian date	Soft song frequency	13.62	1	<0.001*

Table 2-2. Likelihood ratio test comparisons of the effect of treatment group, interactive effect of male age class and treatment group, and Julian date on the frequency of close-range interactions with conspecific females. An “X” indicates an interaction between variables. A “*” indicates statistical significance.

Model	Explaining	χ^2	*df*	P
Treatment	Close-range interactions with females	0.34	1	0.56
Age class X treatment	Close-range interactions with females	6.32	2	0.10
Julian date	Close-range interactions with females	8.39	1	0.004*

Table 2-3. Effect of plumage manipulation according to treatment group on mean territorial-type songs (broadcast, counter, and total songs) per 30 minutes.

Model	Compared with	χ^2	*df*	*P*
Broadcast songs	Null model	0.30	1	0.583
Counter songs	Null model	0.18	1	0.890
Total songs	Null model	0.60	1	0.437

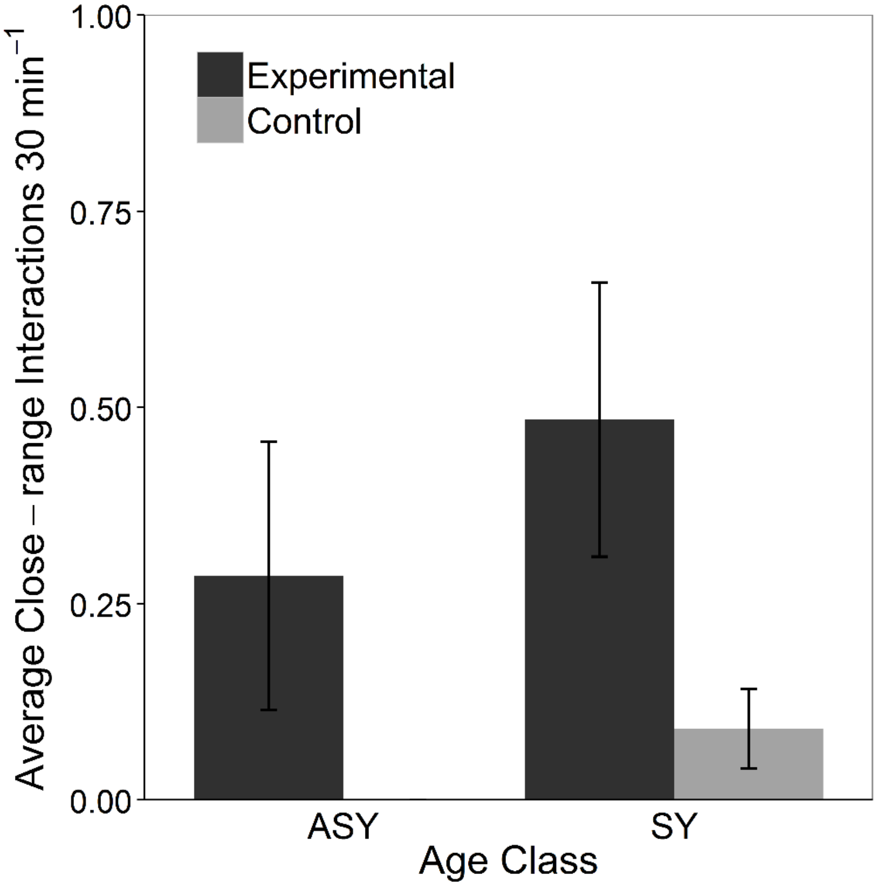

Figure 2-1. Effects of male age class by treatment group on average close-range male-male interaction frequency per 30 minutes. No close-range interactions were observed for ASY control males. Standard errors are shown.

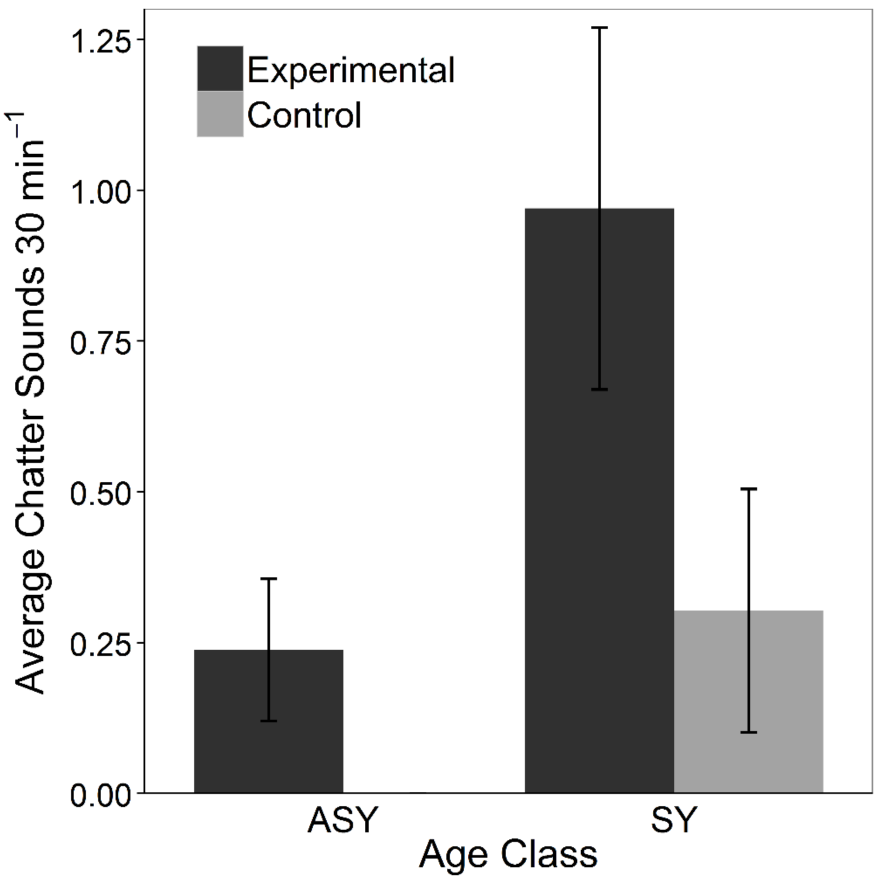

Figure 2-2. Effects of male age class and treatment group on mean chatter sound frequency per 30 minutes. No chatter sounds were observed for ASY control males. Standard errors are shown.

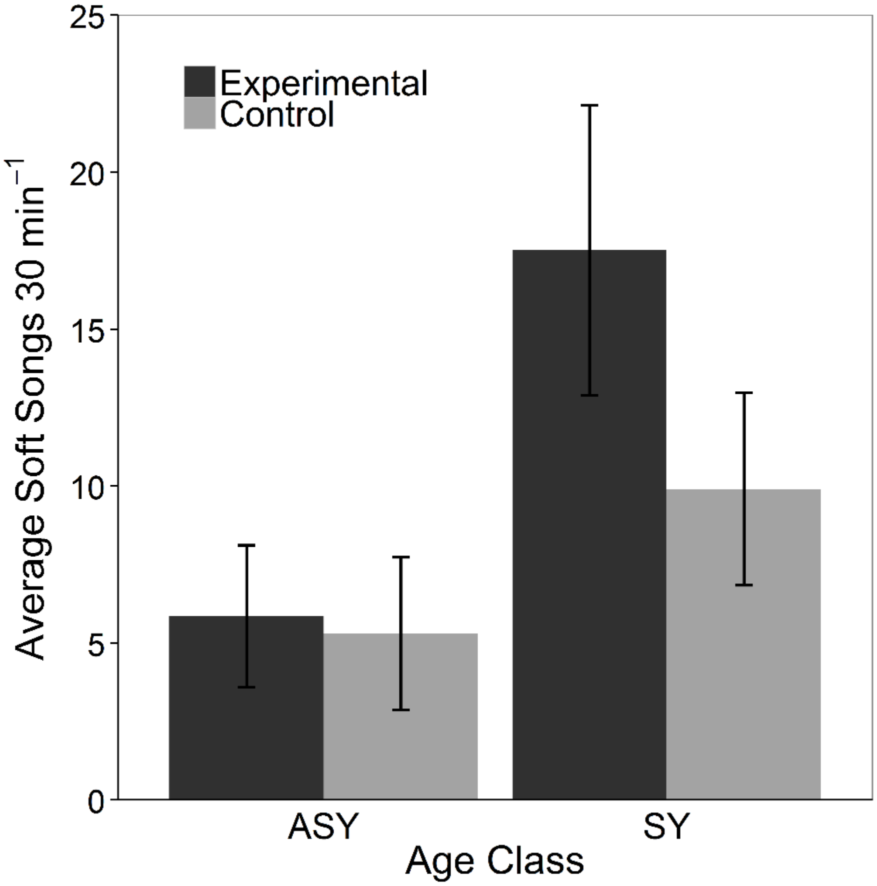

Figure 2-3. Effects of male age class by treatment group on average soft song frequency per 30 minutes. Standard errors are shown.

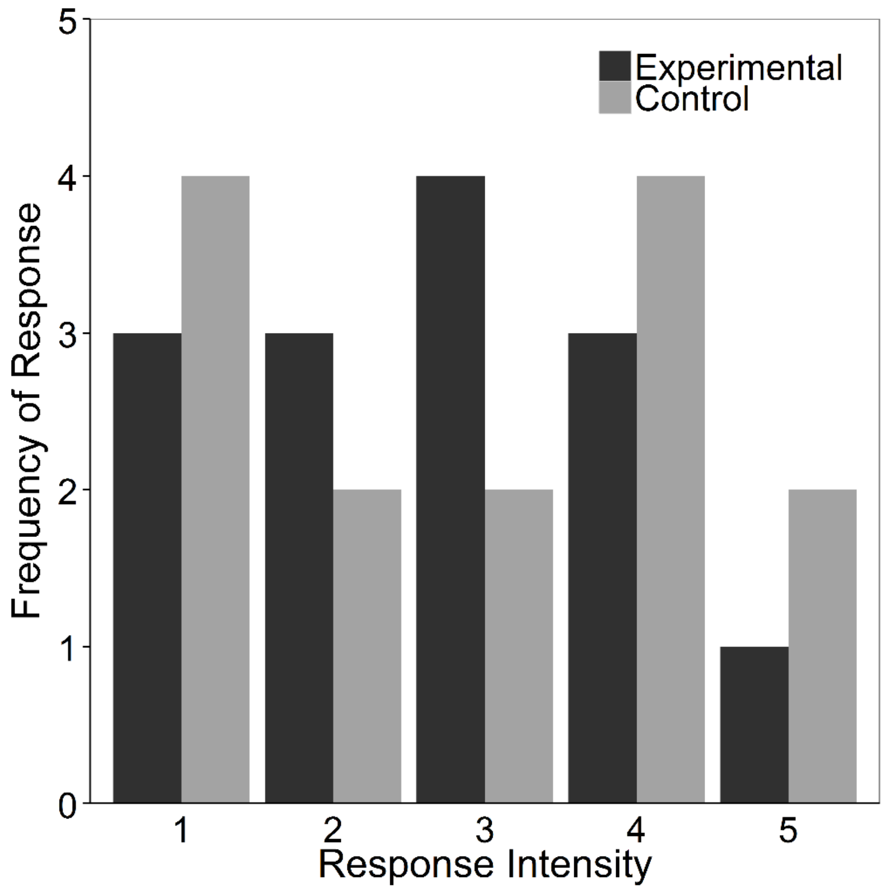

Figure 2-4. Effect of plumage manipulation on male response to a simulated conspecific intruder according to treatment group. The frequency of each type of response intensity is shown. Response intensities were: (1) none, (2) weak (counter-sang from a distance of > 75 m), (3) medium-weak (counter-sang from a distance of approximately 25–75 m), (4) medium-strong (counter-sang from a distance of approximately 10–25 m, with some searching for the intruder), and (5) strongly aggressive response (approached speaker within 10 m, actively searched for an intruder, and produced either aggressive chatter or soft song).

CHAPTER 3

DETERMINING PREDICTORS OF EXTRA-PAIR PATERNITY IN A MIGRATORY SONGBIRD[1]

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[1] Cline, M. H., Michael J. Conroy, Robert J. Cooper, Joanna L. Hatt, Sara A. Kaiser, Lindsey Nietmann, T. Scott Sillett, and Michael S. Webster. To be submitted to Behavioral Ecology and Sociobiology.

Abstract Females often use male characteristics to assess male quality, particularly with regard to male quality as a mate, including as an extra-pair mate. I sought to better understand what male characteristics explain extra-pair paternity in Black-throated Blue Warblers (*Setophaga caerulescens*). Black-throated blue warbler males exhibit a conspicuous achromatic plumage characteristic on their wing, the wing spot. I hypothesized that wing spot length, male age class, and male size were important in explaining extra-pair paternity in this species. I used data collected during the warblers' breeding period at two spatially distinct study sites and an information theoretic approach to model selection to assess my predictions that males with longer wing spots, older males, and larger males would sire more extra-pair offspring. The best-supported model was an interaction between male age class and size, meaning larger males generally had more extra-pair offspring per breeding season, but this effect differed between male age classes. That is, the oldest and largest males sired the greatest number of extra-pair offspring. I found that the male Black-throated Blue Warbler white wing spot was correlated with age, but no evidence to support my prediction that male wing spot length was related to number of extra-pair offspring produced. Though male wing spot length may not predict extra-pair paternity, results from my study may lend support for further study in the context of the good genes hypothesis, that females may choose older and larger extra-pair mates in order to produce offspring with superior viability.

Introduction

Identifying the drivers of variation in male mating success and why some males reproduce with greater success than others is a central question in biology. While the predominant avian mating system is social monogamy, within this system many studies have discovered prevalent extra-pair paternity (Griffith et al. 2002). Understanding the causes and correlates of variation in extra-pair paternity remains an important question (Forstmeier et al. 2014), as extra-pair mating can be an important component of male reproductive success in socially monogamous birds (Webster et al. 2007). Furthermore, understanding the patterns of extra-pair reproduction and why some individuals are more successful in acquiring extra-pair fertilizations is important to understanding how selection operates (Yezerinac et al. 1995). In birds, increased frequency of extra-pair paternity can be related to certain male traits or characteristics including showier plumage (Yezerinac and Weatherhead 1997), increased age (Richardson and Burke 1999), and larger body size (Kempenaers et al. 1997). Further, extra-pair paternity can be important for sexual selection in situations where it provides variation in male mating success upon which sexual selection can act (Schlicht and Kempenaers 2011, Cleasby and Nakagawa 2012)

Sexual selection (Darwin 1871) is an evolutionary mechanism by which secondary sexual traits (typically expressed in males) that are useful in competition for access to females are produced and maintained through non-random mating, with female preference favoring the bearer of the traits. In many species, females prefer males that display elaborate ornaments (Andersson 1994) and these ornaments can serve as indicators that transfer information about male quality to the female (Doucet and Montgomerie 2003). In birds, females may use any number of cues to assess mate quality (Mountjoy and Lemon 1996, Buchanan and Catchpole 1997, Bronson et al. 2003) including plumage characteristics (Jennions and Petrie 1997). Such male plumage traits may act as an intrasexual signal conveying information about social status or ability to provide care to offspring (Møller 1989, Doucet and Montgomerie 2003). Females may assess these male plumage traits in the context of extra-pair paternity and males with more elaborate plumage often have more extra-pair offspring (see Griffith et al. 2002).

Natural selection should work to maximize lifetime reproductive success. Thus, an individual's investment of resources into reproduction may change over its lifetime or between breeding seasons. Life history theory predicts that increased reproductive success with increased age may result from adjustments to resource allocation and increased mating effort with increased age (Stearns 1976, 1992, Lessells 1991). Indeed, in many bird species, first-time breeders reproduce with less success compared to older, more experienced individuals (Curio 1982). Relatedly, multiple hypotheses have been proposed to explain why reproductive success generally increases with age including experience, optimization of reproductive effort (Forslund and Part 1995), and decreased response to stress (Heidinger et al. 2006). As part of reproductive success, male extra-pair paternity often increases with age in birds (Griffith et al. 2002). Additionally, male size can be important in explaining extra-pair mating success (Petrie and Kempenaers 1998). Often, that larger males are better at obtaining extra-pair offspring compared to smaller males and female preference for larger males is cited as support for the good genes hypothesis (Richardson and Burke 1999).

The Black-throated Blue Warbler (*Setophaga caerulescens*) is a strongly sexually dichromatic migratory passerine and intersexual selection is thought to be responsible for most sexual dichromatism (Darwin 1871, Promislow et al. 1992, Andersson 1994). For example, male Black-throated Blue Warblers display a prominent white wing spot at the base of the primary feathers; this plumage characteristic is more pronounced in males compared to females and is known to increase with age (Pyle 1997). Many other bird species display a conspicuous wing spot at the base of the primary feathers and some studies have found this plumage patch to be important for communication purposes (Justice, 2000), as a sexual ornament (Heij et al. 2011), and as a condition-dependent indicator of viability (Török et al. 2003). Thus, it is plausible the male Black-throated Blue Warbler wing spot is used as an intraspecific signal in some social situations. The male wing spot deserves empirical attention and investigation into its potential as an intrasexual signal. If the wing spot is a reliable indicator of male quality it could be a sexually selected trait used by females when they are assessing and choosing a mate, particularly extra-pair mates.

To better understand the predictors of extra-pair paternity in the Black-throated Blue Warbler, I investigated three main hypotheses formulated according to theory and prior research. First, I hypothesized that the male Black-throated Blue Warbler wing spot was related to extra-pair paternity. Specifically, I predicted that males with longer wing spots would sire more extra-pair offspring compared to males with shorter wing spots. Second, I hypothesized that male age was related to extra-pair paternity. Specifically, I predicted that older males would sire more offspring compared to younger males. Finally, I hypothesized that male size would be related to extra-pair paternity. Accordingly, I predicted that larger males with longer wings and greater mass would also sire more extra-pair offspring compared to less massive males with shorter wings.

Methods

Study species

The Black-throated Blue Warbler is a Nearctic-Neotropical migrant songbird that breeds in forested areas of eastern North America and winters mainly in the Greater Antilles. Females build nests in the low shrub layer of hardwood and mixed hardwood-coniferous forests, which allows nests to be readily detected. Males and females are easily distinguished in the field due to plumage differences (Holmes et al. 2005). Both male and female Black-throated Blue Warblers display a white wing spot, produced by white coloration at the base of the primary feathers, although male wing spots are generally longer and much more pronounced. Warblers are territorial and show strong fidelity to breeding sites. Clutch size is generally four, the average length of incubation is 13 days, and the average length of the nestling period is 9 days (Holmes et al. 2005). Females will often re-nest after a failed or successful first attempt (Holmes et al. 1992). Incubation is performed solely by the female, whereas nestlings are fed and cared for by both the male and female. This species is socially monogamous, but extra-pair offspring are common (Webster et al. 2001).

The Black-throated Blue Warbler is well-studied and much work has been conducted regarding extra-pair paternity in this species. Early research used multilocus DNA fingerprinting to investigate Black-throated Blue Warbler extra-pair paternity and found that approximately one third of offspring produced were a result of extra-pair fertilizations and that local synchrony between neighboring females was the best predictor of a nest containing extra-pair young (Chuang et al. 1999). Later, Chuang-Dobbs et al. (2001a) employed microsatellite markers to discover that older (after-second-year; ASY) males that sired all young in their nests provisioned their nestlings at a higher rate when compared to younger males, suggesting older males assess paternity and adjust their parental care investment. Further, Chuang-Dobbs et al. (2001b) discovered males that mate-guarded their social female were less likely to be cuckolded compared to males that were experimentally unable to mate-guard. Webster et al. (2001) found that Black-throated Blue Warbler reproductive interactions occur at a local scale and that the opportunity for selection is limited by this scale. Further, Smith et al. (2005) found no evidence for female Black-throated Blue Warblers choosing extra-pair mates based on heterozygosity. Most recently, Kaiser et al. (2015) found that supplementally fed males in low quality habitat were less likely to lose paternity and less likely to sire extra-pair young than were control males. While much has been discovered regarding patterns of extra-pair paternity in the Black-throated Blue Warbler, any potential role of the wing spot remains an open question.

Study areas

This study was conducted as part of two ongoing, spatially distinct, long-term avian demography studies on two separate breeding populations of Black-throated Blue Warblers. One study is located near the southern edge of the Black-throated Blue Warblers' breeding range while the other is in the northeastern area of the warblers' breeding range. For this research, the southern Black-throated Blue Warbler breeding population was studied during breeding seasons 2011–2013 near the Coweeta Hydrologic Laboratory in Macon County, North Carolina, USA (35°02'N, 83°28'W) at three 35-ha study sites that varied in elevation (1150, 1300, and 1400 m above sea level) within the Nantahala National Forest, hereafter southern study site. The forest is comprised of a diverse assemblage of mainly hardwood trees with a thick shrub layer composed of great laurel (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*). The Black-throated Blue Warbler breeds in this area from mid-April to mid-July. This research was part of a long-term Black-throated Blue Warbler demography study initiated in 2002. The northern Black-throated Blue Warbler breeding population was monitored 2007–2013 at the Hubbard Brook Experimental Forest, in Woodstock, New Hampshire, USA (43°56'N, 71°45'W), hereafter northern study site (for details, see Holmes 2011). Data were collected on three study sites of different elevations (250–400, 600, and 700–850 m above sea level, 85, 65, 35 ha respectively). This northern hardwoods forest has an understory comprised of hobblebush (*Viburnum alnifolium*) and striped maple (*Acer pensylvanicum*). Warblers breed at this location from early May to mid-August.

Demographic monitoring, bird capture, and morphometric measurement

Both populations of Black-throated Blue Warbler were monitored throughout their breeding seasons and field methods were consistent across study sites. Breeding warbler pairs were monitored through direct observation and nests were found via visual searches, mainly by following building females during nest construction. Once located, nests were monitored and checked every other day. Nesting stage, numbers of nesting attempts, and numbers of fledglings produced by each pair were determined. After nest fledging or failure territories were still monitored to find additional nests.

At both study sites, male warblers were captured in their territories using a mist net, playback of a conspecific song recording, and a decoy. Females were captured with a mist net near the nest toward the end of incubation. All adult birds were assigned a unique combination of a numbered U.S. Geological Survey band and three colored plastic leg bands. Adults were aged in-hand using plumage characteristics (Pyle 1997) as SY (second-year) or ASY (after-second-year). During banding, all adult warblers had morphometric measurements taken. Adult mass was measured using digital or Pesola scales with accuracy to the nearest 0.1 gram. Wing length was measured similarly at the two study sites, using unflattened wing chord measurement in mm. These two morphometric measurements were used to calculate a “male size” covariate for analysis, by dividing mass by wing length. Nestlings were banded six days after hatching. Blood samples for both adults and nestlings were collected during banding and stored in lysis buffer.

Also during banding, adult warblers had measurements of the right wing spot taken with digital calipers to the nearest hundredth of a millimeter along the seventh primary feather where the longest extent of white coloration was visible. Wing spot measurements were collected with the bird in-hand with the wing folded in a natural position. For consistency, at the southern study area most (> 85%) measurements were performed by a single observer, MHC. At the northern study area, field wing spot measurements were collected using the same method by multiple observers. For three banders at the northern study site, wing spots were incorrectly measured in a systematic manner. However, because standardized photos were also taken of these birds’ wing spots, “corrected” digital measurements were used in analyses for birds measured by these banders (see Appendix A).

This research was performed under approved animal care protocols and efforts were explicitly made to ensure animal welfare. At the southern study site, banding, marking, and sample collection were conducted under permits from the U.S. Geological Survey (number 22587) and the University of Georgia’s Office of Animal Care and Use in accordance with

Institutional Animal Care and Use Committee polices (number A2012 02-017-Y3-A1). At the northern study site, banding, marking, and sample collection were conducted under a U.S. Geological Survey banding permit (number 22665) and research practices were approved by the Institutional Animal Care and Use Committees of the three institutions participating in this research, Cornell University (number 2009-0133), Smithsonian National Zoological Park (number 08-11, 12-12), and Wellesley College (number 1304).

Genetic analyses and paternity assignment

Genetic analysis for this study followed methods of Kaiser et al. (2015). Specifically, DNA was extracted from blood samples using Qiagen DNeasy blood and tissue kits (Qiagen, Valencia, CA). Adults and nestlings were genotyped at six highly polymorphic microsatellite loci designed for Black-throated Blue Warblers (*S. caerulescens*; *Dca28, Dca32*; Webster et al. 2001), yellow warblers (*S. petechia*; *Dpu16, Dpu01*; Dawson et al. 1997), golden-winged warblers (*Vermivora chrysoptera; Vecr08*; Stenzler et al. 2004) and Swainson's thrushes (*Catharus ustulatus*; *Cuu04*; Gibbs et al. 1999). Each individual had 1 μL of genomic DNA amplified at each locus in a 10 μL polymerase chain reaction containing 6.1 μL dH_2O, 1 μL 10X PCR buffer, 1.2 μL 25 mM $MgCl_2$, 0.2 μL 10 mM deoxyribonucleotide triphosphates, 0.2 μL 10 μM forward (fluorescently labeled) and pigtail reverse primers and 0.1 μL 2.5 U μL^{-1} Taq DNA polymerase. I ran polymerase chain reactions on a thermal cycler. Thermal cycler settings were 30 cycles of 94°C for 1 minute, primer-specific annealing temperature for 1 minute, 72°C for 5 minutes. Polymerase chain reaction products were analyzed on an automated 3730 DNA Analyzer and I scored alleles at each locus using Genemapper 3.7.

Paternity assignment also followed the methods of Kaiser et al. (2015). Paternity was assigned to offspring with known social mothers using the program CERVUS 3.0 (Kalinowski et al. 2007). The program CERVUS assigns parentage using a maximum likelihood method. Allele frequencies were first calculated using data from parents and offspring and then a parentage analysis simulation was conducted allowing for calculation of confidence estimates surrounding the actual parentage analysis. Likelihood scores and decision rules were used to check each CERVUS paternity assignment. The decision rules used are outlined in Smith et al. (2005). Briefly, if the social father had a high likelihood score but mismatched the nestling at 1 or 2 loci, I investigated the possibility of null alleles or mistyping by repeating polymerase chain reactions at mismatched loci and re-scoring the alleles. I accepted the CERVUS assignment of the social father as the genetic sire of a nestling if there was mismatch at ≤ 1 locus. A nestling was considered sired by an extra-pair male if the social father was not listed as a potential candidate father by CERVUS (i.e., had a negative natural log of the likelihood ratio, or LOD, score) or mismatched the nestling at ≥ 2 loci. In these cases I identified the extra-pair sire as the male that mismatched at ≤ 1 locus and had the highest likelihood score. In some cases, no candidate male matched the nestling's genotype (i.e., all had > 2 mismatches with the nestling), and in these cases I considered the nestling to have been sired by an un-sampled male.

Statistical methods

All other statistical analyses were performed in Program R version 3.2.2 (R Development Core Team 2015). Data were initially examined graphically and in tabular form. I determined if there were any correlations between explanatory variables using the "polycor" package (Fox

2015). Polyserial correlations were used for quantitative and ordinal variables and Pearson product-moment correlations were considered for all numeric variables.

To test my *a priori* hypotheses and predictions that (1) males with longer wing spots sired more extra-pair offspring compared to males with shorter wing spots, (2) older males sired more offspring compared to younger males, and (3) larger males would sire more extra-pair offspring compared to smaller males, I constructed eight Poisson generalized linear mixed models with a log link function (Table 3-1). I ranked these models using AIC corrected for small sample size (Akaike 1973, Burnham and Anderson 2002). Male identification number, bander identity, and study site (see Appendix B for details about site differences) were included as random effects in every model. Two interactive models were included in the model set: male age class*male size, to test if any effect of male size was dependent on age class and wing spot, and length*male size, to test if any effect of wing spot length on number of extra-pair offspring sired differed according to male size.

Results

Total sample size for both study sites was 1061, with 879 males at the northern study site and 182 males at the southern study site. Summary statistics regarding patterns of paternity for the southern site are presented in Appendix C. Correlation analyses indicated that the wing spot length and age variables were correlated (≥ 0.70, Table 3-2). Because of this multicollinearity between male wing spot length and age, the wing spot variable was never included in a model with age (Burnham and Anderson 2002). This result is largely because wing spot length increases with male age (Figure 3-1; for more details see Appendix D). Older (ASY) males generally have longer wing spots (10.90 ± 0.16 SE) compared to younger (SY; 7.70 ± 0.09) males. Coefficients for all other variable combinations were < 0.15, indicating low correlation.

Results from model selection used to test my hypotheses explaining extra-pair paternity for Black-throated Blue Warblers are presented in Table 3-3. There was a clear top model, with 83% weight, indicating that an interactive effect of male size and age class was best at explaining number of extra-pair young sired by Black-throated Blue Warbler males per breeding season (Figure 3-2). Examination of the beta coefficients of this top model showed directional influence congruent with my hypotheses that larger, older males had more extra-pair paternity (Table 3-4).

Discussion

My prediction that larger and older males would sire more extra-pair offspring per breeding season compared to smaller, younger males was supported by model selection results. The top-ranked model included an interactive effect of male size and age class, indicating that male size was important in explaining extra-pair paternity, but this effect differed between age classes. Essentially, being large in size was more important for older males compared to younger males regarding the number of extra-pair young sired per male per breeding season (Figure 3-2). By contrast, other than older males tending to have larger wing spots than younger males, I did not find support for my prediction that males with longer wing spots would have more extra-pair young per breeding season compared to males with shorter wing spots.

Predictors of male extra-pair reproductive success

Results from my model selection indicated that the model containing an interaction between male size and age class was best in explaining per-breeding-season male extra-pair reproductive success. That is, generally, the largest Black-throated Blue Warbler males in the older age class produced the greatest number of extra-pair young per breeding season. Regarding male age and extra-pair paternity, my results are similar to some previous studies that have found older birds often have more extra-pair offspring compared to younger birds (Forslund and Pärt 1995, Akçay and Roughgarden 2007). Differences in breeding experience between older and younger male birds is one explanation for older birds having greater success obtaining extra-pair fertilizations than younger males (Wetton et al. 1995, Weatherhead and Boag 1995, Poesel et al. 2006, Cleasby and Nakagawa 2012). Because successfully obtaining extra-pair fertilizations may require reproductive experience, yearling male birds may be at a disadvantage and less able to produce them (Forslund and 1995). Often, the pattern of older males gaining more extra-pair fertilizations compared to younger males is interpreted as support for the good-genes hypothesis (Andersson 1994, Griffith et al. 2002). For instance, simply via longevity, older males have already proven their survival ability and this may make these males preferred by females. Thus, females may prefer to mate with older, better-quality males in order to provide offspring with superior genetics (Richardson and Burke 1999).

Regarding male size and extra-pair paternity, previous empirical work has found generally similar results to this study. While there are many ways in which ornithologists measure the size of an individual birds, different measures of size have proven important in explaining patterns of extra-pair paternity (Griffith et al. 2002). In tree swallows (*Tachycineta* *bicolor*), successful extra-pair sires had longer wings than cuckolded males (Whittingham and Dunn 2014). Increased male mass has also been shown to relate to greater extra-pair paternity in avian studies. For example, Weatherhead and Boag (1995) showed that female red-winged blackbirds (*Agelaius phoeniceus*) preferred to mate with males with larger body size, and in this population of larger birds had higher survival. Thus, female red-winged blackbirds may also prefer males that have superior survival ability. From these results, Weatherhead and Boag (1995) proposed that the good genes hypothesis was supported, that is, females preferred to mate with high-quality mates to improve their offsprings' viability and reproductive success (e.g., Smith 1988, Strohback et al. 1998). Because I used mass to calculate Black-throated Blue Warbler male size (mass/wing length), this measure could incorporate information about male condition as well as size. Male birds with greater mass are generally in better condition compared to males with lower mass (e.g., Whittingham and Dunn 2000). Thus, female Black-throated Blue Warblers may be choosing extra-pair mates based on condition. This possibility deserves more research attention.

Though patterns documented in my study align with some ornithological studies that investigated the predictors of extra-pair paternity, others have found contrasting results. Kempenaers et al. (2001) found no difference in wing length between within-pair and extra-pair sires, suggesting that wing length, and potentially male size, was not particularly important to obtaining extra-pair fertilizations. Additionally, male size has been found to be unrelated to the likelihood of a male siring extra-pair offspring in yellow warblers (*Dendroica petechia*; Yezerinac and Weatherhead 1997). Female choice of extra-pair mates is a complicated process and likely differs between species.

Do males with longer wing spots have more extra-pair offspring?

I did not find evidence to support my prediction that male Black-throated Blue Warblers with longer wing spots have more extra-pair offspring compared to males with shorter wing spots. More research into the relevance of male wing spot to reproductive success is needed and further questions remain regarding if the male wing spot transfers information to conspecific females (but see Chapter 2 of this dissertation for details regarding wing spot and male-male communication). Other male Black-throated Blue Warbler plumage characteristics could transfer information to females and act as a cue for mate choice, including for extra-pair paternity. Many avian studies have found that male birds' ornamentation is important in explaining success in extra-pair paternity and exemplifies sexual selection (Andersson 1994, Møller and Birkhead 1994, Møller and Gregersen 1994, Møller and Tegelström 1997). Although I did not find that Black-throated Blue Warbler females prefer males with longer wing spots as extra-pair mates, females may assess males using other plumage characteristics; this should be explored further.

Uncovering any costs associated with the production and maintenance of the male Black-throated Blue Warbler white wing spot may help to understand its function. White plumage is produced by reflected light being scattered in all directions from unpigmented feather keratin (Prum et al. 1999). As such, white plumage is often regarded as energetically inexpensive because its production requires no special feather structure or pigment. However, white feathers are generally weaker than feathers pigmented with melanin, especially regarding abrasion resistance (Bonser 1995). Thus, rather than its production, the maintenance of white plumage may be energetically costly. This idea, coupled with the knowledge that white plumage patches are used as ornaments in numerous bird species (Höglund et al. 1990, Gustafsson et al. 1995, Hill et al. 1999, Kose et al. 1999, Sheldon and Ellegren 1999, Mennill et al. 2003, Török et al. 2003, McGlothlin et al. 2005, Woodcock et al. 2005, McGlothlin et al. 2007), lends support to the existence of an energetic cost associated with white wing spot. It is plausible that the male Black-throated Blue Warbler wing spot may entail associated costs and knowing these costs could support the idea that bearing a wing spot has benefits.

The subject of extra-pair paternity in birds in complex and much attention has been given to its function (see Griffith et al. 2002). Nonetheless, extra-pair paternity is only part of total reproductive success. For many socially monogamous species, extra-pair paternity can be a source of variation in male reproductive success on which sexual selection may act (Webster et al. 2007). However, if extra-pair paternity and within-pair paternity have a negative association, this could lessen the importance of extra-pair paternity's role in sexual selection (Webster et al. 1995). Investigating male Black-throated Blue Warbler wing spot in the context of extra-pair, within-pair, and total paternity would provide a more complete picture of whether the wing spot is important to male reproductive success.

My results suggest that the male Black-throated Blue Warbler wing spot should be studied further in the context of the good genes hypothesis. In Black-throated Blue Warblers, extra-pair paternity is greatest for older, larger males. Female choice is ultimately driving extra-pair paternity and this study provides evidence that females are preferentially selecting extra-pair mates based on individual characteristics.

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Table 3-1. Description of *a priori* hypotheses and corresponding statistical models explaining extra-pair paternity (EPP) of Black-throated Blue Warbler males breeding at two study sites, the Nantahala National Forest in North Carolina, USA and the White Mountain National Forest in New Hampshire, USA. A null model is not shown in this list, but was included in modeling.

Model	*a priori* Hypothesis
Age class	Age is related to EPP
Male size (mass/wing length)	Male size is related to EPP
Wing spot length	Wing spot is related to EPP
Age class + male size	Age and male sized are related to EPP
Wing spot length + male size	Wing spot and male size are related to EPP
Age class * male size	Male size is related to EPP, but this effect depends on age
Wing spot length * male size	Wing spot is related to EPP, but this effect depends on male size

Table 3-2. Correlations between variables considered in analyses to explain male extra-pair reproductive success at two study sites, the Nantahala National Forest, North Carolina, USA and the White Mountain National Forest in New Hampshire, USA from 2007–2013. Polyserial correlations were used for quantitative and ordinal variables and Pearson product-moment correlations were used between numeric variables.

	Wing spot length	Size	Age
Wing spot length	X	0.08	0.70
Size		X	0.12
Age			X

Table 3-3. Model selection results explaining number of extra-pair young sired per breeding season by Black-throated Blue Warbler males breeding at two study sites, the Nantahala National Forest, North Carolina, USA and the White Mountain National Forest in New Hampshire, USA from 2007–2013. Random effects included in every model were bander (observer) identity, male identification number, and study site. Models were ranked using Akaike's Information Criterion corrected for small sample size (AICc). Column K indicates number of model parameters and LL indicates log likelihood.

Model	K	AICc	ΔAICc	Weight	LL
Age class * size	7	1209.23	0	0.83	-597.50
Age class + size	6	1212.37	3.14	0.17	-600.10
Wing spot length * size	7	1222.65	13.42	0	-604.21
Wing spot length + size	6	1224.57	15.353	0	-606.20
Size	5	1230.21	20.98	0	-610.05
Age class	5	1345.34	136.11	0	-667.62
Wing spot length	5	1352.82	143.60	0	-671.36
Null	4	1373.02	163.80	0	-682.48

Table 3-4. Estimates of beta coefficients and their 95% confidence intervals (CI) from the top-ranked model of number of extra-pair young produced by male Black-throated Blue Warblers per breeding season. Data were collected from 2007–2013 at two breeding locations, one in the Nantahala National Forest, North Carolina, USA and the other in the White Mountain National Forest, New Hampshire, USA.

Parameter	Mean estimate	Lower CI	Upper CI
Intercept	-4.365	-9.132	0.402
Age class (SY)	6.478	0.595	12.362
Size	26.854	-4.762	58.471
Age class (SY) * size	-47.438	-86.452	-8.424

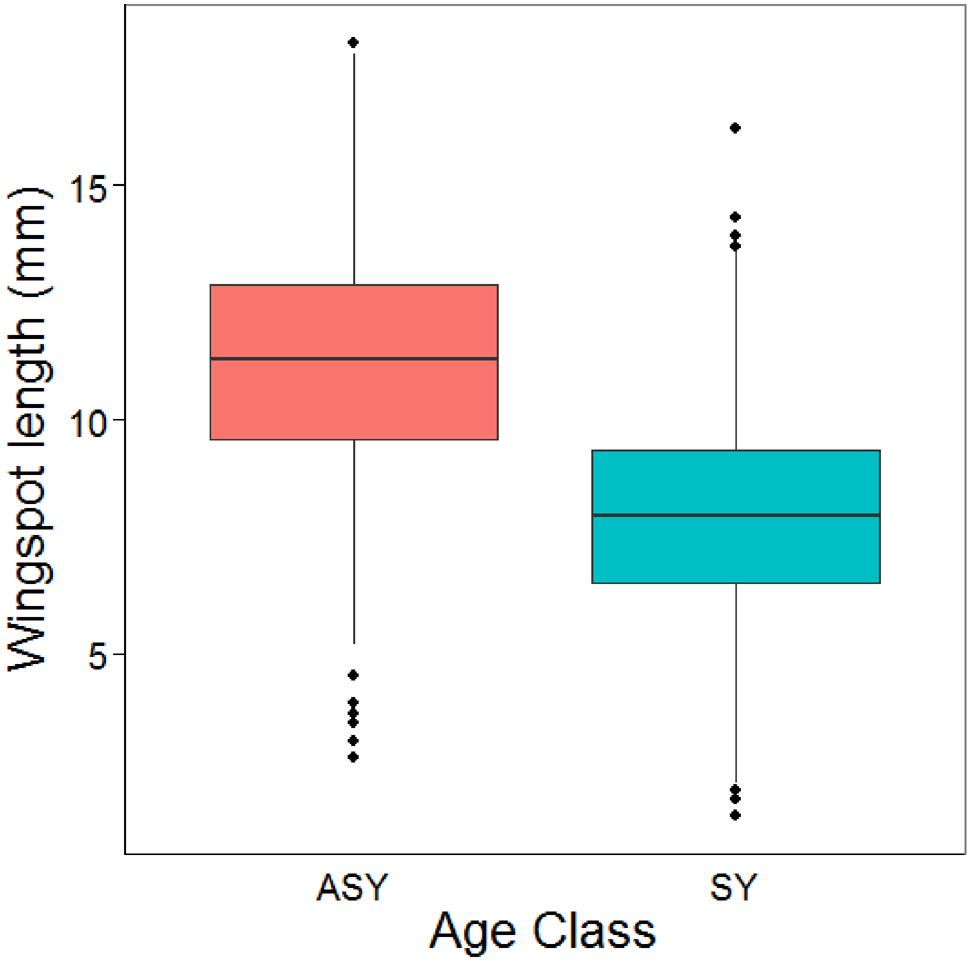

Figure 3-1. Relationship between age class and wing spot length for male Black-throated Blue Warblers breeding at two study sites, the Nantahala National Forest in North Carolina and the White Mountain National Forest in New Hampshire. Data were collected from 2007–2013. Older males are represented by the ASY (after-second-year) age class, while younger males are represented by the SY (second-year) age class.

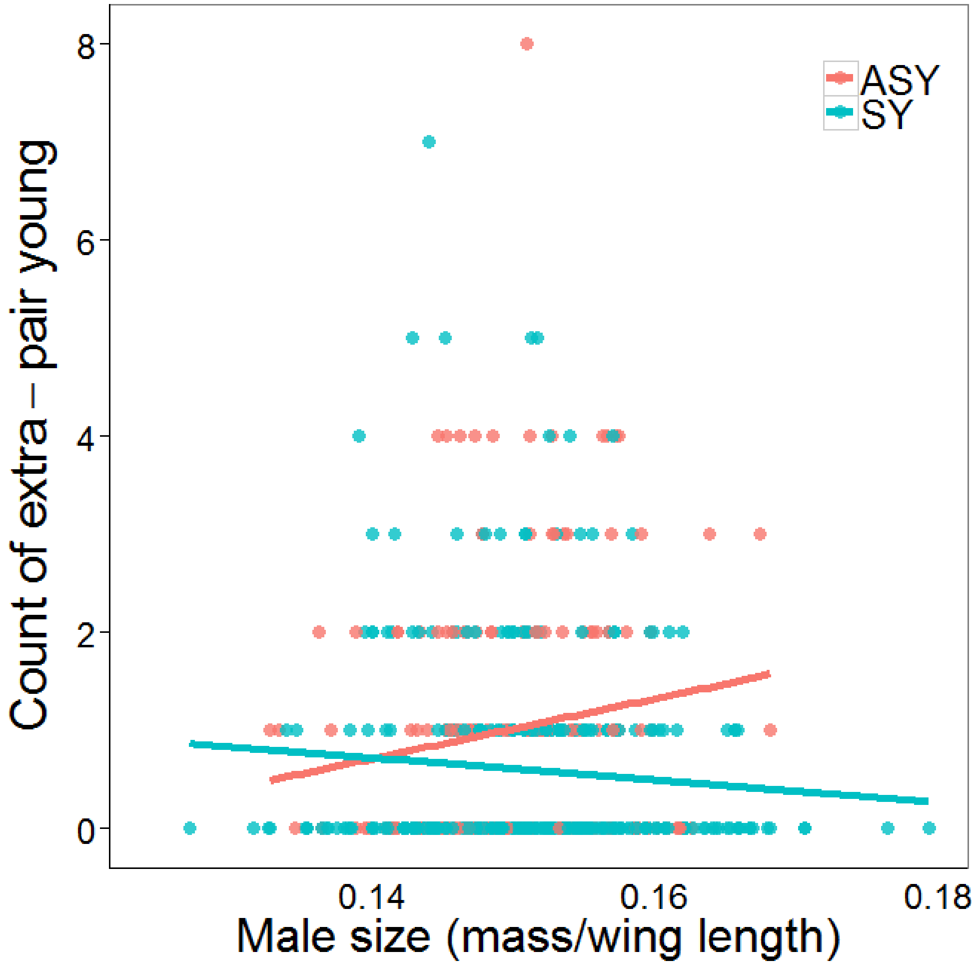

Figure 3-2. Number of extra-pair offspring sired by male Black-throated Blue Warblers was best explained by an interaction between male size (mass/wing length) and age class. Larger males in the older age class (ASY; after-second-year) sired the greatest number of extra-pair offspring per breeding season. Data were collected at two study sites from 2007–2013, one in the Nantahala National Forest, North Carolina, USA and the other in the White Mountain National Forest in New Hampshire, USA.

CHAPTER 4

SURVIVAL AND MOVEMENT OF BLACK-THROATED BLUE WARBLERS BREEDING IN THE SOUTHERN APPALACHIANS[1]

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ABSTRACT—Populations of Black-throated Blue Warblers (*Setophaga caerulescens*) have recently declined in the southernmost part of their breeding range (Sauer et al. 2014), but the cause of decline remains elusive. I used mark-resight data collected from 2010–2015 in the Nantahala National Forest, North Carolina, USA to assess two sets of hypotheses and corresponding predictions. First, I hypothesized that differences existed between adult male and female Black-throated Blue Warblers with regard to annual survival and movement probabilities. To assess my predictions corresponding to this hypothesis, I constructed models explaining apparent annual survival and movement probabilities and used an information theoretic approach for model comparison. My prediction that males had higher annual survival compared to females had limited support while my prediction that females had higher probability of temporary emigration compared to males was supported. Second, I hypothesized that individual characteristics affected apparent annual survival of adult Black-throated Blue Warblers. To assess my predictions corresponding to this hypothesis, I constructed Cormack-Jolly-Seber models explaining apparent annual survival probabilities according to individual covariates and used an information theoretic approach for model comparison. Consistent with predictions, female warblers attempting a greater number of nests in season *t* had a lower probability of surviving to season *t*+1 compared to females attempting fewer. However, I found no support for my prediction that apparent annual survival of male warblers was related to age or wing spot length.

INTRODUCTION

Population dynamic processes and vital rates must be understood for effective conservation of species. Annual survival is one important parameter that must be examined to understand a population's fluctuations. Breeding populations of many Neotropical migratory bird species have declined in recent years (Robbins et al. 1989, Sauer et al. 2014). In eastern North America declines of several species have been greatest at the southern periphery of their breeding areas, such as the high-elevation southern Appalachians. Such declines lend a sense of urgency to the need to estimate and understand migratory breeding bird population vital rates, including annual survival, in this southern Appalachian region.

The Black-throated Blue Warbler (*Setophaga caerulescens*) is a Neotropical migrant with a mainly northern United States and Canadian range that breeds in the southern Appalachians and, like other songbird species, has faced recent declines in this area (Sauer et al. 2014; Figure 4-1). However, causes of the decline remains unclear. Survival has been investigated for adult Black-throated Blue Warblers in this area (Stodola et al. 2013), but this study lacked critical information on movement patterns and how individual-level characteristics influence survival probability. Movement estimates are needed for this species because adult movement, particularly emigration, has the potential to bias survival estimates (Lebreton et al 1992). While permanent emigration can be a source of bias for survival estimates under many models, survival estimates can also be biased if temporary emigration movement is not random (Burnham 1993, Kendal et al. 1997) and via the interpretation of detection estimates. Thus, understanding emigration in this population of Black-throated Blue Warblers could help to produce less-biased survival estimates. Additionally, knowledge of Black-throated Blue Warbler adult annual survival and movement in this geographic area could inform why other members of the southern Appalachian breeding migratory bird community have been showing population-level declines (Robbins et al. 1989, Sauer et al. 2014).

Our understanding of how adult survival differs between males and females also is limited with regard to migratory songbirds (Stutchbury et al. 2009). Some studies examining these potential differences have found that annual survival is lower for females compared to males (Liker and Székely 2005, Fairbairn et al. 2007). In birds, lower rates of annual survival for females compared to males is often attributed to a higher cost of reproduction and higher risk of predation (Breitwisch 1989, Cilimburg et al. 2002, Sillett and Holmes 2002). Further, for Neotropical migrants, habitat segregation according to sex is common during the wintering period and females often occupy lower quality habitat than do males which can lead to lower annual survival for females (Marra and Holmes 2001). However, intersexual differences in annual survival are not always found in empirical investigations (Chase et al. 1997, Møller and Szép 2002). More research is needed regarding how annual survival, as well as immigration and emigration, differs between sexes in migratory birds and the mechanisms behind any variation.

Many factors can influence adult annual survival in birds (Aebischer and Coulson 1990, Karr et al. 1990, García-Pérez et al. 2014). For example, many researchers have found a general trend of younger birds surviving at lower rates compared to older birds (reviewed in Martin 1995a, Tavecchia et al. 2001). For short-lived migratory birds, annual survival often increases from the youngest age class to an older age class, but decreases in the oldest age class as a result of senescence (Møller and De Lope 1999). Additionally, empirical evidence has shown increased investment in reproduction is related to lowered survival for some birds (Santos and Nakagawa 2012). However, while reproduction is energetically costly, potential survival costs may be offset by individual quality (Mitchell et al. 2012). Related to individual quality, some individual characteristics are correlated with avian survival. For example, birds expressing more elaborate plumage coloration often have increased survival (Griffith et al. 2003, Galván and Møller 2013). A possible mechanism for increased survival corresponding with showier plumage could include energetic benefits conferred from reduced agonistic interactions with conspecifics (Cline et al.

2015; Chapter 2). Alternatively, plumage coloration may be unrelated to adult survival (Delhey and Kempenaers 2006). As part of this study, I examined the relationship of sex, age, reproductive investment, and plumage coloration to adult annual survival in the Black-throated Blue Warbler.

The Black-throated Blue Warbler is well studied (Holmes et al. 2005) and adult survival throughout the annual cycle has been estimated previously using capture-recapture methods (Sillett and Holmes 2002). This research found that the majority of mortality occurred during the migratory and wintering periods and that males generally had a higher survival rate than did females during the breeding season. More recently, Zipkin et al. (2014) investigated demographic rates for the Black-throated Blue Warbler breeding at the northern portion of their range. They used N-mixture models, which use count data, to estimate demographic rates and compared their results from this method to estimates using capture-recapture methods. Hatt et al. (2015) studied Black-throated Blue Warbler fledgling survival in the southern Appalachians. However, population parameters have not been formally investigated for adult Black-throated Blue Warblers breeding at the southern end of their breeding range, an area where this species has faced recent declines (Sauer et al. 2014). My objective in this study was to examine adult Black-throated Blue Warbler annual survival according to two sets of competing candidate models (hypotheses) developed according to theory, previous empirical works, and my prior observations.

HYPOTHESES

First, I constructed a candidate model set that corresponded to my hypotheses concerning differences between adult male and female Black-throated Blue Warblers in regard to apparent annual survival, temporary immigration, and temporary emigration. I predicted that males would have higher apparent annual survival compared to females and that females would have higher rates of movement (i.e., temporary immigration and emigration) compared to males based on evidence from previous work (Sillett and Holmes 2002, Cline et al. 2013). To investigate these predictions, I constructed models estimating adult Black-throated Blue Warbler apparent annual survival and movement, using a robust design capture-mark-resight framework and an information theoretic approach to models selection. My specific set of competing candidate hypotheses, and their representation in model form, are presented in Table 4-1.

Second, I constructed two additional sets (one for males and one for females) of competing candidate models to explain how individual characteristics affected year-to-year survival of adult Black-throated Blue Warblers. I constructed each of these model sets separately for each sex using individual covariates that represented my predictions. Specifically, I predicted that year-to-year survival of male Black-throated Blue Warblers was related to age and wing spot length with older males and males with larger wing spots having a higher apparent annual survival probability compared to younger males and males with smaller wing spots. Additionally, I predicted that annual survival of female Black-throated Blue Warblers was related to age and reproductive effort with older females with fewer nesting attempts having higher apparent annual survival probability compared to younger females that produced many nesting attempts. I ranked each model set using an information theoretic approach. Models are detailed in Table 4-2.

METHODS

Study area—My study locations were adjacent to the Coweeta Long Term Ecological Research Station (hereafter, Coweeta) within the Nantahala National Forest in Macon County, North Carolina, USA. Coweeta is located at 35°00'N, 83°30'W. My research was conducted as part of a long-term study of Black-throated Blue Warbler breeding ecology that was started at Coweeta in 2002. Specifically, my research was conducted from 2010–2015 at two 35-ha study sites located about 1150 m and 1400 m above sea level. Study sites are characterized by cove hardwood and northern hardwood forest types (Day et al. 1988) and consist of a diverse assemblage of mainly hardwood trees such as red oak (*Quercus rubra*), American beech (*Fagus grandafolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula allegheniensis*), black birch (*B. lenta*), Fraser magnolia (*Magnolia fraseri*), and pignut hickory (*Carya glabra*). Dominant shrub-layer plants include great laurel (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and American chestnut (*Castanea dentata*), and saplings of canopy trees. The Black-throated Blue Warbler breeds in this area from early mid-April to mid-July.

Species description—The Black-throated Blue Warbler (*Setophaga caerulescens*) is a Nearctic-Neotropical migratory songbird that breeds in forested areas of eastern North America and winters mainly in the Greater Antilles. Males and females of this species are markedly different in appearance, which allows the sexes to be easily distinguished in the field (Holmes et al. 2005). Males are territorial and show strong fidelity to breeding sites. Males have a prominent white wing spot at the base of their primary feathers and this plumage characteristic has been demonstrated to be important to male-male interactions (Cline et al. 2015, and see Chapter 2). Female Black-throated Blue Warblers build nests in the low shrub layer of the forest, which allows nests to be readily detected and checked. Females will re-nest after a failed nesting attempt and will often attempt a second brood after a successful first attempt (Holmes et al. 1992). Nest construction and incubation is performed solely by the female.

Field methods—During my study period, warbler pairs on the study sites were tracked and all breeding activities monitored. Nests were located by following females during the nest-building or incubation periods. All nests were checked at least every other day. Through this direct observation, numbers of nesting attempts for each warbler female were determined. Males were captured in their territories using mist nets, playback of conspecific song, and a decoy. Females were captured with mist nets near the nest during the final days of incubation. All adult birds were assigned a numbered United States Geological Survey band and a unique combination of three colored leg bands. Morphometric measurements were taken during banding and these included a measurement of male wing spot length, i.e., the longest extent of white coloration along the seventh primary feather, using digital calipers. Birds were aged as either SY (second-year; young birds in their first breeding season) or ASY (after-second-year; older birds in at least their second breeding season) using plumage characteristics (Pyle 1997). Animal use permits were obtained through the UGA Office of the Vice President for Research and my research was conducted in accordance with IACUC standards. All bird banding and marking was approved and permitted through USGS permit #22587.

Study design for apparent survival estimation—To examine adult survival of this population, I established a resighting survey protocol consisting of primary and secondary sampling periods (see Appendix E for details). As there are two sets of time intervals involved with the robust design (Pollock 1982, Kendall et al. 1995), each breeding season (2010–2015) was considered a primary sampling period. Data from primary occasions were also used for modeling the factors that affected apparent annual survival. Surveys during the breeding season were considered secondary sampling periods, during which the population is assumed demographically closed. The assumption of closure during secondary sampling periods is realistic due to the Black-throated Blue Warblers’ life history during these periods. Warblers are strongly territorial during the breeding season and exhibit extremely low levels of movement from these territories (Holmes et al. 2005). Additionally, floaters (wandering, unmated individuals) are essentially nonexistent in this species during the breeding season (Holmes et al. 2005). I conducted 30 secondary sampling periods within each of the six primary sampling periods. Secondary sampling occasions consisted of resighting surveys (i.e., sampling with replacement) of the study plots during which every part of the study plot was surveyed. Secondary sampling occasions occurred every other day from May 15th to July 15th in each year of the study (see Appendix E). During these surveys, sightings of both marked and unmarked adult warblers were recorded. When a marked individual was encountered its identity was noted.

Statistical analyses—I analyzed mark-resight data collected in the robust design framework using Program MARK version 8.0 (White and Burnham 1999). My study used an approach similar to those outlined in McClintock and White (2009) and McClintock et al. (2009). That is, I used a zero-truncated Poisson log-normal estimator, (Z)PNE, to model apparent annual survival (φ) and state-transition (γ' and γ'') parameters. I used the (Z)PNE mark-resight model because sampling within secondary periods is with replacement and the number of marked individuals in the population is not exactly known (McClintock and White 2012). I included males and females as different groups in analysis according to my hypotheses. Within Program MARK, I constructed eight models that corresponded to my competing hypotheses shown in Table 4-1. In all models I assumed α (intercept on the log scale for mean resighting rate during primary interval *j*), σ (resighting rate parameter, individual heterogeneity), and U (number of unmarked individuals in the population) were constant. I used model selection based on Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AICc; Burnham and Anderson 2002) to rank these models. Because goodness-of-fit tests are lacking for these type of mark-resight models, AICc was used to evaluate model fit (Burnham and Anderson

2002). When there was no clear top model, I averaged across models to generate estimates of the parameters of interest (Johnson and Omland 2004).

To investigate adult warbler annual apparent survival as related to individual covariates, encounter history data collected during primary sampling occasions (see above and Appendix E) were used in Cormack-Jolly-Seber (CJS) modeling with males and females considered separately. Probabilities of Black-throated Blue Warbler apparent survival (ϕ) and detection (p) were modeled with a state-space formulation of the CJS mark-recapture model (Lebreton et al. 1992). I created two candidate sets of five models each for males and females. Models were specified with individual-specific covariates to test my predictions (see Table 4-2). I checked for multicollinearity of all covariates used in each model set using Pearson's coefficient. All analyses were conducted in Program R version 3.2.2 (R Core Team 2015) and OpenBUGS (Thomas et al. 2006) using the R2OpenBUGS package (Sturtz et al. 2005). I conducted hierarchical analysis of apparent survival and detection in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods. Models were constructed using a mixed model formulation in a Bayesian paradigm that is analogous to generalized linear mixed models (Bolker et al. 2009). I used a logit link and included individual as a random effect in every model. I specified uninformative priors for the variance of all individual covariates. For each model, I ran three overdispersed parallel MCMC chains to evaluate model convergence. 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 250,000 iterations with 50,000 burned iterations and a thinning interval of 3 for posterior summarization.

Model selection and evaluation of hierarchical model uncertainty is an active field of research where little consensus has been reached (Link and Barker 2009, Kéry and Schaub

2012). Deviance Information Criterion (DIC) is often used for Bayesian non-hierarchical model selection (Link and Barker 2009, Spiegelhalter et al. 2002, Spiegelhalter et al. 2012). However, Bayesian hierarchical model selection is complicated because the number of model parameters derived from random factors is not easily estimable (Kéry 2010). Thus, DIC is problematic when random effects models are being ranked because it attempts to estimates the effective number of parameters to be used as a penalty. Therefore, I ranked models using a penalized posterior deviance (Akaike 1973). I approximated the number of parameters in each model by counting each component of the model that came from a separate distribution as a single parameter. I then computed AIC as deviance + 2*k*, where *k* equaled the number of parameters for a model. I considered this approach sufficient to determine an approximate, and relative, indicator of the best model for each sex. Estimates of the beta coefficients from the top-ranked model were produced and their 95% Bayesian credible intervals (CI) were examined to ensure that they were informative (i.e., exhibited change from the priors). To determine the influence of each variable on apparent survival, I calculated odds ratios for the parameter estimates of the top model.

RESULTS

I tested my hypotheses using a dataset consisting of 310 Black-throated Blue Warblers, 164 males and 146 females. The top-ranked model explaining apparent annual survival and movement probabilities consisted of survival varying by sex and constant temporary immigration and emigration probabilities; this model had 23% weight (Table 4-3). However, four other models were within two delta AICc units from this top model. Thus, there was no clear best model in my candidate set. Annual survival was estimated to be 0.45 ± 0.04 for males and 0.41 ± 0.04 for females (Table 4-4). Generally, female Black-throated Blue Warblers had a slightly greater probability of temporary emigration compared to male and my analyses showed similar male and female apparent survival rates.

Model selection indicated that male apparent survival was not explained by any of the covariates included, as there was no clear top model, with the null model being the best-fitting model (Table 4-5). However, for females, number of nesting attempts produced per season was important to explaining apparent annual survival (Tables 4-5 and 4-6). While the age parameter was included in the second-ranked model explaining female survival, this was an uninformative parameter that I did not interpret as having an ecological effect (Arnold 2010). Examination of the beta coefficients of this top model showed directional influence congruent with the hypotheses that females with more nesting attempts had lower apparent survival (Table 4-7). As an example, odds-ratio calculations indicated that females with three attempts had a 15% lower apparent annual survival probability than females with two attempts (Table 4-7, Figure 4-2). Mean detection probability estimated from this model was 0.87 (95% CI: 0.74–0.96).

DISCUSSION

This study examined apparent annual survival and movement parameters of a breeding population of Black-throated Blue Warblers in the southern Appalachians. Consistent with my prediction, female Black-throated Blue Warblers had a greater probability of between-breeding season temporary emigration than did males. However, my analyses did not reveal marked differences in male and female apparent survival rates and provided limited support for a model explaining differences in survival by sex. Investigation of the individual characteristics that I predicted would affect apparent annual survival produced mixed results. Reproductive effort was important in explaining female apparent survival. Female warblers with a greater number of nesting attempts in season *t* had a lower probability of surviving to season *t*+1 compared to females that had fewer nesting attempts. By contrast, results for males did not provide insight into the individual characteristics that affect apparent annual survival, as survival probability was not found to be related to age or wing spot size.

Apparent annual survival and movement estimation—Regarding my first set of hypotheses and predictions (Table 4-1), the top-ranked model explaining apparent annual survival and movement probabilities consisted of survival varying by sex with constant temporary immigration and emigration; this model had 23% of the weight (Table 4-3). However, there was no clear best model according to selection results and the second-ranked model included temporary emigration probability varying according to sex. Additionally, average resighting rate was high and did not differ between sexes (0.99 ± 0.24 SE; Table 4-4). Thus, I found some support for sex differences in apparent annual survival and movement probabilities.

Related to my prediction that adult males would have higher apparent annual survival probabilities compared to females, model-averaged estimates for apparent annual survival probability were suggestive of differences between males and females with a lower estimate for females compared to males (Table 4-4). However, estimated confidence intervals based on unconditional standard errors overlapped, suggesting small, non-statistical differences in underlying rates. Sillett and Holmes (2002) found that for Black-throated Blue Warblers breeding in New Hampshire males had higher apparent annual survival (0.51 ± 0.03) compared to females (0.40 ± 0.03). I did not find such distinct differences in apparent survival probabilities between males (0.45 ± 0.03) and females (0.41 ± 0.03), and this was consistent with findings from Stodola et al. (2013). Thus, it appears there could be a subtle differences in apparent annual survival between these two breeding locations.

I found partial support for my prediction that adult female warblers have higher probability of movement (i.e., temporary immigration and emigration) compared to males. According to model-averaged estimates, females had a higher probability of temporary emigration (specifically, moving from an observable to unobservable state) compared to males (Table 4-4), but both estimates were generally low. Thus, because overall mean resighting rate was high and temporary emigration estimates were low, it is unlikely that the associated survival estimates are biased. Temporary immigration probability estimates did not differ for males and females, a finding that does not support my prediction. Movement needs to be considered when attempting to estimate survival, especially when vagile organisms are the subjects of interest (Szé 1999). Sillett and Holmes (2002) indicated that differences in adult annual survival estimates between male and female Black-throated Blue Warblers may have resulted, at least in part, from differences in permanent emigration patterns between the sexes. If females had a higher probability of permanent emigration, apparent survival estimates would be lower than demographic survival. The idea that females undergo longer-distance breeding dispersal compared to males is supported by findings from New Hampshire by Cline et al. (2013). My finding of sex-differences in temporary emigration probability estimates from this current study also supports this idea.

Predictors of apparent annual survival for female and male warblers—I found support for my prediction regarding female Black-throated Blue Warbler apparent survival in relation to reproductive effort. Female Black-throated Blue Warblers that had more nesting attempts in year *t* were less likely to survive to year *t*+1 (Figure 4-2). This is consistent with previous avian research that found increased reproductive effort to be linked to decreased survival (Lindén and Møller 1989, Martin 1995b, Blomberg et al. 2013). Female Black-throated Blue Warblers perform all nest construction and incubation (Holmes et al 2005) and the energetic costs of these activities could contribute to reduced annual survival for individuals with many nesting attempts. However, this result should be taken in the context of results presented in the previous paragraph—females have higher temporary emigration probabilities compared to males. Furthermore, Cline et al. (2013) found females that fledged few offspring (and had many nesting attempts) in year *t* were more likely to undergo breeding dispersal movement in year *t*+1 compared to females that fledged many offspring. Survival estimation using CJS methods does not account for permanent emigration, therefore mortality and movement can be confounded when detection is low (see Appendix F). However, estimates from my models indicated high detection probability (0.87), thus this was likely not a concern for my study.

Contrary to my predictions, age was not important in explaining apparent annual survival for male or female Black-throated Blue Warblers. This finding is consistent with Sillett and Holmes (2002), who also found age did not affect survivorship on the breeding or wintering grounds. Moreover, I did not find evidence to support my predictions that adult male Black-throated Blue Warbler apparent annual survival probability differed according to wing spot length. More research grounded in solid theory is needed to understand which, if any, male plumage characteristics might be related to apparent annual survival. While females in this species generally invest more in reproduction compared to males, there is male investment and some males invest more than others (Sillett et al. 2005). Thus, a metric of male reproductive effort (e.g., provisioning rate) could aid in explaining adult male annual survival. Also, modeling that includes a larger suite of variables could better elucidate patterns of male Black-throated Blue Warbler annual survival. Specifically, extrinsic factors should not be overlooked as they have also been found to have an influence on this species' survival (Sillett et al. 2000).

To fully understand Neotropical migrant songbird population declines in the southern Appalachians, studies of more species across a range of habitats are needed. In addition, other population parameters need to be estimated for this and other songbird species. Estimates of apparent survival from this study were similar to those found by Sillett and Holmes (2002) for a stable population (Figure 4-1). However, adequate adult survival is only one component of population persistence. Long-distance migratory birds have complex annual cycles (Greenberg and Marra 2005) and events on both migration and the wintering period can have a strong influence on population dynamics (Sillett and Holmes 2002, Marra et al. 2015). Survival estimates from my study coupled with other population parameters to be estimated in the future will contribute to a better understanding of songbird population declines in the southern Appalachians.

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Table 4-1. Hypotheses and corresponding models describing apparent annual survival and movement for adult Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. Each of the eight models represents a competing hypothesis. “Constant” indicates the parameter is neither sex-dependent nor time-dependent. Parameters varying by “g” denote expected differences by two groups, males and females.

Hypothesis	Model description
Apparent survival, temporary immigration, and temporary emigration are constant	φ(.) γ’’(.) γ’(.)
Apparent survival differs by sex; temporary immigration and temporary emigration are constant	φ(g) γ’’(.) γ’(.)
Apparent survival is constant, temporary immigration differs by sex, temporary emigration is constant	φ(.) γ’’(.) γ’(g)
Apparent survival and temporary immigration are constant; temporary emigration differs by sex	φ(.) γ’’(g) γ’(.)
Apparent survival and temporary immigration differ by sex; temporary emigration is constant	φ(g) γ’’(.) γ’(g)
Apparent survival differs by sex; temporary immigration is constant; temporary emigration differs by sex	φ(g) γ’’(g) γ’(.)
Apparent survival is constant; temporary immigration and temporary emigration differ by sex	φ(.) γ’’(g) γ’(g)
Apparent survival, temporary immigration, and temporary emigration differ by sex	φ(g) γ’’(g) γ’(g)

Table 4-2. Descriptions of models used in my analyses explaining apparent annual survival of Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. Each model represents a competing hypothesis. Models were constructed separately by sex and ranked according to AIC. In all cases, the covariate of interest was measured in year *t* and investigated to determine whether it affected survival to year *t*+1. A "+" indicates an additive model while a "*" indicates an interactive model.

Hypotheses explaining apparent annual survival	
Males	Females
Null	Null
Wing spot length	Number of nesting attempts
Age	Age
Wing spot length + age	Number of nesting attempts + age
Age * wing spot length	Number of nesting attempts * age

Table 4-3. Model selection results explaining apparent annual survival and movement for adult Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. Each model corresponds to a competing hypothesis. Akaike's Information Criterion corrected for small sample size (AICc) was used to rank models. Parameters varying by "g" denote differences by two groups, males and females. Explanation of parameters presented: φ is apparent survival between primary intervals, γ'' is the probability of transitioning from an observable state to an unobservable state, γ' is the probability of transitioning from an unobservable state to an observable state. Column *k* indicates number of model parameters.

Model	*k*	AICc	ΔAICc	Weight	Deviance
φ(g) γ''(.) γ'(.)	7	5571.36	0	0.23	5557.16
φ(.) γ''(g) γ'(.)	7	5571.85	0.49	0.18	5557.65
φ(g) γ''(g) γ'(.)	8	5572.15	0.79	0.16	5555.89
φ(.) γ''(.) γ'(.)	6	5572.17	0.81	0.15	5560.02
φ(g) γ''(.) γ'(g)	8	5573.28	1.92	0.09	5557.02
φ(.) γ''(g) γ'(g)	8	5573.52	2.15	0.08	5557.25
φ(g) γ''(g) γ'(g)	9	5574.22	2.85	0.06	5555.89
φ(.) γ''(.) γ'(g)	7	5574.22	2.86	0.05	5560.02

Table 4-4. Model-averaged parameter estimates (± unconditional standard errors) for apparent annual survival and movement probabilities by sex. Presented are estimates for: apparent survival between primary intervals (φ), probability of transitioning from an observable state to an unobservable state (γ’’), probability of transitioning from an unobservable state to an observable state (γ’), and overall mean resighting rate (λ). Data were collected 2010–2015 at two sites in the Nantahala National Forest, North Carolina, USA.

	φ	γ’’	γ’	λ
Males	0.45 ± 0.04	0.06 ± 0.04	0.05 ± 0.25	0.99 ± 0.24
Females	0.41 ± 0.04	0.11 ± 0.07	0.05 ± 0.20	0.99 ± 0.24

Table 4-5. Model-selection results for models explaining male apparent annual survival for Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. A random effect of individual was included in each model. Akaike's Information Criterion (AIC) was used to rank models. Number of parameters (*k*) was approximated. A "+" indicates an additive model while a "*" indicates an interactive model.

Model	*k*	AIC	ΔAIC	Weight	Deviance
Null	2	229.82	0	0.49	225.84
Wing spot	3	231.37	1.52	0.23	225.37
Age	3	231.93	2.09	0.17	225.93
Age+wing spot	4	233.33	3.48	0.09	225.33
Age*wing spot	5	236.44	6.60	0.02	226.44

Table 4-6. Model-selection results for models explaining female apparent annual survival for Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. A random effect of individual was included in each model. Akaike's Information Criterion (AIC) was used to rank models. Number of parameters (*k*) was approximated. A "+" indicates an additive model while a "*" indicates an interactive model.

Model	*k*	AIC	ΔAIC	Weight	Deviance
Number of nesting attempts	3	208.54	0	0.60	202.54
Age+number of nesting attempts	4	210.00	1.47	0.29	202.00
Age*number of nesting attempts	5	212.42	3.89	0.09	202.42
Null	2	216.18	7.65	0.01	212.18
Age	3	217.57	9.03	0.01	211.57

Table 4-7. Estimates of beta coefficients and their 95% Bayesian credible intervals (CI) from the top-ranked model of female apparent annual survival. Data were collected 2010–2015 at two sites in the Nantahala National Forest, North Carolina, USA.

Parameter	Mean estimate	Lower CI	Upper CI
Number of nesting attempts	-0.635	-1.096	-0.235
Random effect of individual	0.510	0.005	1.980
Intercept	0.717	-0.056	1.621

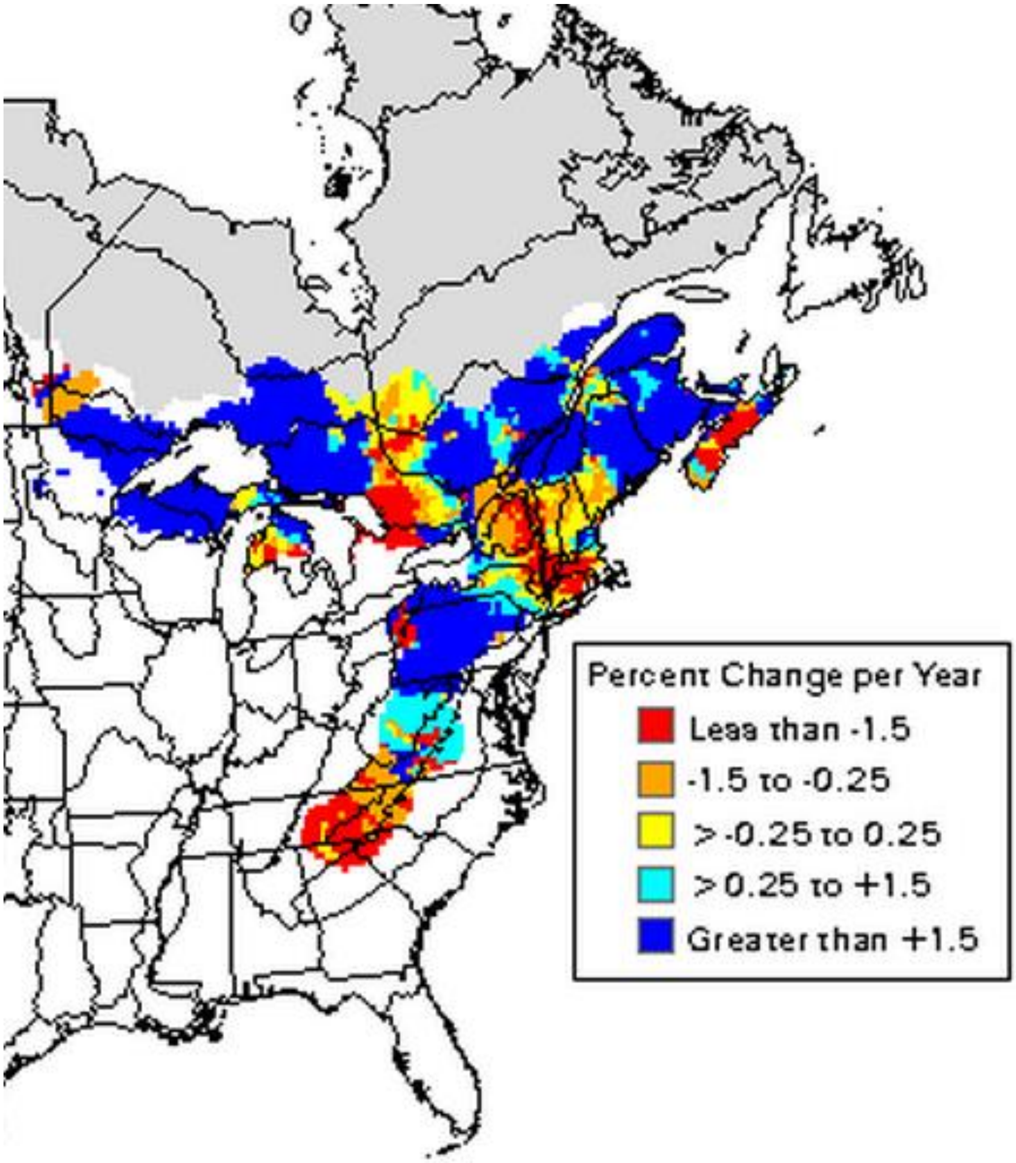

Figure 4-1. Breeding bird survey trend map for the Black-throated Blue Warbler, 1966–2013. Colors indicate percent change per year with the southern Appalachians region showing a declining population trend. Figure is from Sauer et al. (2014).

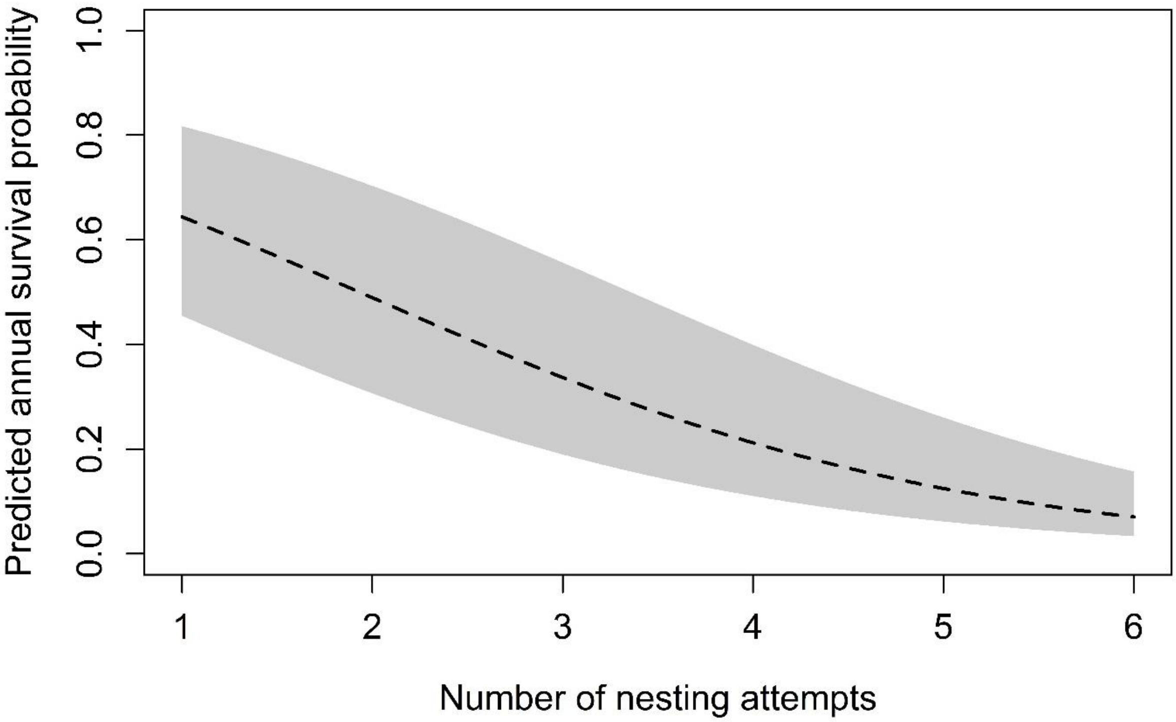

Figure 4-2. Predicted apparent annual survival probability (dashed line) decreased with number of nesting attempts for female Black-throated Blue Warblers breeding in the Nantahala National Forest, North Carolina, USA. Gray area surrounding the dashed line indicates upper and lower bounds of the 95% Bayesian credible interval.

CHAPTER 5

CONCLUSIONS AND SYNTHESIS: UNDERSTANDING BEHAVIOR, SURVIVAL, AND MOVEMENT IN A MIGRATORY SONGBIRD, WITH EMPHASIS ON THE IMPORTANCE OF A PROMINENT PLUMAGE CHARACTERISTIC

This dissertation focused on social signaling, extra-pair paternity, and survival and movement in Black-throated Blue Warblers (*Setophaga caerulescens*) breeding in the southern Appalachians. I placed particular emphasis on how male wing spot, a prominent plumage characteristic, may be related to intraspecific communication and survival. Many bird species display elaborate plumage characteristics. Often, plumage characteristics are important for social signaling (Lyon and Montgomerie 1986). These plumage traits may be used for intraspecific communication in both intersexual and intrasexual contexts (Berglund et al. 1996). Elaborate plumage characteristics can incur costs to their displayer, including survival costs (Hooper and Miller 2008). The utility and cost surrounding prominent plumage characteristics can vary and identifying the circumstances in which prominent plumage characteristics convey information. By studying the possible functions and survival costs associated with this conspicuous plumage trait in this migratory songbird I have contributed to the greater knowledge of avian behavior, communication systems, and annual survival. Information gained from this research will provide clues to help better comprehend how these traits and systems may have evolved. Conspicuous plumage is important in many different contexts and may have multiple functions. For instance, the role of the female Black-throated Blue Warbler wing spot and identifying any non-survival costs associated with male wing spot were not examined in this study and remain fertile areas for future research. Additionally, the importance and function of the Black-throated Blue Warbler wing spot during the wintering period should be studied. In the paragraphs below, I briefly summarize the important findings of each chapter, followed by a synopsis of the entire study.

SOCIAL SIGNALING

In Chapter Two, I investigated the social communication function of a conspicuous plumage characteristic in male Black-throated Blue Warblers, after breeding territory establishment when individuals are familiar with neighbors. Via experimental manipulation of males' white wing spots, and subsequent observation of their behavior, I found that males with experimentally eliminated wing spots had more frequent close-range interactions with conspecific males. Also, these manipulated males had more agonistic interactions involving aggressive vocalizations compared to control males, though effects differed according to male age class. However, the wing spot did not appear to be important for interactions with conspecific females; frequency of close-range interactions with female conspecifics was not influenced by wing spot manipulation. Finally, wing spot manipulation did not influence males' territorial song rates or responses to a simulated intruder, indicating no change in individual self-perception. My study provides evidence that, even when individuals are familiar with each other and on established territories, social status signals continue to convey important information. Additionally, the male Black-throated Blue Warbler wing spot appears to be more important in male-male communication compared to male-female communication. However, the role of the male wing spot in interactions with females is not clear and deserves more empirical attention.

EXTRA-PAIR PATERNITY

In Chapter Three, I sought to better understand what male characteristics explain extra-pair paternity in Black-throated Blue Warblers. I hypothesized that wing spot length, male age class, and male size were important in explaining extra-pair paternity. I used data collected during the warblers' breeding period at two spatially distinct study sites and an information theoretic approach to model selection to assess my predictions that males with longer wing spots, older males, and larger males would sire more extra-pair offspring. I found the most support for a model including an interaction between male age class and size. Specifically, larger males generally had more extra-pair offspring per breeding season, but this effect differed between male age classes. That is, the oldest and largest males sired the greatest number of extra-pair offspring. I found that the male Black-throated Blue Warbler white wing spot was correlated with age, but no evidence to support my prediction that male wing spot length was related to number of extra-pair offspring produced.

SURVIVAL AND MOVEMENT

In Chapter Four, I studied adult annual survival of this Black-throated Blue Warblers breeding in the southern Appalachians. To do this, I used mark-resight data collected from 2010–2015 in the Nantahala National Forest, North Carolina, USA to assess two sets of hypotheses and corresponding predictions. First, I hypothesized that differences existed between adult male and female Black-throated Blue Warblers with regard to apparent annual survival and temporary immigration and emigration probabilities. To assess my predictions corresponding to this hypothesis, I constructed models explaining apparent annual survival and movement probabilities and used an information theoretic approach for model comparison. My prediction that males had higher apparent annual survival compared to females had limited support while my prediction that females had higher probability of temporary emigration compared to males was supported. Second, I hypothesized that individual characteristics affected apparent annual survival of adult Black-throated Blue Warblers. To assess my predictions corresponding to this hypothesis, I constructed Cormack-Jolly-Seber models explaining apparent annual survival probabilities according to individual covariates and again used an information theoretic approach for model comparison. Consistent with predictions, female warblers attempting a greater number of nests in season *t* had a lower probability of surviving to season *t*+1 compared to females attempting fewer. However, I found no support for my prediction that apparent annual survival of male warblers was related to age or wing spot length.

SUMMARY

I found that the Black-throated Blue Warbler male wing spot was important in intraspecific male-male communication even in situations where males were familiar with one another. However, I did not find support for male wing spot length being important in explaining extra-pair paternity in this species; more important were male age and male size. Regarding survival, male wing spot length was not important in explaining male annual survival, thus there does not appear to be an obvious survival cost associated with displaying a longer wing spot. There may be other associated costs with displaying the wing spot plumage trait, but any cost remains unclear. Furthermore, any function of the male wing spot in communicating with conspecific females is still uncertain. While I did not find wing spot length to be important in explaining patterns of extra-pair paternity, female Black-throated Blue Warblers may still use the male wing spot as a signal, but the type of information conveyed and how it is perceived by a female receiver remains a question. In sum, results from my dissertation research suggest that the male Black-throated Blue Warbler wing spot is most relevant in male-male communication, at least during the breeding period, but any male-female communication function remains unclear.

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APPENDIX A: DIGITAL WING SPOT MEASUREMENT

At the northern study area, photographs were taken during banding to measure the wing spot length of a subset of males (n=365). Using ImageJ software (Rasband 2014), each image was scaled to a ruler included in the photo and the extent of white barbs along the feather shaft in the outer vane of primary flight feather p7 was measured, starting from the primary coverts (Figure A-1). The extent of white was measured twice and averaged.

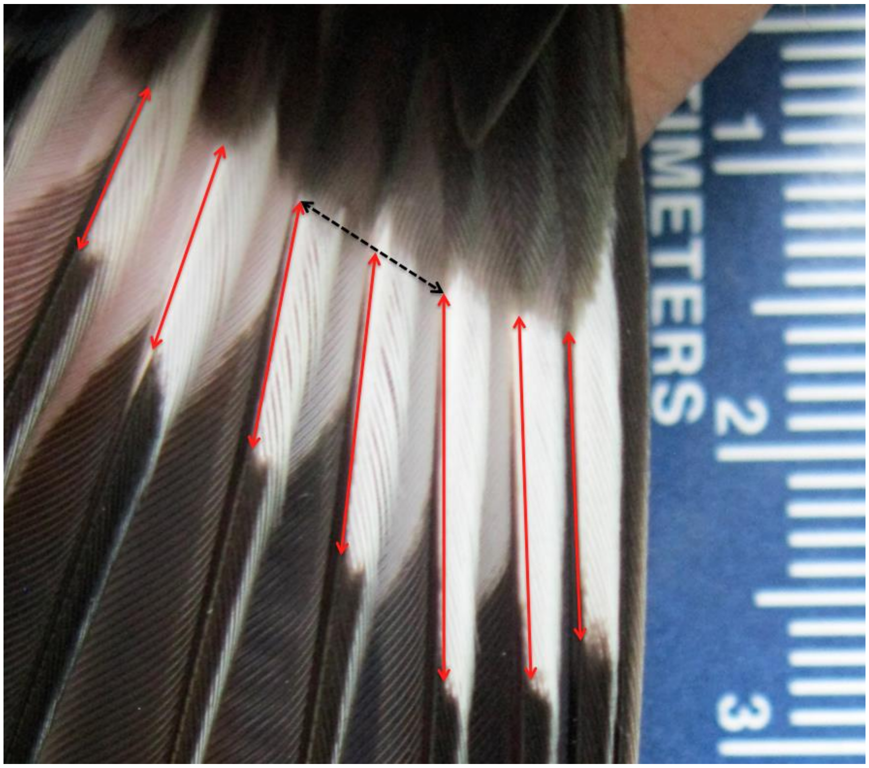

Figure A-1. Photo explaining digital wing spot measurement for male Black-throated Blue Warblers breeding in the White Mountain National Forest in New Hampshire, USA. Images were scaled to the ruler and the measurement was taken along the feather shaft of primary seven (third red line from right) from the tip of the coverts to the end of the white barbs in the outer vane. If the tip of a covert did not cover the feather shaft, measurement was started by estimating the point at which a line drawn between the two nearest coverts would cross the feather shaft (black dashed line). Photo credit: Lindsey Nietmann.

APPENDIX B: SITE DIFFERENCES

Age distribution between sites

Differences existed between the Black-throated Blue Warbler subpopulation breeding at the southern site and the subpopulation breeding at the northern site. For one, male age structure was different (Figure B-1) with a greater proportion of older (ASY; after-second-year) males at the southern site compared to the northern site. A model including the effect of age was better than a null model at explaining differences between study sites (binomial GLMM with random male ID; LRT: $\chi^2 = 5.00$, df=1, $p = 0.026$).

Age differences in morphometrics according to site

For both study sites wing spot length, wing length, and number of extra-pair young sired increased with male age. In contrast to the northern site, total young produced per male per breeding season did not differ between age classes at the southern study site (Table B-1 and B-2). Investigation into this site-level difference between breeding populations deserves attention. Regarding Tables B-1 and B-2: The dataset used in *t*-test analyses included multiple observations and measurements of the same individual males because some males returned to the study sites in multiple breeding seasons. However, when additional analyses were run after removing duplicate birds (i.e., (1) only the first record of a male was used or (2) when only one randomly selected male record was used) no change in inference resulted.

Table B-1. Age differences in morphometrics and reproductive variables for male Black-throated Blue Warblers breeding at the southern study site in the Nantahala National Forest in North Carolina, USA. Older males are represented by the ASY (after-second-year) age class, while younger males are represented by the SY (second-year) age class. EPY indicates extra-pair young, WPY indicates within pair young.

	ASY males		SY males			*t*-test	
Variable	Mean	SE	Mean	SE	*t*	df	*p*
Wing spot	11.94	0.32	8.24	0.16	10.43	91.9	<0.001
Wing length	65.05	0.18	63.71	0.14	5.81	134.7	<0.001
Mass	9.40	0.10	9.52	0.06	-0.99	30.3	0.33
WPY	1.86	0.21	2.00	0.23	-0.45	86.9	0.65
EPY	1.10	0.20	0.29	0.09	3.72	81.9	<0.001
Total young	2.57	0.27	2.15	0.21	1.23	103.8	0.22

Table B-2. Age differences in morphometrics and reproductive variables for male Black-throated Blue Warblers breeding at the northern study site in the White Mountain National Forest in New Hampshire, USA. Older males are represented by the ASY (after-second-year) age class, while younger males are represented by the SY (second-year) age class. EPY indicates extra-pair young, WPY indicates within-pair young.

	ASY males		SY males		*t*-test		
Variable	Mean	SE	Mean	SE	*t*	df	*p*
Wing spot	10.93	0.16	7.85	0.10	15.97	448.5	<0.001
Wing length	64.32	0.08	63.30	0.06	10.35	506.4	<0.001
Mass	9.66	0.03	9.58	0.02	2.34	519.6	0.02
WPY	1.86	0.12	1.62	0.10	1.59	566.5	0.11
EPY	1.35	0.10	0.58	0.06	6.48	420.4	<0.001
Total young	3.21	0.16	2.21	0.11	5.22	481.4	<0.001

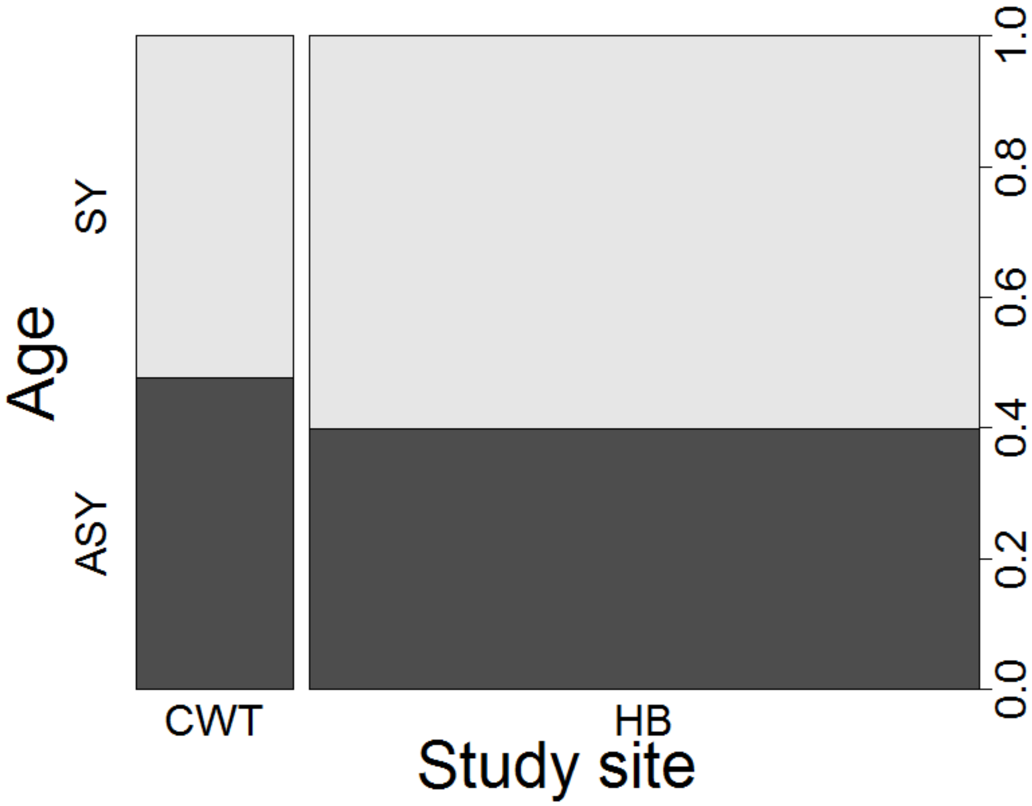

Figure B-1. There were a greater proportion of males in the older (ASY; after-second-year) age class at the southern study site (CWT) compared to the northern site (HB). The older age class (ASY) is indicated by the dark shading while the younger, yearling (SY; second-year) age class is shown in light gray. Relative sample size is indicated by bar width in this plot.

APPENDIX C: ADDITIONAL GENETIC SUMMARY STATISTICS FOR THE SOUTHERN STUDY SITE

At the southern study site, 34 banded males were identified as siring at least 1 extra-pair young. When the extra-pair sire could be identified, 69% were males holding territories directly next to the female. Out of 121 nests sampled at the southern study site, 99 had complete reproductive data (i.e., nestlings and both social parents had blood samples collected). The 22 nests lacking complete reproductive information contained 68 nestlings total. The percentage of nests containing at least one extra-pair young was 65%. Among nests containing at least 1 extra-pair young, the mean proportion of extra-pair young in these nests was 68%. The number of nests that had at least two extra-pair young was 46. In clutches with at least 2 extra-pair young, and where sires could be identified, 58% contained offspring from 2 different sires. The total number of nestlings sampled and genotyped from nests for which I had complete reproductive data was 393. In these complete nests, 82 total extra-pair young could be assigned to a known male while 67 total extra-pair young could not be assigned to any sampled male. Thus, total nestlings identified as extra-pair was 149 and the percentage of offspring (from these complete nests sampled) that were extra-pair was 38%.

APPENDIX D: LONGITUDINAL (WITHIN-MALE) CHANGE IN MORPHOMETRICS, REPRODUCTIVE VARIABLES, AND WING SPOT LENGTH

I examined how wing spot length changes within an individual over time. Sample sizes were limited (n=62), with the majority of data points coming from the northern study site (southern study site n=5; northern study site n=57). Estimates (± SE) for mean change from year *t* to *t*+1 in morphometric and reproductive variables are summarized in Table D-1. Also shown are results from paired t-tests. Both wing spot and wing length increased from year *t* to *t*+1 (Figure D-1).

Table D-1. Longitudinal age effects on morphometrics and reproductive variables for male Black-throated Blue Warblers breeding at two study sites, the Nantahala National Forest in North Carolina, USA and the White Mountain National Forest in New Hampshire, USA. EPY indicates count of extra-pair young, WPY indicates count of within-pair young. Results from paired t-tests indicated that, within-individual, wing spot and wing length increase from year *t* to *t* + 1.

	Year *t*		Year *t* + 1		Paired *t*-test		
Variable	Mean	SE	Mean	SE	*t*	df	*P*
Wing spot	9.04	0.38	11.50	0.29	6.81	51	<0.001
Wing length	63.51	0.23	64.51	0.18	5.43	51	<0.001
Mass	9.56	0.07	9.68	0.07	1.25	43	0.22
WPY	1.59	0.32	1.98	0.30	1.41	29	0.17
EPY	0.90	0.25	1.27	0.28	0.67	27	0.51
Total young	2.44	0.36	3.12	0.42	1.50	29	0.15

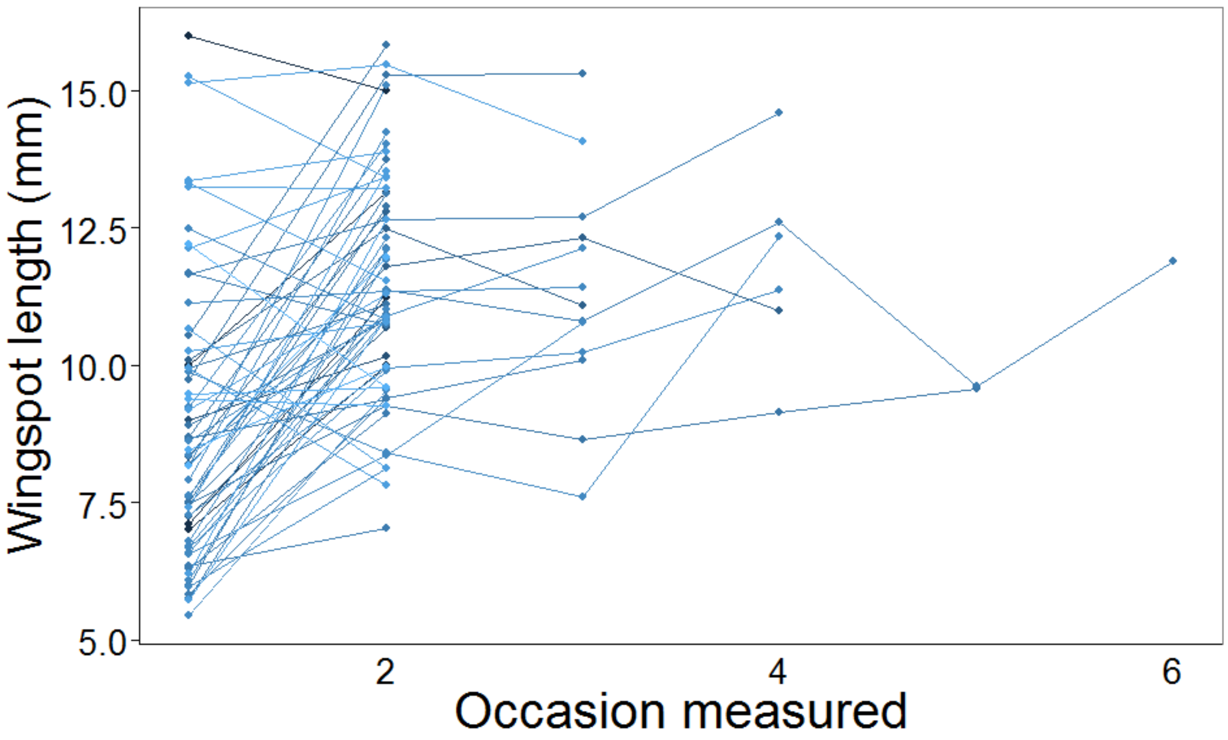

Figure D-1. Longitudinal (within-male) changes in wing spot length over time (with increasing age) for Black-throated Blue Warblers breeding at two study sites, the Nantahala National Forest, North Carolina, USA and the White Mountain National Forest in New Hampshire, USA.

APPENDIX E: ROBUST DESIGN SAMPLING FRAMEWORK

Figure E-1. Illustration of my sampling under the robust design framework; shown is a schematic of the first three years of sampling. A primary sampling occasion occurred from May 15th to July 15th each year, 2010–2015. Within each primary sampling occasion were 30 every-other-day secondary sampling occasions, during which the population is assumed to be closed. The intervals between primary periods represent the time between breeding seasons. Between primary periods the population is assumed to be open to additions (birth and recruitment) and losses (death and permanent emigration).

Primary periods	1 (2010)						2 (2011)						3 (2012)					Sampling continued through 2015
Secondary periods	1	2	...	29	30		1	2	...	29	30		1	2	...	29	30	
Population status	Closed					Open	Closed					Open	Closed					

APPENDIX F: DETAILS REGARDING SURVIVAL ANALYSES

A brief overview of survival analysis methods using capture-recapture data—Capture-recapture methods are a common way to estimate population parameters, including survival and population size. These methods have a rich history and have been continually improved since their seminal formulation in the 1960s (Cormack 1964, Jolly 1965, Seber 1965). In such capture-recapture studies, animals of interest are captured, given identifying marks, and released back into the population. Following the initial capture event, subsequent sampling occasions are used to recapture or resight these marked individuals. The resulting data are then used to estimate population vital rates of interest.

Research investigating survival rates, especially in populations of vagile organisms such as small migratory songbirds, can be complicated by practical issues of data collection and statistical analysis. In particular, one issue that poses statistical challenges is individual detection. The main problem surrounding individual detection is the separation of mortality from permanent emigration, i.e., often it is impossible to differentiate between an organism that has died and one that has permanently moved away from the study area. Survival is confounded with permanent emigration (probability) in traditional mark-recapture models like Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965). If the statistical models used to estimate survival do not take into account permanent emigration, the resulting survival estimator will have a negative bias. Thus, to reduce bias it is important to account for detection in analyses, as do modern methods of estimation.

Mark-recapture studies and models come with sets of assumptions that must be met in order to generate reliable inference. Two major types of models have been developed around an “open” (Pollock et al. 1990, Lebreton et al. 1992) or “closed” (Otis et al. 1978) population assumption. This assumption deals with whether a population of interest is considered demographically open or closed during data collection. In other words, an open population is subject to changes via birth, death, immigration, and emigration to which a closed population is not subject. In many cases these assumptions are biologically unrealistic. Additionally, neither open nor closed type models are designed to deal with temporary emigration, the process of when an animal is temporarily unavailable for recapture or resight (Kendall et al. 1997). The need to avoid an unrealistic assumption of population closure and account for temporary emigration were important factors leading to the development of the robust design method for determining population parameters (Pollock 1982).

Survival analysis, details surrounding the robust design—The robust design (Pollock 1982) combines both open and closed mark-recapture models and is designed to deal with issues of individual detection probability. In the robust design, there are k primary sampling periods which consist of l closed capture occasions. The robust design allows for detection probability to be derived from information gathered from the secondary capture occasions within the primary periods. Information about survival (more precisely, an apparent survival estimate) and probability of state transition (e.g., from an observable to an unobservable state) is derived from information across primary sampling periods. State transition probabilities *sensu* McClintock and White (2009, 2012) correspond to the gammas of standard robust design notation, γ' (gamma prime) and γ'' (gamma double prime). The gammas define the probability of movement between the observable and unobservable states (Kendall et al. 1995, 1997). Both apparent survival and temporary emigration estimates are defined at an interseasonal scale.

The robust design produces less biased estimates of population size and survival in the face of temporary emigration (Kendall et al. 1997, Dinsmore et al. 2003) compared to traditional methods. Compared to open sampling designs, the robust design provides more estimable parameters with less bias and greater precision (Kendall and Nichols 2002, Kendall 2004). Moreover, recent advances in the robust design allow estimation of parameters within a maximum likelihood framework (Kendall et al. 1995). Additionally, use of the robust design allows for the estimation of additional parameters such as temporary immigration (Kendall et al. 1997) and recruitment between sampling periods (Pradel 1996).

Mark-resight methods of data collection and analysis are slightly different compared with more traditional mark-recapture methods often used in the robust design framework (McClintock and White 2009, McClintock et al. 2009, McClintock and White 2012). Instead of a requirement to physically recapture previously marked animals, mark-resight methods allow for the accounting of individuals through visual observations of individually-identifiable marks on the animals. Mark-resight data allow estimation of many of the same population parameters as in analysis of mark-recapture data, while also accounting for imperfect detection. This approach also allows incorporation of data on unmarked individuals to be used in the estimation of parameters. In a robust design framework, mark-resight data can be used to estimate apparent survival and abundance as well as transition probabilities between observable and unobservable states (Kendall and Nichols 2002). The robust design has, thus, been cast as a multistate model (Figure B-1).

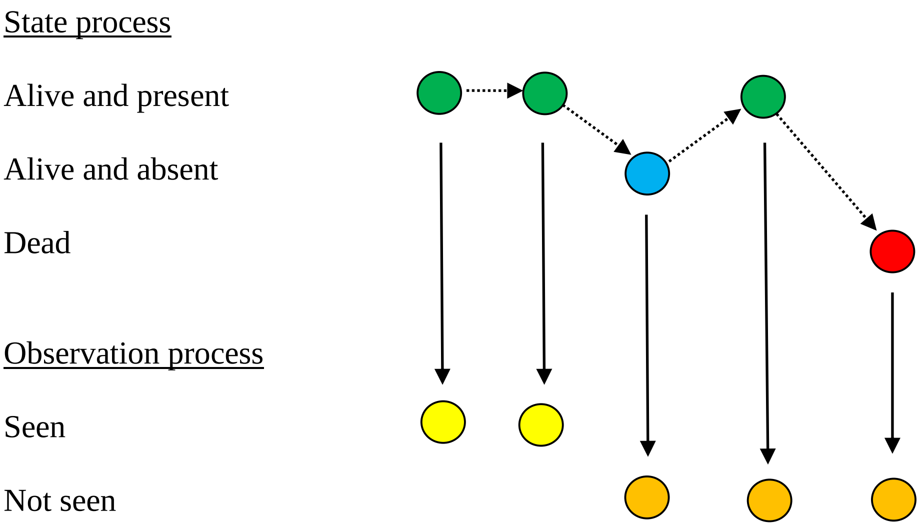

Figure B-1. The robust design as a multistate model. This temporary emigration model is hierarchical (it models both the state and observation process) and multistate. The diagram above illustrates a hypothetical state and observation process for a particular marked individual. Specifically, in the first and second occasions the animal was alive and present for resight/recapture. On the third occasion the animal was alive and unavailable (had temporarily moved off the study area). In the fourth occasion the animal was alive and present for resight/recapture but not seen. In the fifth occasion the animal was dead. Essentially, concerning multistate models, the state is often described as a categorical individual covariate that can change over time (Kéry and Schaub 2012). States here are: 1) alive and available, 2) alive and unavailable, and 3) dead. Figure adapted from Kéry and Schaub (2012).