INVESTIGATION OF MALE GOLDEN-WINGED WARBLER PLUMAGE TRAITS AS SEXUALLY SELECTED ORNAMENTS

A Thesis
by
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Abstract

INVESTIGATION OF MALE GOLDEN-WINGED WARBLER PLUMAGE TRAITS AS SEXUALLY SELECTED ORNAMENTS

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In his originating theory of sexual selection, Darwin hypothesized that males with the most elaborate plumage ornaments were able to outcompete rivaling males to gain access to females and vital resources, as well as better attract females during courtship. Substantial evidence has now demonstrated that fertilization competition selects for the most effective status-signaling and female-stimulating ornaments and that females measurably benefit from choosing males with the most elaborate ornaments. Studying sexually selected traits begins with characterizing ornaments, identifying signaling functions, and testing whether highly ornamented males achieve high fitness. In this study, I characterized ornamentation of the carotenoid-based crown plumage, melanin-based throat plumage, and structurally derived tail white plumage of breeding male Golden-winged Warblers in the Appalachian Mountains. I tested for geographic and age-based variation of plumage traits and investigated their quality indicating and behavioral signaling functions. I found a latitudinal gradient of variation in crown and throat coloration and regional differences in body condition, with the southern birds showing less ornamentation and lower body condition. Plumage traits were not indicative of body condition but older birds displayed more white on their tails and co-variation of crown and throat coloration. Males with less-ornamented crowns were more aggressive to simulated territorial intrusions while males with greater tail white ornamentation provisioned nestlings more often. To further investigate the influence of sexual selection on these plumage traits, plumage manipulation studies and refined body condition measures are needed to confirm signaling functions and female preferences need to be tested. My study has demonstrated that there is measurable variation and signaling potential in male Golden-winged Warbler plumage traits, thus suggesting these ornaments are sexually selected traits.

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I would like to thank the many individuals and organizations who have helped me in my research and the making of this thesis. My success would not be possible without my advisor, Dr. Lynn Siefferman. Not only did she provide the doorway into my graduate career, but she also led me to the funding opportunities which made it possible for me to afford the relocation from my home state, Virginia, and support myself through the past two years of challenges and monumental change. Dr. Siefferman's unceasing encouragement and guidance kept me focused on my work as I underwent personal transformation, and her renowned expertise in my field of study provided a safe haven for me to return to for guidance when I felt lost in my research. My other committee members, Dr. Mike Gangloff and Dr. Jeremy Hyman, have provided insightful and diverse perspectives, as well as valuable critiques, on my research and on the world of academia as a whole. I would not have been able to study such a fascinating avian system if it were not for Audubon North Carolina who allowed me to join a regional Conservation Easement Assessment Project on Golden-winged Warblers, funded by the Natural Resources Conservation Service. My field mentor and Audubon advocate, Curtis Smalling, passed on his birding expertise to me and the field crew and without him, none of my field study would be possible. In addition, the collaboration of researchers responsible for the making of this regional study allowed me to expand my questions and experience cooperative science, and I must thank Dr. Jeff Larkin, Dr. Marja Bakermans, Dr. Petra Wood, Dr. David Buehler, Kyle Aldinger, D.J. McNeil, and Justin Lehman for all of their data contribution, editorial help, and creative support. I also

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Dedication

I dedicate this thesis to all that is Love.

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Foreword

Chapters 2 and 3 of this thesis will be submitted for publication to *The Auk: Ornithological Advances*, an international, peer-reviewed journal published by the American Ornithologists' Union. The chapters being submitted have been formatted according to the style guide for that journal.

Chapter 1

General Introduction

The theory of sexual selection was originally proposed by Darwin (1871) and was inspired, in large part, by elaborate and sexually dimorphic plumage of birds (reviewed in Hill and McGraw 2006). Darwin hypothesized that males with elaborate plumage traits were more capable of gaining access to females and successfully courting them, thus achieving higher fitness than less ornamented males (Darwin 1871). Darwinian sexual selection can be described as social competition, almost always among males, for mating opportunities (i.e., competition for fertilization) which can occur in two different, but typically interacting, contexts (reviewed in West-Eberhard 2014). First, male-male competition involving battle and threats among rivals selects for the most effective weapons and status-signaling ornaments which gain access to females, breeding territories, and food resources, and second, male-male competition of attractiveness in the presence of a potential mate (i.e., courtship) selects for individuals best capable of stimulating females (reviewed in West-Eberhard 2014).

Many researchers would agree that the extensive empirical and theoretical evidence to date demonstrates sexual selection has genetic mechanisms and is shaped by environment, such as social context, ecological nuances, and natural selection influences (reviewed in Smith 1991, Andersson and Simmons 2006, West-Eberhard 2014). Despite the acknowledged complexity of this form of social selection, patterns have emerged across taxa demonstrating that females measurably benefit from choosing the males with the most elaborate traits. Many of these direct fitness benefits lead to increased offspring quality and survival (Hoelzer 1989). The indicator model explains that the benefits of female preference for elaborate ornaments are the product of high-quality individuals capable of handling the energetic costs of producing ornaments above the costs of basic survival (Zahavi 1975). If a male is high enough quality to produce expensive plumage ornaments, he is also likely capable of providing excellent parental care (Senar et al. 2002, Siefferman and Hill 2003), securing high quality resources (Møller 1988, Wolfenbarger 1999, Keyser and Hill 2000), or successfully defending his offspring (Reyer et al. 1998, Jawor and Breitwisch 2004).

Many avian species express multiple plumage ornaments that are subject to independent or simultaneous social selective forces. Moreover, different signals (including different components of the same plumage patch in some cases) under the various forms of sexual selection can provide either independent (‘multiple messages’ hypothesis) or redundant (‘back-up signal’ hypothesis) information about the individual to signal receivers (reviewed in Møller and Pomiankowski 1993, Candolin 2003). The ‘multiple messages’ hypothesis explains the evolution of complementary but different ornaments by arguing that they can each provide limited information about different aspects of mate quality that, when evaluated together, reflect overall male quality (Møller and Pomiankowski 1993). One the other hand, the redundant or ‘backup signal’ hypothesis (reviewed in Candolin 2003) argues that multiple traits may reflect the same quality, but may facilitate the reliability of signals to the receivers (Johnstone 1996, 1997, reviewed in Candolin 2003).

On the contrary, ornaments may not always be reliable indicators of quality because traits under sexual selection are not necessarily favored because of their effectiveness at indicating quality, but rather because of their stimulating effect on the receivers in population (reviewed in West-Eberhard 2014, Prum 2013). This is less likely in systems where male-male battles exert a stronger selective pressure on weapons and ornaments because the traits are constantly being tested, but it is possible in systems where trait function has diverged from battle or status signaling purposes and courtship, directed by female preference, is the dominating form of male competition (reviewed in Berglund et al. 1996). However, natural selection is still acknowledged to interact with sexual selection, explaining correlations between elaboration of ornaments and forms of quality (reviewed in West-Eberhard 2014).

The implications of sexual selection acting on phenotypes and behaviors may scale up in ecological impact. A mated pair is the foundational unit from which population and community relationships are shaped and the bottom-up effect of selective forces acting on the pair level has evidentiary support (Björklund and Gustafsson 2013). Because a population's viability is rooted in reproduction, studying sexual selection of fragile taxa can be beneficial. In the process of making effective management decisions, a thorough understanding of behaviors such as reproduction, resource acquisition, and movement is important (Buchholz 2007). Conservation research has begun to incorporate behavioral approaches in light of the current global diversity loss (reviewed in Buchholz 2007). The enormous variety of sexually selected traits alone warrants continual study for the sake of characterizing diversity, hopefully faster than it is being lost.

Sexual selection research has gained much momentum and intricacy since Darwin first presented his ideas. The field’s progression does not appear to be slowing anytime soon in light of advanced genomic exploration, modeling techniques, and refined experimental designs. Studying sexual selection begins with characterizing ornaments, identifying signaling functions, and testing whether highly ornamented males achieve high fitness. This fundamental research can lead to greater findings and impact many fields of biology.

Chapter 2

Associations between plumage, age, body condition, and geographic region in male Golden-winged Warblers

ABSTRACT

Plumage displays frequently play a primary role in avian communication and are often energetically expensive. Models suggest that only higher-quality individuals are able to produce elaborate plumage, and ample research has demonstrated plumage can reveal honest information about individual phenotypic quality and age. Two primary mechanisms that produce plumage color in birds are pigment deposits (carotenoid and melanin pigments being the most common) and reflectance of feather microstructure. Little research has examined variation and honest signaling of Golden-winged Warbler (*Vermivora chrysoptera*) plumage despite their growing popularity among avian conservationists. In this study, I characterized ornamentation of the carotenoid-based crown plumage, melanin-based throat plumage, and structurally derived tail white plumage of breeding male Golden-winged Warblers in the Appalachian Mountains. I investigated whether these plumage traits vary 1) across the breeding range, 2) with age class, and 3) with body condition. Finally, I tested whether these multiple ornamental traits co-vary. I found that crown and throat coloration as well as body condition varied across the Appalachian Mountain range and followed a latitudinal gradient, with the more southern birds showing less ornamentation and also lower body condition compared to birds in more northern populations. These geographic differences may result from either

genetic or environmental differences between populations and there may be regional differences in selection strength or resource availability during molt. Although I found that plumage traits were not correlated with the proxy of body condition (body mass adjusted for structural size), older birds displayed tails with greater extent of white than did younger birds. Among older males (but not younger males) those with more-ornamented crown color also displayed more-ornamented throat coloration. Although I did not find evidence that plumage traits signal body condition, tail white may be a reliable signal of age and thus could be assessed by potential rivals or mates. Finally, this species also demonstrates some potential for both redundant (facial coloration) and independent (tail white) signaling. Future research should investigate the signaling function of multiple plumage ornaments in Golden-winged Warblers.

INTRODUCTION

Male plumage coloration is often considered the classic example of sexual selection—selection for traits that are associated with differential mating success of males (reviewed in Hill and McGraw 2006). Because feather ornamentation is often energetically expensive (reviewed in Dale 2006), it is expected that only the highest quality individuals will be able to produce and maintain elaborate plumage displays and therefore these displays can act as honest signals of a male's quality (Zahavi 1975, Hill 1991, Andersson 1994). Numerous studies have shown that females prefer to mate with males that communicate the most elaborate expression of an ornamental trait (e.g., Andersson 1982, Møller 1988, Hill 1991, von Schantz et al. 1994). Females may gain either direct or indirect benefits from mating with more-ornamented and presumably higher quality males. Direct benefits include better quality territories, more courtship feedings, more help in parental duties, and better protection from predators while indirect genetic benefits are gained for offspring (reviewed by Andersson and Simmons 2006). Additionally, ornamentation can influence intrasexual contests for mates or high-quality territories (reviewed in Senar 2006, Santos et al. 2011).

Plumage may also vary with male age; older males typically display the most elaborate ornaments (reviewed in Dale 2006). Delayed plumage maturation in birds is defined as the delayed acquisition of a definitive color or pattern of plumage until after the first potential breeding period, resulting in a distinctive appearance for two or more age classes within a breeding population (Hawkins et al. 2012). Yet, not all avian species show such extreme age-based variation and when the age classes overlap in plumage appearance variation may result from differences in quality and foraging ability between younger and older birds (e.g., Griffith and Pryke 2006). Age-based color variation is likely a life-history strategy associated with delayed reproductive investment as a result of an inability of sub-adults to compete with adults for limited resources, particularly breeding opportunities (reviewed in Hawkins et al. 2012).

Two primary mechanisms that produce plumage color in birds are pigment deposits and reflectance of feather microstructure. The most common pigments in bird plumage include carotenoids which produce yellow, orange, and red plumage, and melanins which produce brown to black plumage (McGraw 2006a, b). Birds ingest carotenoid pigments from plants that synthesize carotenoids, or via insect herbivores of those plants; these are then metabolized and deposited into the keratin during feather growth (McGraw 2006a). Carotenoid pigments also have important immune functions and serve as essential vitamin A precursors (McGraw 2006a). Because of diet-dependency, carotenoid-based plumages reveal information about individual quality in many species and are frequently the target of sexual selection (Hill 2006a). Melanin pigments are produced de novo (reviewed in McGraw 2006b), however, melanin-based plumage traits have also been linked to individual condition (reviewed in Griffith et al. 2006). In some species, melanin-based plumage is a reliable indicator of testosterone production, social dominance and aggression (reviewed in McGraw 2006b, Dale 2006).

Structural coloration is produced by microstructures in the reflective keratin of the feather that scatter light and reflect the shortest wavelengths (reviewed in Prum 2006). White plumage reflects the non-organized microstructure while ultraviolet, blue, and iridescent color is produced from highly organized feather microstructure (reviewed in Prum 2006). Although less studied than the vibrant structural colors, there is some evidence that white plumage (both brightness and patch size) may signal quality in Dark-eyed Juncos (*Junco hyemalis*; McGlothlin et al. 2007).

Plumage displays can be complex and traits can be measured in multiple ways including quantifying aspects of color (e.g., brightness, hue, and chroma) and by patch size (Badyaev et al. 2001). Moreover, many taxa express multiple plumage traits. Different plumage traits and different measures of the same trait can be redundant, partially independent, or independent signals of male condition, indicating the possibility of multiple selection pressures, signaling functions, or receivers (Møller and Pomiankowski 1993; Candolin 2003).

Study Species

The Golden-winged Warbler (*Vermivora chrysoptera*) is a neotropical migratory songbird that has experienced range-wide declines for >40 years (Sauer et al. 2014). It is currently listed by the International Union for Conservation of Nature as near-threatened (BirdLife International 2012) and as a special concern species by North Carolina Wildlife Resources Commission (15A NCAC 10I.0105). Its historical breeding range extended from the southern Appalachian Mountains to New England and west to the Great Lakes region (Confer et al. 2011). Today, the distribution is fragmented into two regional breeding populations: the Great Lakes population and the Appalachian population (Buehler et al. 2007). Appalachian populations have experienced steep declines (North Carolina: -11.87% per year during 2002-2012; Sauer et al. 2014). Although Golden-winged Warblers once commonly occurred in the northeastern states, New York and New Jersey are now sparsely populated and only relic populations remain in Vermont, Massachusetts, and Connecticut (Sauer et al. 2014).

Breeding territories consist of open patches of early successional habitat adjacent to mature forest stands (Ficken and Ficken 1968, Confer et al. 2011). Early successional habitat has been declining in the breeding range of Golden-winged Warblers due to reforestation of fallow lands, modern development, and fire suppression (Klaus and Buehler 2001, Buehler et al. 2007). Because they are a conservation priority, Golden-winged Warblers have been well studied in the past few decades. The majority of this research has been focused on understanding stand-level habitat needs as well as response to management techniques in Pennsylvania (Kubel and Yahner 2008), West Virginia (Aldinger 2010), North Carolina and Tennessee (Klaus and Buehler 2001, Rossell et al.

2003), and Wisconsin (Roth and Lutz 2004, Martin et al. 2007). These collaborative research efforts have been beneficial in understanding broader scale patterns, as well as regional variation, of occupied habitats.

Little prior research has examined variation and signaling function of Golden-winged Warbler plumage despite this species' popularity among researchers, conservation concern, and distinct plumage patterns. The head plumage of males consists of a bright yellow crown patch, black auriculars and throat patches, and white submoustachial stripes (Confer et al. 2011). Honest signaling of individual quality (i.e., body condition) for any of these plumage ornaments has yet to be tested. Two studies have examined the black, melanin-based head plumage of males in the context of mating and reproductive success. McKinnon and Robertson (2008) found that males with more ornamented throat patches (higher UV chroma) mated with females that laid eggs earlier in the season. Leichty and Grier (2006) investigated plumage function as it relates to the hybridization of Golden-winged Warblers and their sister species, the Blue-winged Warbler (*V. cyanoptera*). They used plumage manipulation to mimic hybrids and showed that males that had their black throat patches and auriculars bleached during territory establishment were more likely to lose their territories and not obtain mates.

Although previous studies demonstrate importance of the throat patch in mating success, they do not examine the conspicuous yellow crown plumage, which is raised during interactions, or tail white, which is displayed by tail fanning and flicking during interactions. Crown reflectance is derived from dietary carotenoid pigments and there is evidence that crown ornamentation correlates with territory quality (Jones and Siefferman

2014, Jones et al. *in review*). As in many other warblers, Golden-winged Warblers also have patches of white on their outer 2-3 retrices (Confer et al. 2011).

Here, I focus on coloration and size of the carotenoid-based yellow crown, coloration of the melanin-based black throat, and size of the structurally derived white patches on the outer tail feathers of male Golden-winged Warblers throughout the Appalachian breeding population. Investigating these multi-level variations is the first step towards determining if Golden-winged Warbler plumage potentially functions as a sexually selected trait that could signal information about age, condition, and possibly redundant or multiple messages to different receivers. The objectives of my study were three fold. First, I characterize plumage variation across three breeding populations in the Appalachian Mountains to describe geographical variation in plumage. Second, I test whether plumage traits vary between young and older males. Third, I investigate how each plumage trait varies with male body condition and whether the multiple plumage ornaments co-vary.

METHODS

With the help of collaborators from the Golden-winged Warbler Working Group, I sampled male Golden-winged Warblers across 10 breeding sites in northwestern North Carolina, 8 sites in eastern West Virginia, and 6 sites in eastern Pennsylvania from April 27th to June 23, 2014. Additionally, I collected a subset of North Carolina crown samples during a preliminary field season in 2013. I captured birds via mist-net and conspecific audio playback, tagged them with a numbered U.S. Geological Survey (USGS) aluminum band, and measured wing length (mm) and mass (g). I estimated the age of birds as second-year (SY) or after-second-year (ASY) based on multiple morphology cues:

second year birds retain the flight feathers they grew in the nest, so they typically have dusky brown, pointy, and abraded primaries, primary coverts, and tail feathers compared to those of ASY birds which are less abraded, more truncated, and gray in color (Pyle 1997). Also, SY birds generally lack the crisp light-gray edging of the primary coverts seen in ASY birds (Pyle 1997).

I took standardized photographs of the crown and right side tail white plumage using 10-12 megapixel point-and-shoot cameras. I then measured the area of plumage patches (mm^2) using Adobe Photoshop. I took crown photos with the camera lens perpendicular to the transverse plane of the bird's head. For each bird, I measured bill length (mm) dorsally from the distal tip to the proximal end where crown feathers begin and used this measure as a size standard in photographs for measuring crown area. I took photos to quantify tail white using a perpendicular angle with the right side of the tail placed flat against a background containing a size standard (20 mm line) and feathers spread so that tail white was visible. By using size standards, distance from lens to plumage patch was controlled for.

From the crown and throat, I collected six feathers per patch and stored them in opaque envelopes in a climate-controlled environment until spectral analysis. I taped feathers by the rachis to black non-reflectance paper, imitating how the feathers lie flat naturally on the bird. I recorded spectral data with an Ocean Optics S2000 spectrometer (range 250-880 nm: Dunedin, FL) using a micron fiber-optic probe emitting UV light (deuterium bulb) and visible light (tungsten-halogen bulb) placed at a 90° angle to the feather surface (Siefferman and Hill 2003). Reflectance measures were generated relative to a white standard (Labsphere, Inc.) that reflects 100% of light from the 300-700 nm range. I took three measures of plumage reflectance from different locations on the patch sample. To reduce spectral noise, the average of 20 rapid sequential spectral readings was taken from each location. I then averaged readings from the different locations to create one spectral measure of the plumage patch. I quantified color using two standard descriptors of reflectance spectra: carotenoid chroma reflectance (yellow crown patch) and mean brightness (throat patch). Carotenoid chroma reflectance yields a chromatic measure ($(R_{\lambda 450} - R_{\lambda 700}) / R_{\lambda 700}$) and mean brightness is an achromatic measure; the mean of the summed reflectance from 300-700 nm (Montgomerie 2006).

Statistical Analyses

I used the standardized residuals of a linear regression of body mass on wing length to create a body condition index (Jakob et al. 1996). I tested for geographic regional effects on plumage and body condition using 1-way analyses of variance (ANOVAs) with Tukey's post hoc tests. I used Student's t-tests to assess age class differences in plumage traits and used Pearson correlations to understand co-variation between multiple measures of plumage and how plumage traits relate to body condition. I used SPSS software (v.22 (IBM 2013) for statistical analyses.

RESULTS

I sampled 133 territorial Golden-winged Warbler males across 25 sites in North Carolina, West Virginia, and Pennsylvania. Linear regression models revealed that body mass was significantly positively related to wing length ($r^2 = 0.024$, $F_{1,29} = 5.198$, $P = 0.011$). In North Carolina samples, there was no year effect (2013 versus 2014) on crown carotenoid chroma ($T = 1.373$, $P = 0.175$, $N = 26, 35$) or body condition ($T = 0.663$, $P = 0.510$, $N = 26, 33$), thus both years' data were combined for all future analyses.

There were significant effects of geographic region on yellow crown ornamentation, throat ornamentation, and body condition ($F_{2,129} = 13.948$, $P < 0.001$; $F_{2,102} = 3.822$, $P = 0.025$; $F_{2,130} = 8.220$, $P < 0.001$, respectively; Figures 1-3). Birds in North Carolina had less-ornamented (lower carotenoid chroma) yellow crowns compared to birds in West Virginia ($P = 0.001$) and Pennsylvania ($P < 0.001$). Birds in North Carolina also had less-ornamented throats (i.e., higher throat brightness, duller black) compared to those from Pennsylvania ($P = 0.007$). Birds in North Carolina were in lower body condition than birds in West Virginia ($P < 0.001$) and Pennsylvania ($P = 0.004$). To correct for the significant regional differences when testing for co-variance between morphological measures and when testing for age-related differences, crown chroma, throat brightness, and body condition were standardized to region (z-score).

There were no statistically significant age-related differences in crown chroma, throat brightness, crown area, or body condition (Table 1). However, older birds exhibited significantly more tail white plumage than younger birds (Figure 4, Table 1). Within SY birds, no plumage ornaments were significantly correlated with each other (Table 2). However, within ASY birds, crown ornamentation was significantly correlated with throat ornamentation (i.e., birds with more saturated crowns had darker throats (Figure 5), while no other plumage traits co-varied significantly (Table 3). No plumage traits co-varied significantly with the index of body condition (Table 4).

DISCUSSION

I found that male Golden-winged Warblers display significant variation in yellow crown coloration, black throat coloration, and body condition across their Appalachian breeding range. North Carolina populations, the most southern in this study, display the least-ornamented yellow crown and black throat coloration and are in poorer body condition (i.e., weighed less in relation to their body size) compared to the more northern populations. After controlling for regional differences, I found that older males displayed more extensive tail white than younger males but did not differ in crown size, crown coloration, or throat coloration. Additionally, I found significant covariance in crown and throat coloration among older males; males with more-ornamented yellow crowns also displayed more-ornamented throat coloration. However, I failed to find evidence that these plumage traits co-varied with body condition, but this measure of body condition may be very coarse. Together, these results suggest plumage traits of male Golden-winged Warblers have some potential to signal information about age to mates or rivals.

Geographic Variation

I found clear evidence that the carotenoid-based yellow crown and melanin-based black throat coloration differed among populations and followed a latitudinal gradient, with the more southern birds showing the least ornamentation. These North Carolina populations also showed the lowest body condition compared to northern populations. These geographic regional differences could result from either genetic or environmental differences between the populations. Variation in ornamentation, especially diet derived carotenoid plumage, could be linked to the geographic origin of molt because color is often associated with different environmental resources.

Little research, in general, has investigated how ornamental traits in birds vary across breeding ranges. However, some recent work has focused on how the melanin-based coloration of Barn Swallows (*Hirundo rustica*) can be influenced by molt location (Norris et al. 2009), as well as the carotenoid-based coloration of both House Finches (*Haemorhous mexicanus*; Hill 1992, 1993) and American Redstarts (*Setophaga ruticilla*; Norris et al. 2004). In House Finches, the variation is caused by regional differences in carotenoid availability, and the research on Barn Swallows and American Redstarts suggest that melanin and carotenoid pigment deposition during the time of molt are negatively influenced by the physiological stress of overlapping costly seasonal activities. Among American Redstarts, those that breed later in the summer experience tradeoffs because they experience fall molt during their migration, further south of their breeding grounds, resulting in duller carotenoid-based plumage (Norris et al. 2004). Among Barn Swallows, those that breed later in the summer experience tradeoffs because they molt when they are still caring for young and food sources are declining; suggesting these stressors increase corticosterone levels which affect melanin production (Norris et al. 2009).

To date, among Golden-winged Warblers, researchers do not know the extent to which latitude might influence timing of molt or the extent to which individuals experience overlap in fall molt and breeding. Nonetheless, if regional differences in carotenoid availability or amino acid precursors exist during the time of molt, birds in some regions may have better access to the resources necessary to produce highly-ornamented plumage. Indeed, there is some evidence that Golden-winged Warblers undergo a prealternate molt of some head feathers on the wintering grounds prior to spring migration (March), but further data are needed to assess whether this is a common occurrence (Pyle 1997; L. Chavarría-Duriaux, personal communication).

It is also possible that the history of natural and sexual selection could vary between warbler populations across the latitudinal gradient, potentially resulting in the regional differences of crown and throat coloration. Leichty and Grier (2006) show the importance of Golden-winged Warblers black throat coloration in the context of retaining territories and obtaining mates, suggesting a strong influence of sexual selection on this species' appearance. Birds in the New England region frequently co-occur and hybridize with populations of Blue-winged Warblers (Gill 2004). It is possible that interspecific competition for access to females may have driven the selection of more ornamented plumage in the northern portion of the Appalachian breeding population, where hybrid zones are more prevalent.

It is also important to consider the effects of the winter season on this migratory species. These varying conditions may affect the quality of plumage when birds arrive on the breeding grounds several months after molting (i.e., by feather wear and bacterial degradation) and may result in the puzzling geographic variation observed with body condition. Birds sampled in this study were captured within the same time frame across the study region, so it is unlikely that natural fluctuations in body weight throughout the breeding season caused this effect. Because local populations of Golden-winged Warblers tend to be faithful to certain migration paths (Confer et al. 2011), perhaps conditions during migration were more strenuous for the birds of North Carolina populations and resulted in lighter birds at the beginning of the breeding season when samples were being collected. Bergmann's rule (1847) may also explain the subtle differences in body condition found between regions, with birds in the higher latitudes of Pennsylvania being heavier for their body size (i.e., higher condition) compared to the birds in North Carolina.

Age Variation in Coloration

Older males exhibited tails with greater extent of the white coloration than did younger males. This age variation is consistent with extensive repeated measurements of banded Golden-winged Warblers (Pyle 1997) and is likely a consequence of the adult versus juvenile prebasic molt pattern. Adult Golden-winged Warblers undergo a complete prebasic molt on or near the breeding grounds after breeding while the hatch-year birds undergo a partial molt of the body and head, but not flight feathers (Pyle 1997). Thus, hatch year Golden-winged Warblers retain their fledgling flight feathers until undergoing a complete prebasic molt after their first (SY) breeding season (Confer et al. 2011). Indeed, many other species of wood-warblers show similar age variation in the amount of white, or other contrasting colors, on the rectrices (Pyle 1997). The extent of white on the tail is likely a useful signal that could be assessed by potential mates and rivals because Golden-winged Warblers spread their tails during courting and territorial displays (Ficken and Ficken 1968).

Among wood-warblers, age related plumage variation in carotenoid chroma and melanin brightness occurs in the American Redstart, which exhibit classic delayed plumage maturation; first year breeders resemble females (Sherry and Holmes 1997).

Although tail white varied with age class, neither the carotenoid-based yellow crown nor the melanin-based black throat patch differed between younger and older males. Thus, this species does not fit the definition of delayed plumage maturation; age class differences are quite subtle and are restricted to tail regions. However, it is possible that age-related variation in throat patch size in Golden-winged Warblers functions similar to melanin badges in House Sparrows (*Passer domesticus;* Møller 1988) and Cerulean Warblers (*Setophaga cerulea*; Boves et al. 2014). However, measuring throat patch size proved difficult because males often erected throat feathers while being handled. Future studies should develop a standardized and accurate method to measure the throat patch to characterize patch size variation.

Honest Signaling

I found no evidence that any measure of plumage coloration was significantly associated with the index of body condition. I expected the yellow carotenoid-based crown coloration to vary with condition because, in many other species, carotenoids act as quality indicators (reviewed in McGraw 2006a). Carotenoids serve other important physiological functions, mostly immunoenhancing functions, thus tradeoffs may exist between pigment production and other metabolic pathways necessary for survival (McGraw 2006a). However, most research on condition dependency of carotenoid-based plumage focuses on granivorous rather than insectivorous species (see McGraw 2006a). Golden-winged Warblers are insectivorous gleaners (Confer et al. 2011) thus carotenoids pass through additional trophic levels before birds have access to them. In the context of foraging behavior, there is also no evidence in this species that higher-quality individuals actively seek, or are capable of identifying, carotenoid-rich prey (see McGraw 2006a). It may be that Golden-winged Warblers are opportunistic gleaners, foraging on several arthropod taxa (e.g., Lepidoptera larvae, arachnids, Hemipterans; personal observation) in between bouts of territorial song displays.

Lack of a significant correlation between body condition and the melanin-based throat patch was not surprising, although some species have demonstrated condition dependence in melanin-based plumage production (e.g., Pied Flycatcher (*Ficedula hypoleuca*), Slagsvold and Lifjeld 1985, and House Sparrow, Veiga and Puerta 1996). In many species, melanin ornaments are hormonally regulated (see Jawor and Breitwisch 2003) and the level of male ornamentation may be related to social environment during time of molt (Møller 1988, McGraw et al. 2003). Leichty and Grier (2006) demonstrated that Golden-winged Warbler throat plumage plays a role in territory retention, suggesting that the throat patch may be a hormonally controlled signal of aggression or dominance. However, Leichty and Grier completely removed the black throat patch by bleaching the plumage. A study manipulating throat patch coloration within the natural variation would help to clarify this ornaments role in dominance signaling.

White plumage is related to body condition in some passerine species (e.g., Rock Sparrows (*Petronia petronia*), Griggio et al. 2011, and Dark-eyed Juncos, McGlothlin et al. 2007). For example, in Dark-eyed Juncos, healthy individuals have larger and brighter white patches and birds fed supplemented diets produced more-ornamented tails (McGlothlin et al. 2007). However, I did not find evidence of associations between condition and tail white in male Golden-winged Warblers. The mechanism behind honest signaling of white plumage remains ambiguous, despite the frequent and obvious importance of white plumage in an array of avian displays (Galván 2008). White plumage does not require deposition of pigments or special feather structure and is assumed to be relatively inexpensive to produce (Prum 2006). It may also be that the natural diets of Golden-winged Warblers in my study are less variable than diets fed during the manipulative study of McGlothlin et al. (2007). This may explain the observation that tail white plumage was not related to body condition in my study.

Finally, my measure of body condition is likely very coarse and I may have failed to detect true condition dependency of some plumage traits. Methods of measuring body condition that use residual mass indices attempt to estimate an individual's energy reserves with the assumption that more mass equates to more energy (e.g., fat) reserves (Green 2001). The residual index method I used (Jakob et al. 1996) is based on the assumption that relative mass is a reliable indicator of overall good body condition and energy reserves. However, morphometric approaches are often not well correlated with body fat (reviewed in Labocha and Hayes 2011) and it is likely that overall condition is affected by multiple physiological variables, each of which may or may not have an effect on energy reserves (reviewed in Hill 2011). For example, coccidia are gut parasites that limit carotenoid pigmentation most likely by preventing carotenoid absorption in the digestive system (reviewed in Hill 2006b). Yet, parasite load often does not affect the mass of birds but results in birds molting into duller plumage. Better approaches include experimental manipulations and more sophisticated measures of the capacity of individuals to maintain optimal functionality of vital cellular systems (reviewed in Hill 2011). However, such invasive approaches are difficult with studies of rare animals.

Co-variation of Multiple Plumage Ornaments

The co-variation of crown and throat ornamentation in older males suggests that these plumage traits may be redundant signals. In theory, females would benefit most from assessing the single most reliable signal, making the production of costly redundant signals unfavorable for males (Schluter and Price 1993). However, Golden-winged Warbler males may show this tendency for dual ornamentation to more reliably signal overall quality (i.e., redundant signals). Also, if the individual traits reflect different aspects of quality, females could better gauge overall quality by assessing them (i.e., multiple signals). For example, it is possible that high quality males may signal both resource holding capacity with crown coloration and another currently unknown phenotypic quality with throat coloration. In contrast, it is possible these traits are inexpensive and may not be honest indicators of quality but attractive to females and an evolutionary product of female aesthetic preference (Møller and Pomiankowski 1993, Prum 2013). It is unclear what the more likely explanation is for this correlation in Golden-winged Warbler head plumage, especially because there is limited literature on female preference for these traits and I found no relationship between plumage and body condition. However, recent research on the behavioral signaling of male Golden-winged Warbler plumage in North Carolina suggests the crown coloration is correlated with territorial aggression (Chapter 3), and territory quality (Jones et al., *in review*) and thus could potentially function as an intersexual signal of resource holding potential. This, in combination with initial studies of throat ornamentation, suggests that females could pay attention to these plumage traits for a more reliable assessment of mate quality.

Conclusions

This is the first study to comprehensively characterize the plumage variation in male Golden-winged Warblers. First, I found clear evidence of geographic variation in plumage traits. I also found that tail white is a reliable predictor of age. I found some evidence of redundancy in signaling; among older males, those with more-ornamented yellow crowns also display more-ornamented black throat patches. Although I failed to detect condition dependence of plumage traits, research from the North Carolina population suggests that multiple traits may signal different information to different receivers. Male Golden-winged Warblers with greater extent of tail white provision nestlings more often while males with more chromatic yellow crown coloration are less aggressive to simulated conspecific intruders on their territories (Tisdale *in prep*).

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TABLES AND FIGURES

TABLES

Table 1. Results of Student’s T-tests comparing second year and after second year plumage traits and body condition in male Golden-winged Warblers after controlling for regional variation.

Plumage Trait	**Age**	**N**	**Mean**	**T**	**P**
Crown Chroma (zscore)	SY	39	-0.136	-1.262	0.210
	ASY	76	0.107		
Crown Area (mm^2)	SY	23	151.542	1.730	0.088
	ASY	50	141.033		
Throat Brightness (zscore)	SY	29	0.148	0.895	0.373
	ASY	66	-0.053		
Tail White Area (mm^2)	SY	23	235.049	-3.231	**0.002**
	ASY	54	295.772		
Body Condition (zscore)	SY	40	-0.103	-0.761	0.448
	ASY	76	0.039		

Table 2. Results of Pearson's correlation analyses between plumage traits in second-year male Golden-winged Warblers after controlling for regional variation.

		Crown Area (mm^2)	**Throat Brightness (zscore)**	**Tail White Area (mm^2)**
Crown Chroma (zscore)	r	-0.037	-0.175	-0.183
	P	0.870	0.372	0.414
	N	22	28	22
Crown Area (mm^2)	r		-0.306	0.039
	P		0.156	0.871
	N		23	20
Throat Brightness (zscore)	r			0.159
	P			0.468
	N			23

Table 3. Results of Pearson's correlation analyses between plumage traits in after-second-year male Golden-winged Warblers after controlling for regional variation.

		Crown Area (mm^2)	**Throat Brightness (zscore)**	**Tail White Area (mm^2)**
Crown Chroma (zscore)	r	0.106	-0.350	0.053
	P	0.469	**0.004**	0.709
	N	49	66	53
Crown Area (mm^2)	r		-0.162	-0.203
	P		0.272	0.177
	N		48	46
Throat Brightness (zscore)	r			-0.016
	P			0.910
	N			53

Table 4. Results of Pearson's correlation analyses between body condition index and plumage traits in male Golden-winged Warblers after controlling for regional variation.

		Crown Chroma (zscore)	**Crown Area (mm^2)**	**Throat Brightness (zscore)**	**Tail White Area (mm^2)**
Body Condition (zscore)	r	0.035	-0.035	0.049	0.138
	P	0.697	0.766	0.630	0.232
	N	126	73	100	77

FIGURES

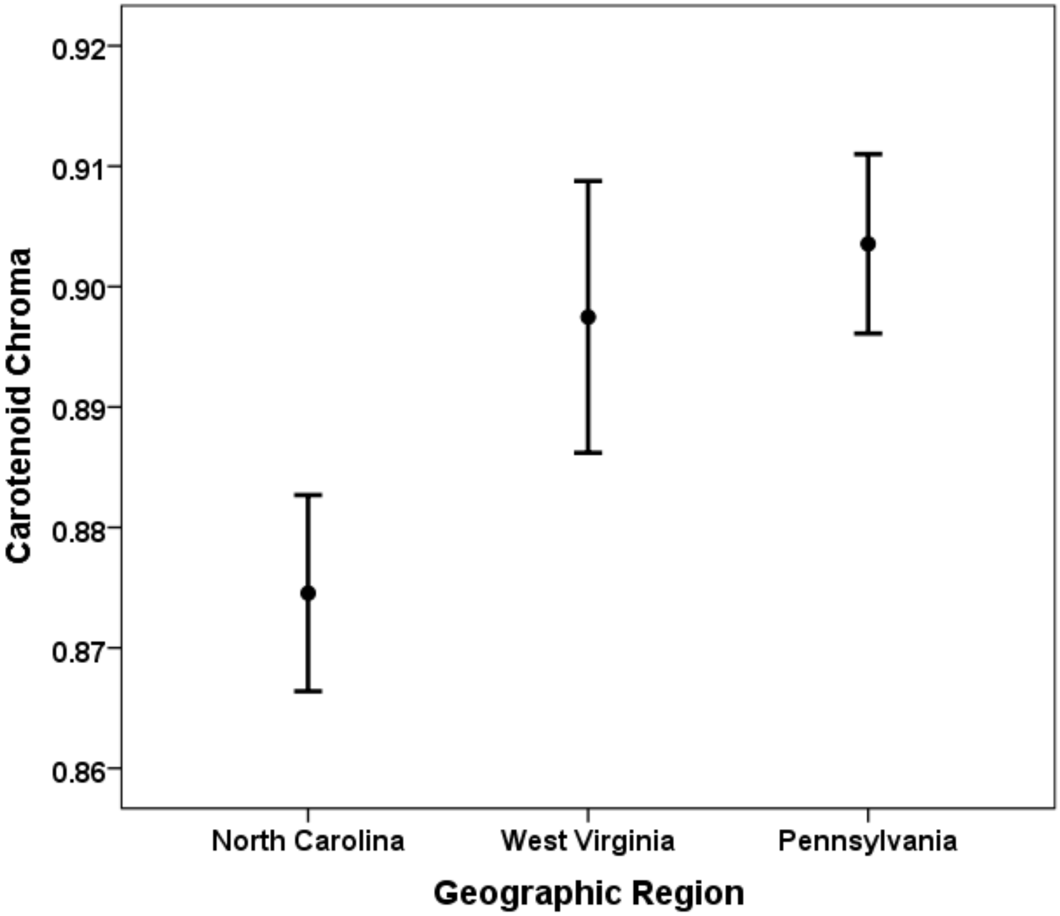

Figure 1. Comparisons in carotenoid chroma reflectance of crown plumage between North Carolina, West Virginia, and Pennsylvania male Golden-winged Warblers. Bars depict the 95% confidence interval for mean of sampled sites within each state. Higher reflectance values correspond to brighter, more ornamented crown feathers.

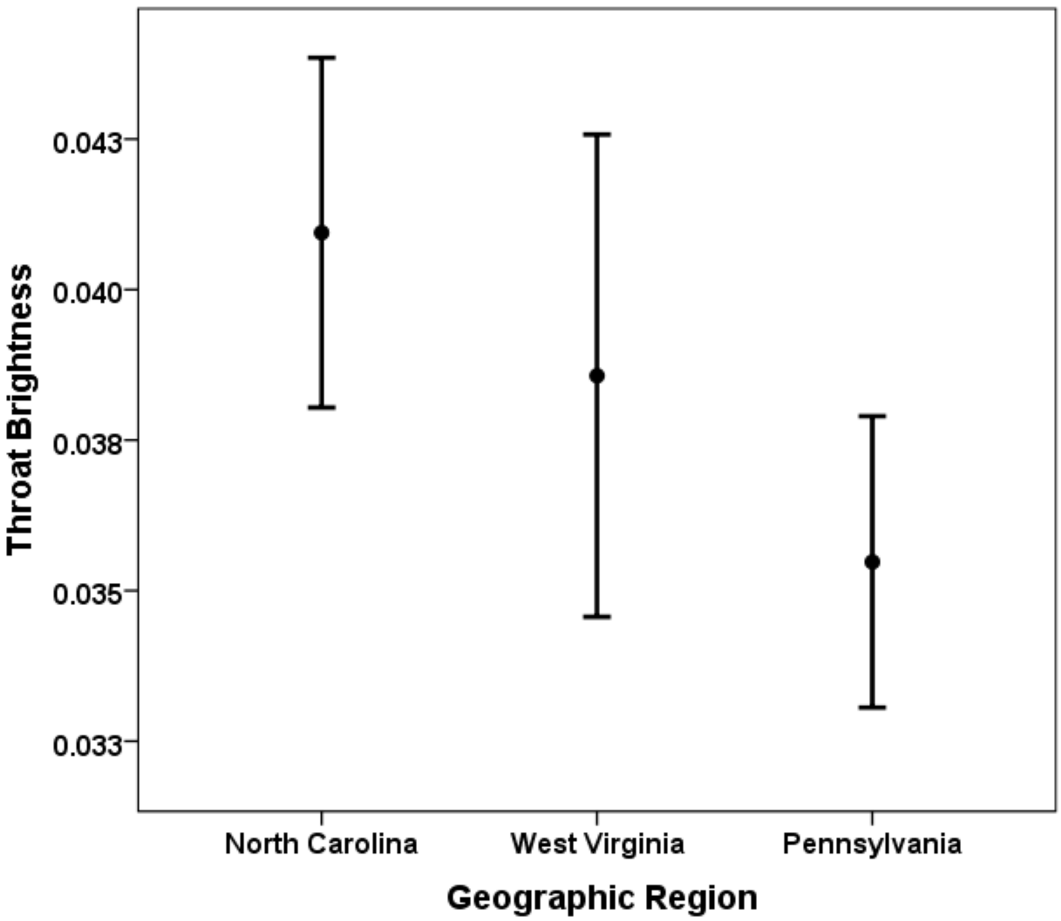

Figure 2. Comparisons in mean brightness (mean reflectance across spectral curve) of melanin throat plumage between North Carolina, West Virginia, and Pennsylvania male Golden-winged Warblers. Bars depict the 95% confidence interval for mean of sampled sites within each state. Lower reflectance values correspond to darker, more-ornamented throat feathers.

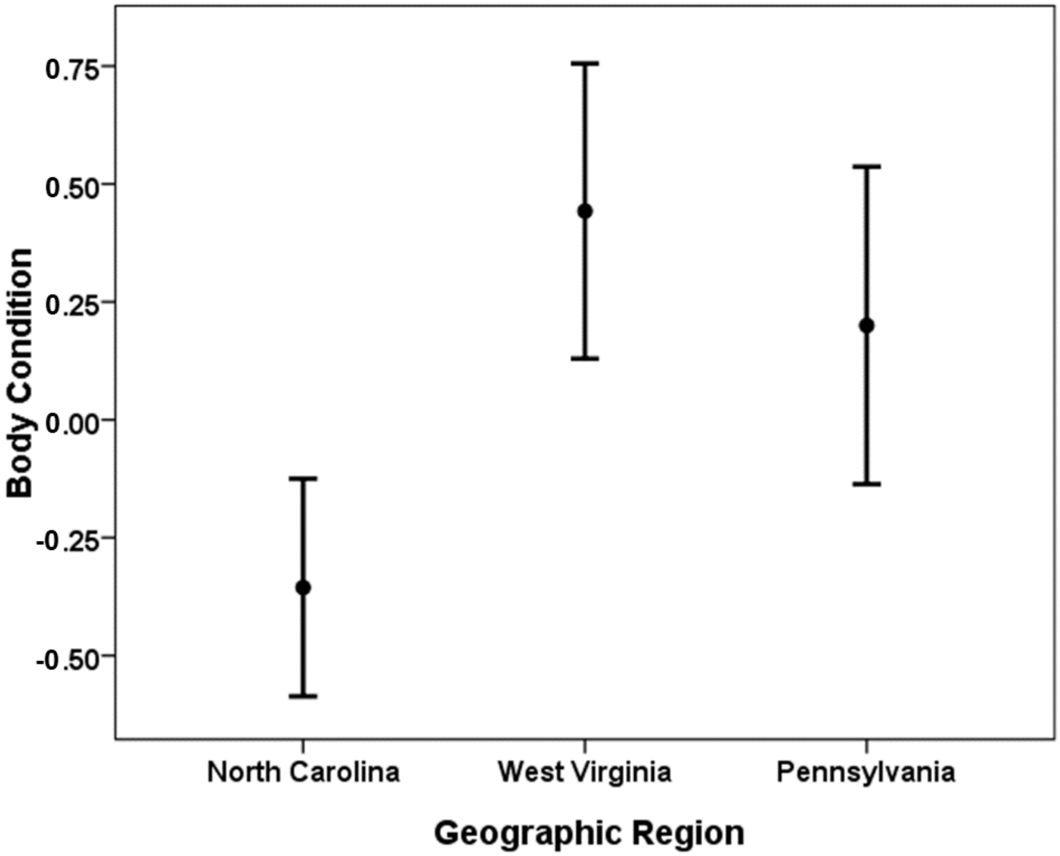

Figure 3. Comparisons in body condition (standardized residuals of mass on wing linear regression) between North Carolina, West Virginia, and Pennsylvania male Golden-winged Warblers. Bars depict the 95% confidence interval for mean of sampled sites within each state. Positive values indicate heavier birds relative to their size and negative values indicate lighter birds relative to their size.

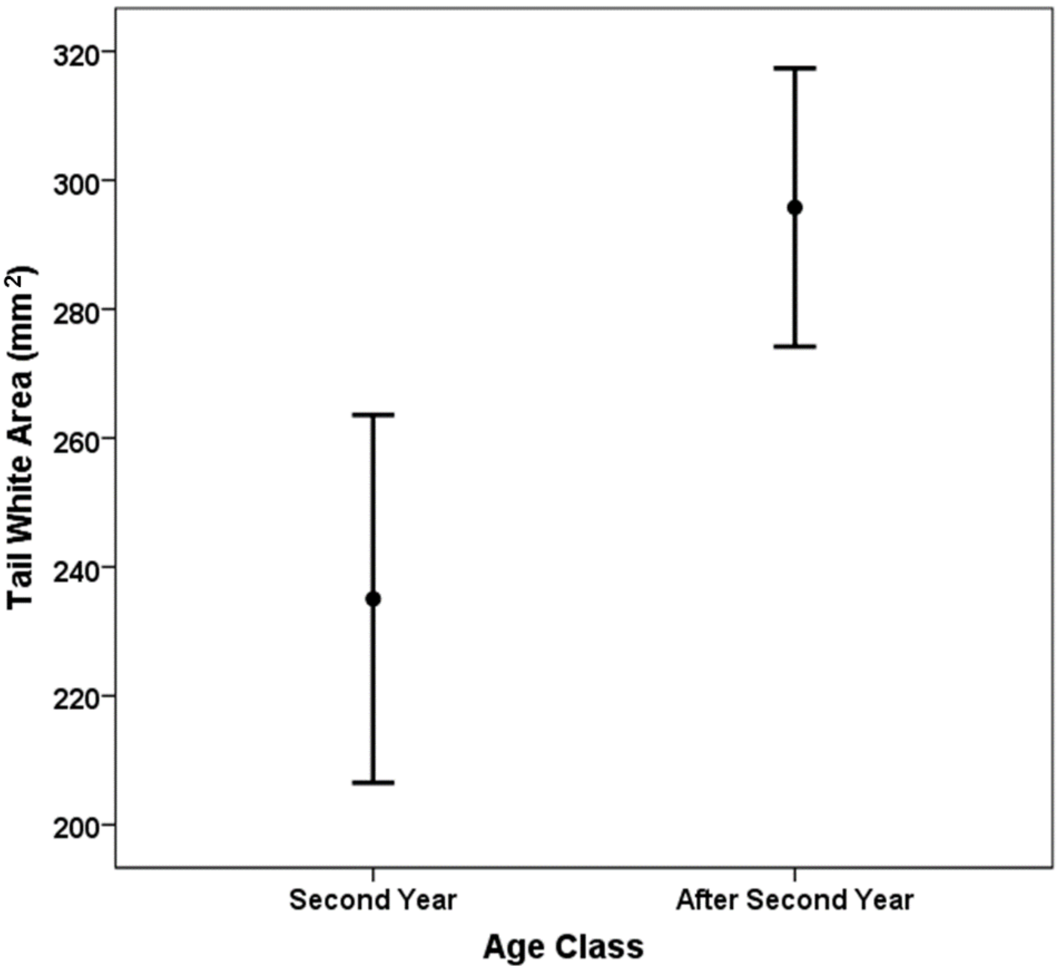

Figure 4. Comparisons in amount of tail white on the outer right retrices between second year and after second year male Golden-winged Warblers sampled in North Carolina, West Virginia, and Pennsylvania. Bars depict the 95% confidence interval for mean of each age class.

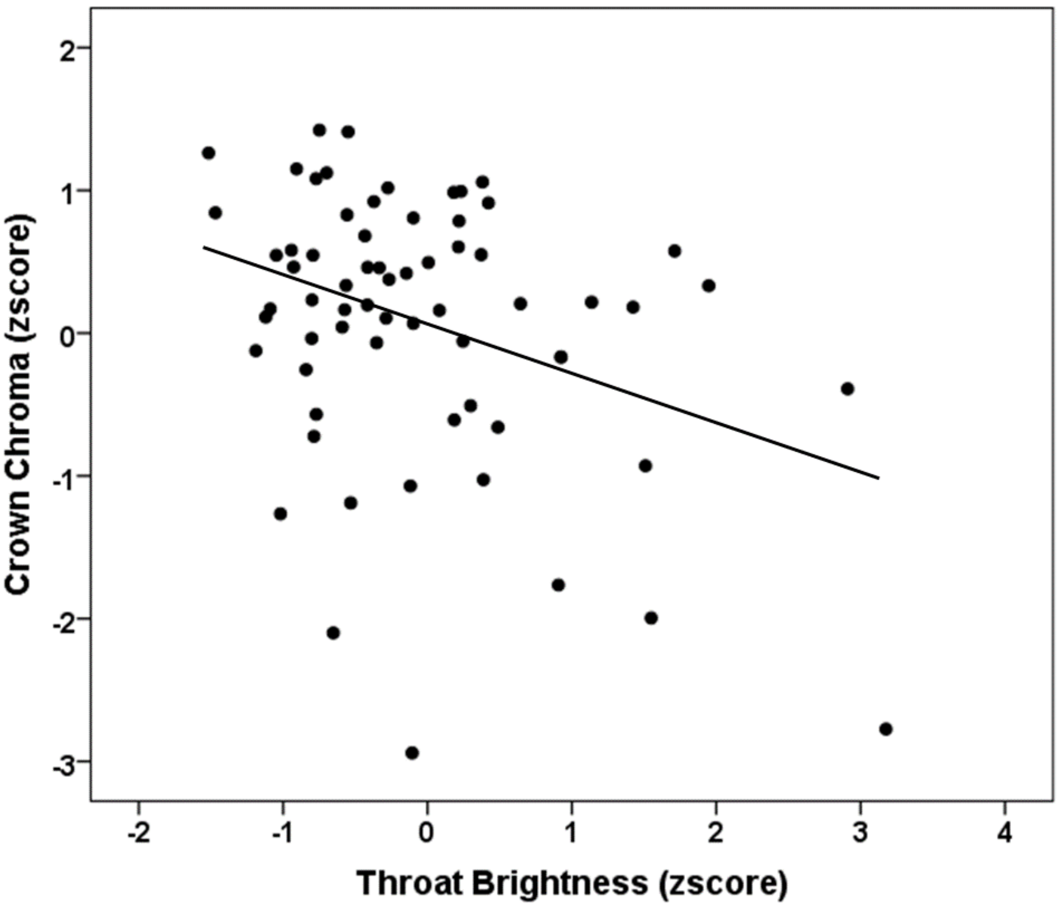

Figure 5. Relationship (Pearson's correlation) between crown ornamentation and throat ornamentation in after second year male Golden-winged Warblers sampled in North Carolina, West Virginia, and Pennsylvania. Plumage scores standardized to regional means to account for regional variation in ornamentation. Higher crown chroma values and lower throat brightness values are considered more ornamented, and birds that were more ornamented in one head plumage trait also tended to be more-ornamented in the other trait.

Chapter 3

Ornamental plumage, aggression, and parental care in male Golden-winged Warblers

ABSTRACT

Competition for mating opportunities is well known to result in ornamental traits that greatly influence mate selection. Male Golden-winged Warblers (*Vermivora chrysoptera*) have ornamental plumage coloration consisting of a brilliant yellow crown, black facial pattern, and white outer tail feathers. The yellow crown coloration is produced from carotenoid pigments deposited in feathers, whereas the black throat coloration is produced by melanin pigments, and the tail white is a product of non-organized feather microstructure. I tested the hypothesis that plumage coloration could be a reliable indicator of reproductive investment in male Golden-winged Warblers, a socially monogamous, sexually dichromatic passerine. I investigated whether male ornamentation correlates with male territorial aggression and parental effort. I found that males with less-ornamented yellow crown coloration were more aggressive to simulated territorial intrusions while males with greater tail white ornamentation (greater extent of tail white) provisioned nestlings more often. These results suggest that multiple plumage traits could be reliable indicators of male aggression and mate quality that can be assessed by competitors and females. Future plumage manipulation studies are needed to confirm that yellow crowns function as a badge of status used in male-male competitive interactions and females assess tail white when choosing mates.

INTRODUCTION

Female preference for ornamental male traits has long been acknowledged to be a selective force acting on individual mating success (Darwin 1871, Andersson 1994, Hill 2006a). There are several theories to explain this tendency, but most mechanisms describe females receiving benefits from mating with elaborately-ornamented males. For example, the reliable indicator model argues that only males of high phenotypic or genetic quality can afford to produce highly-ornamented traits and therefore these traits may be honest signals of quality (Zahavi 1975, Andersson 1994). Elaborate plumage is a common avian ornament and ample experimental evidence shows coloration or size of plumage ornaments can signal quality to females; thus plumage may be used in mate-choice decisions (reviewed in Griffith and Pryke 2006). Females benefit indirectly when offspring inherent genes of highly-ornamented males and direct benefits to females include: more incubation feedings (e.g., Siefferman and Hill 2005), more help in parental duties (e.g., provisioning nestlings; Senar et al. 2002, Siefferman and Hill 2003), as well as better protection from predators (e.g., Norris 1990, Grunst et al. 2015).

In addition to functioning in mate choice, elaborate plumage is often related to aggressive behavior and can signal social dominance (reviewed in Senar 2006). Males of many bird species defend contested breeding territories containing limited resources, and individuals must have adequate fighting ability to acquire and maintain those territories (Lack 1968, Ligon 1999). Territory acquisition and defense is critical, as the pair's reproductive success is dependent on available nest sites and habitat resources (Lack 1968, Ligon 1999). Assessments of rivals may be made in part by the males' ability to predict how aggressively a rival might fight over a territory (Vedder et al. 2010, also see

Mercadante and Hill 2014). When a plumage trait reliably signals an individual's fighting ability, it can be considered an honest status signal in agonistic interactions (reviewed in Senar 2006). A dominance hierarchy is then established amongst males in a linear fashion; the most dominant signaler defeats all others and the least dominant signaler is subordinate to all others (Hill 2002). Female mate choice may also influence badges of status if females use them to determine quality, resulting in ornamental traits with dual signaling functions (reviewed in Berglund et al. 1996).

Plumage coloration results from the reflection of either pigments deposited during feather growth or light scattering off the feather microstructure (McGraw 2006a, b, Prum 2006). Diet derived carotenoids (yellow to red plumage), and intrinsically derived melanins (brown to black plumage), are the most prevalent feather pigments (reviewed in McGraw 2006a, b). Condition-dependent carotenoid plumage is frequently maintained via sexual selection and can be a reliable indicator of individual quality because it is typically related to foraging ability (reviewed in Hill 2006a, Griffith and Pryke 2006), but can also signal dominance over high quality territories (e.g., Red-collared Widowbirds (*Euplectes ardens*), Pryke et al. 2001). Melanin-based plumage often signals aggression and dominance because of the pigment's regulation by testosterone (reviewed in Senar 2006, McGraw 2006b), the main hormone responsible for controlling aggression (Wingfield et al. 1987). White plumage is derived from light reflected off non-organized feather microstructure (Prum 2006) and is believed to be the most common form of structural coloration (Galván 2008). Tail displays are common in birds and tail white may influence mate choice (e.g., Dark-eyed Juncos (*Junco hyemalis*), Hill et al. 1999) or advertise male dominance or territorial prowess (e.g., Dark-eyed Juncos, Balph et al.

1979, and Rock Sparrows (*Petronia petronia*), Griggio et al. 2011). In the context of plumage badges of status, positive correlations between ornamentation and aggression are typical (reviewed in Senar 2006). However, in House Finches (*Haemorhous mexicanus*), drabber males tend to dominate brighter ones during both breeding and nonbreeding seasons (Belthoff et al. 1994, McGraw and Hill 2000).

In this study, I tested the hypothesis that male Golden-winged Warblers (*Vermivora chrysoptera*) use plumage to signal dominance and quality to conspecifics. Golden-winged Warblers are a rapidly declining Neotropical migratory songbird and have recently received much attention from conservation biologists (Roth et al. 2012, Sauer et al. 2014). My previous work has shown that males exhibit substantial within-population variation in the chroma of carotenoid-based yellow crown coloration, the brightness of melanin-based black throat coloration, and the extent to which tail feathers are white (Tisdale *in prep*). Older males have larger patches of white on their tails (hereafter referred to as 'tail white') compared to younger males, and among older males, those that expressed greater chroma (more-ornamented) of the yellow crowns also express significantly darker (more-ornamented) throats (Tisdale *in prep*). Melanin-based throat plumage is likely a sexually selected trait in this species; initial research suggests the level of throat ornamentation is related to earlier nesting (McKinnon and Robertson 2008). Also, males with throat color experimentally removed to mimic Brewster's Warblers, the hybrid phenotype resulting from crosses between Golden-winged and Blue-winged Warblers (*V. cyanoptera*, Gill et al. 2001), tend to lose their territories to competitors and fail to mate (Leichty and Grier 2006). Given the results of the research on coloration of Golden-winged Warblers to date, I predicted that plumage coloration in this species may signal behaviors associated with reproductive investment.

My objective was to quantify ornamentation of the crown, throat, and tail white plumage of male Golden-winged Warblers and test for correlations with proxies of aggression and parental care, which are two phenotypic qualities that potentially lead to higher reproductive success. Because carotenoid-based plumage is strictly diet derived and well known to signal foraging ability in other species (reviewed in Griffith and Pryke 2006), I predicted males with more-ornamented yellow crown ornamentation would provision offspring at higher rates. Because melanin-based plumage is often related to steroid hormone levels (reviewed in Senar 2006), I predicted that males with darker (more-ornamented) throat coloration would express more aggressive territorial defense behavior. Finally, because tail white is an indicator of male age (Tisdale *in prep*), I expected males with greater extent of white on their tails would both provision offspring well and defend territories aggressively.

METHODS

Plumage Collection

I studied male Golden-winged Warblers at eight breeding sites in the southern Appalachian Mountains of western North Carolina from April 27-June 17, 2014. Early in the breeding season, I captured birds via mist-net and conspecific audio playback. I banded birds with both a numbered U.S Geological Survey aluminum band and three colored bands to create a unique combination of colors to confirm identity during behavioral observations. I measured body condition using a standardized residual index from a linear regression of body mass (m) on wing length (mm) (Jakob et al. 1996). I photographed the tail white of the right outer retrices using 10-12 megapixel point-and-shoot cameras. I took tail white photos from a perpendicular angle with right side of the tail placed flat against a background containing a size standard (20 mm line) and feathers spread so that tail white was visible. By using this size standard, distance from lens to plumage patch was controlled for. Tail white area (mm^2) was measured using Adobe Photoshop.

From the crown and throat, I collected six feathers per patch and stored them in opaque envelopes in a climate-controlled environment until spectral analysis. I taped feathers by the rachis to black non-reflectance paper, imitating how the feathers lie flat naturally on the bird. I recorded spectral data with an Ocean Optics S2000 spectrometer (range 250-880 nm: Dunedin, FL) using a micron fiber-optic probe emitting UV light (deuterium bulb) and visible light (tungsten-halogen bulb) placed at a 90° angle to the feather surface (Siefferman and Hill 2003). I generated reflectance measures relative to a white standard (Labsphere, Inc.) that reflects 100% of light from 300-700 nm range. I measured plumage reflectance from three different locations on the patch sample. To reduce spectral noise, I averaged 20 rapid sequential spectral readings taken from each location. I then averaged readings from the three locations to create one spectral measure of the plumage patch. I quantified yellow crown coloration using carotenoid chroma reflectance $(R_{\lambda 450} - R_{\lambda 700}) / R_{\lambda 700})$; birds with greater chroma are considered more-ornamented (Montgomerie 2006). I quantified throat ornamentation as mean brightness, calculated as the mean of the summed reflectance from 300-700 nm; birds with lower brightness (i.e., darker) are considered more-ornamented (Montgomerie 2006).

Simulated Territorial Intrusions

To quantify individual aggression, I used song playback experiments within a male's territory and observed their aggressive behavior. Because males are known to move around during the first week after returning to the breeding grounds, and males can drastically change their territorial behavior after nesting commences, I performed simulated territorial intrusions (STIs) one week after a male's initial arrival and before his female began laying. I obtained STI observations for some males prior to plumage collection because males had been captured in prior years and already had color bands for identification.

I conducted playback experiments in the morning, weather permitting, when males were most actively defending their territory (~0600-1100 EDT). Once I confirmed males via color bands in their territories, I set a speaker 1-3 m above the ground adjacent to a known perch. I took behavioral observations from a distance of ~30 m from playback source. The playback protocol was as follows: 1 min ambient noise, 2 min control song (Field Sparrow, *Spizella pusilla*), 1 min ambient noise, 10 min Golden-winged Warbler song, alternating between segments of type 1 song (commonly used while perched) and a type 2 song (commonly used during interactions). Sound files were obtained from Xeno-Canto online database and the Golden-winged Warbler song portion of the playback was comprised of recordings of different individuals from the same geographic region as the study population. My proxy of aggression was rate of aggressive dives within 1 m of the speaker (Jones et al. *in review*). I used aggressive dives as my measure of aggression because this behavior is only seen during aggressive interactions, whereas singing occurs during non-aggressive territorial displays from perches as well as during aggressive interactions, thus it may not be a reliable measure of aggressive intent.

Nestling Provisioning

For a subset of males, I found nests within known territories and I monitored nests every three days for contents and hatching. When nestlings were six days old (+1 for inclement weather), I set up video cameras ~1 m from nests so the field of view allowed parent identification and the number of feeds each nestlings received was quantifiable. I recorded nests for 4 hours from 0700-1100 EDT. I took cameras down if weather became unsuitable because females typically return to the nest to brood their nestlings during rainy weather. I used the footage to measure number of male feeds per chick per hour so each male had a feeding rate standardized to brood size and footage time.

Statistical Analyses

I used Pearson correlations to test for associations between plumage characteristics and 1) aggression, 2) provisioning rate, and between aggression and provisioning rates. I also used Pearson correlations to test for associations between body condition and 1) aggression and 2) provisioning rate. I used SPSS software (v.22 (IBM 2013) for statistical analyses.

RESULTS

The carotenoid chroma of the yellow crown was significantly negatively correlated with dive rate (Table 1; Figure 1); birds with greater crown ornamentation dove less often at the playback source. Neither throat brightness nor tail white area was significantly correlated to aggression (Table 1). Crown carotenoid chroma and throat brightness were unrelated to provisioning rates, but males with more extensive tail white fed nestlings at significantly higher rates (Table 1; Figure 2). As with a larger regional dataset, this North Carolina subset of data showed no relationship between plumage traits and body condition (Table 1; see Chapter 2). Body condition was not significantly associated with dive rate or provisioning rate ($r = -0.097$, $P = 0.669$, $N = 22$; $r = 0.226$, $P = 0.626$, $N = 7$, respectively). Although birds that dove more often tended to feed offspring less often, this relationship was not statistically significant ($r = -0.665$, $P = 0.221$, $N = 5$).

DISCUSSION

I found that males with more-ornamented yellow carotenoid-based crowns were less aggressive towards conspecific playback whereas males with greater extent of tail white provisioned offspring more often. My data demonstrate no association between melanin-based black throat ornamentation and either conspecific aggression or parental provisioning. Further, there is some indication that the males that feed offspring more often tend to defend their territories less aggressively. Although no plumage traits appear to signal body condition, these data suggest a potential role of yellow crown coloration in male-male interactions and a role of tail white in female choice of mates.

Although contrary to my predictions, there was no relationship between provisioning rates and carotenoid-based crown coloration. Because crown coloration was unrelated to body condition, the expression of this plumage may not be dependent on foraging ability. Rather, it could be that carotenoid derived ornamentation is a signal of competitive ability or resource holding potential (e.g., Red-collared Widowbirds, Pryke et al. 2001) The negative correlation between crown carotenoid chroma and aggressive behavior is surprising and contrasts to previous studies demonstrating positive correlations between ornamental coloration and territorial aggression (reviewed in Senar 2006). However, less-ornamented male House Finches are more aggressive than brighter males, yet males with brighter red carotenoid-based plumage are preferred by females as mates (reviewed in Hill 2002). In House Finches, aggressive behavior has been explained as a compensatory strategy whereby duller males invest heavily in singing and aggression (Stoehr and Hill 2000, Hill 2002). Indeed, aggression, signals of status, and dominance are not necessarily redundant (McGraw and Hill 2000, Vedder et al. 2010) and male-male interactions can be complex. For example, the relative coloration of each of the two competing males could also affect the behavioral responses of both contenders; a pair of bright males and a pair of dull males may display significantly more aggression towards each other than a pair of males drastically different in ornamentation (Mateos and Carranza 1997). A brighter male may choose not to interact if he does not perceive the intruder as a threat or of similar status (e.g., Greene et al. 2000).

Although it is not clear whether crown coloration functions as a signal of status and predicts dominance in male Golden-winged Warblers, it may be that like House Finches, males with duller crowns are less attractive to potential mates and thus duller males behave aggressively to compensate. Experimental tests manipulating Golden-winged Warbler model crown plumage are needed to determine true status signaling, but the crown could still be used as predictor of aggressive responses to territorial intrusions. In addition, Golden-winged Warbler males with greater yellow chroma do nest in habitat that is believed to be higher quality (Jones et al., *in review*), suggesting more-ornamented males have greater resource holding potential.

My data show no evidence that the black melanin-based throat plumage in Golden-winged Warblers signals aggression like in other species (e.g., House Sparrow (*Passer domesticus*), Møller 1988). These observations may seem at odds with the extensive literature on melanin coloration. Many studies of melanin ornaments consistently show positive relationships with resource holding potential. However, the great majority of studies of melanin coloration and dominance have focused on badge size and not coloration *per se* (Senar 2006). Indeed, in general, there is little variation in the reflectance of black melanin-based plumage (reviewed in Jawor and Breitwisch 2003). The size of plumage patches, therefore, may be a more effective signal in Golden-winged Warblers. Unfortunately, I did not quantify throat patch size for Golden-winged Warblers.

As expected, the melanin-based throat ornamentation was unrelated to provisioning rates. However, in an Ontario Golden-winged Warbler population, associations between a male's black throat coloration (higher UV chroma) and his mate's egg laying date have been documented (McKinnon and Robertson 2008). It is difficult to interpret how variation in UV chroma influences melanin plumage ornamentation (these pigments show little variation across the UV and visible spectrum; McGraw 2006b). McKinnon and Robertson (2008) interpreted this spectral variation (reported <0.5%) as a gradient of ornamentation. However, avian visual models (Maia et al. 2013) demonstrate that the chromatic variation among the black throats of the males at my field sites would not be discernable to birds, thus very unlikely to be a signal, but the achromatic variation (brightness) is discernable (J. A. Jones, personal communication). Further, although variation in brightness was experimentally induced by Leichty and Grier (2006) which led to reduced fitness, the researchers fully removed both the black throat and facial mask to mimic hybrids; males were altered far beyond the natural range of phenotypic variation in this species. Thus, it is possible that conspecifics only discriminated against odd looking males (see Hill 2006a). Manipulations of plumage coloration within the natural range of variation, coupled with mate choice and male-male competition experiments, would help clarify any melanin-based throat plumage signaling functions.

Male Golden-winged Warblers with larger tail white regions fed offspring more often, suggesting that tail white might also function to signal paternal care investment. Certainly, the provisioning data set suffers from small sample size and further data are needed to confirm that tail white is a reliable signal of paternal investment. However, older male Golden-winged Warblers have significantly more tail white than first time breeders (Chapter 2). Together these data suggest a benefit for females to mate with older males and, among older males, those with the greatest tail white.

Finally, I found a nonsignificant trend suggesting that the males that provision more often are less aggressive to STIs; the strength of the effect was strong but a larger sample size is needed to confirm this trend in Golden-winged Warblers. This negative relationship is consistent with theory that generally assumes a trade-off between the investment in provisioning and levels of aggressiveness (e.g., Ketterson and Nolan 1999). This evidence of behavioral trade-off further suggests males may use different, and possibly compensatory, reproductive strategies that are signaled by different plumage ornaments.

To date, I have little data to speculate about whether Golden-winged Warblers assess plumage during interactions; no clear associations exist between studied plumage traits and measures of reproductive success. However, when considering the potential for crown color to signal aggression, the age-based variation in the tail white plumage, and the fact that among older males, those with brighter crowns tend to have darker throats (suggesting redundant signaling; Chapter 2), there is great potential that conspecifics assess plumage traits to gain information about potential mates and rivals. The amount of tail white could signal paternal investment and yellow crown may signal aggression and potentially the outcome of agonistic interactions. Thus, the results of my study suggest that Golden-winged Warbler plumage may serve important signaling functions and variation in plumage may be maintained by sexual selection. To test the role of plumage coloration in mate choice and male-male competition, experimental studies are warranted.

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TABLES AND FIGURES

TABLES

Table 1. Results of Pearson's correlations between plumage ornamentation (yellow crown carotenoid chroma, black throat brightness, and area of tail white (mm^2)) and 1) aggression proxy (dive rate), 2) provisioning rate (feeds/chick/hour) and 3) body condition (standardized residuals of mass on wing linear regression) in male Golden-winged Warblers. Significant P values are bolded.

		Crown Chroma	**Throat Brightness**	**Tail White Area (mm^2)**
Dive Rate	**r**	-0.515	0.061	-0.12
	P	**0.014**	0.782	0.648
	N	22	23	17
Provisioning Rate	**r**	0.322	-0.003	0.895
	P	0.437	0.995	**0.016**
	N	8	8	6
Body Condition	**r**	-0.07	0.342	0.396
	P	0.75	0.102	0.116
	N	23	24	17

FIGURES

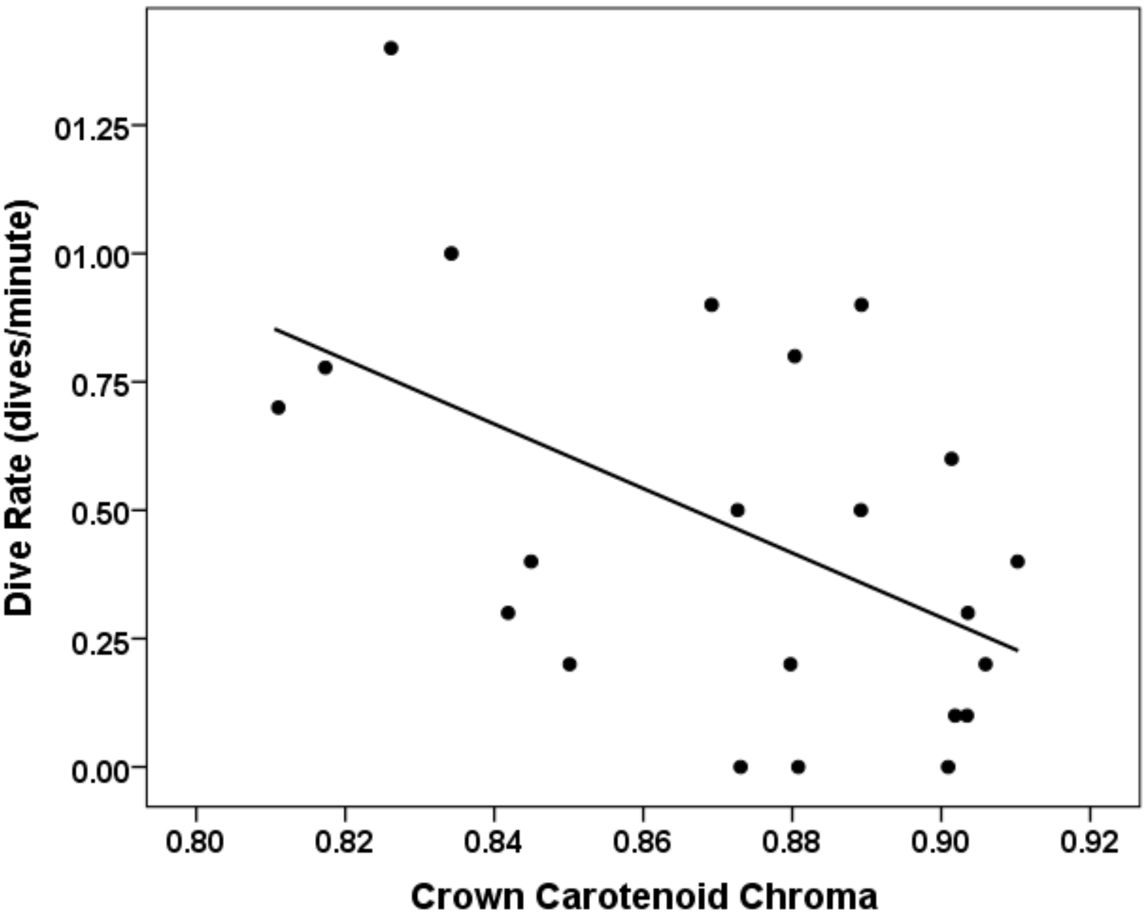

Figure 1. Relationship (Pearson's correlation) between yellow carotenoid chroma of crown plumage and dive rate (number of aggressive dives per minute) over playback source during simulated territorial intrusions in male Golden-winged Warblers.

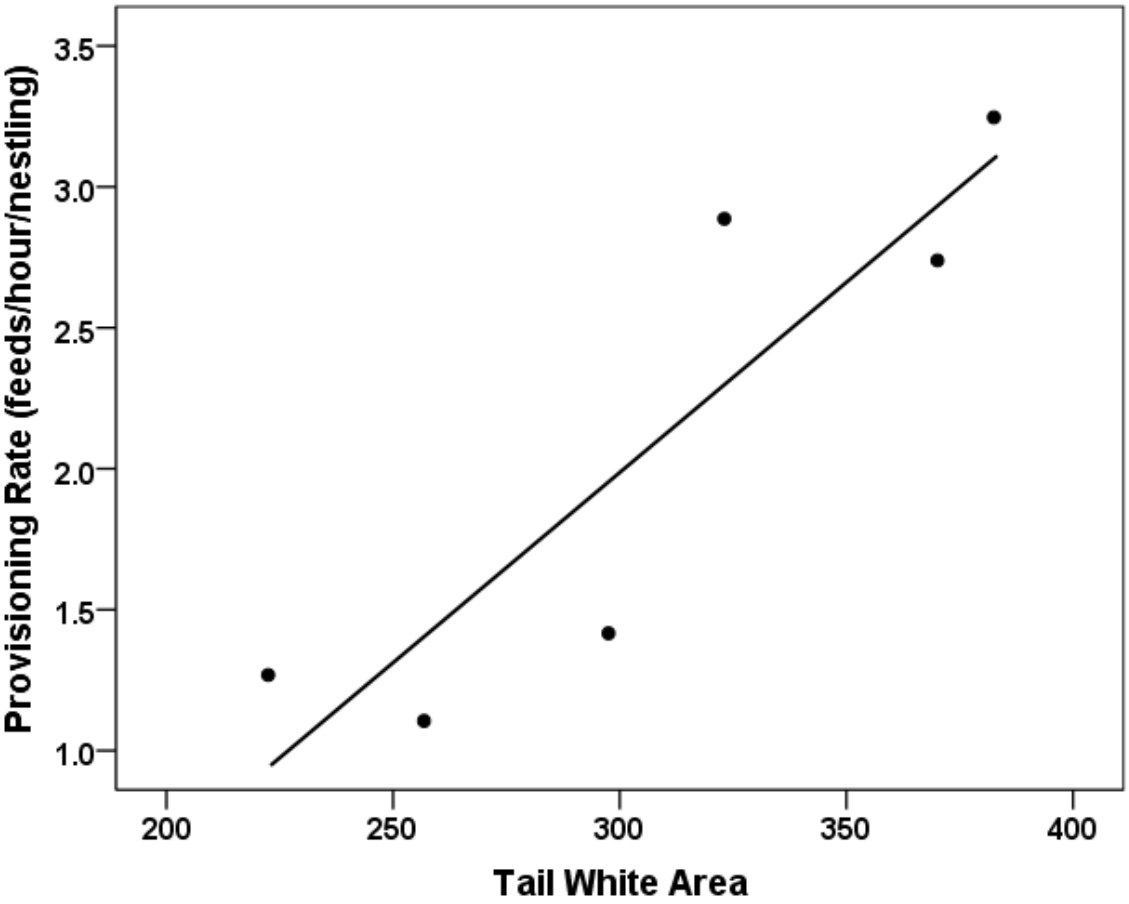

Figure 2. Relationship (Pearson's correlation) between amount of white in right tail plumage (mm^2) and provisioning rate in male Golden-winged Warblers.

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Vita

Anna Chewning Tisdale was born in Richmond, Virginia in 1989 to her parents Maria Jones Tisdale and George Mabry Tisdale III. She attended elementary, middle, and high school in western Henrico County and graduated from Mills E. Godwin High School with honors in 2007. She enrolled at Virginia Commonwealth University in Richmond, Virginia in 2007 and in her final semester she traveled to Panama for a study abroad trip focus in avian ecology. She was awarded a cum laude Bachelor of Science degree from Virginia Commonwealth University in 2011. To explore different career options, she worked the next two years in various education environments and did a variety of field work based in avian ecology. She was then accepted into the Master of Science program in the biology department at Appalachian State University in 2012 and in 2013 she was awarded an out of state tuition waiver from the graduate school as well as a research assistantship from Audubon North Carolina. Anna moved to Boone, North Carolina in April 2013 for a pilot field season studying Golden-winged Warblers and began the Master program the following fall. She received her Master of Science degree for a focus in Ecology and Evolutionary Biology in August 2015. Anna is now exploring a career in science education and community outreach in the high country of North Carolina.