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Source: The Wilson Journal of Ornithology, 130(1) : 286-296

Published By: The Wilson Ornithological Society

URL: https://doi.org/10.1676/16-198.1

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The Wilson Journal of Ornithology 130(1):286–296, 2018

Geography and age are related to plumage coloration of male Golden-winged Warblers (*Vermivora chrysoptera*)

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ABSTRACT—Although plumage displays often reliably signal individual condition and age, how these sexually selected traits vary with geographic region is not well understood. Golden-winged Warbler (*Vermivora chrysoptera*) populations are fragmented and declining precipitously in the Appalachian Mountains. Limited research suggests that Golden-winged Warbler facial plumage ornaments may be under sexual selection; black throat (melanin-based) coloration is associated with mate acquisition while yellow crown (carotenoid-based) coloration is associated with aggression and habitat quality. We tested whether multiple plumage traits (crown, throat, and tail coloration) (1) varied across the Appalachian breeding range, (2) varied with age class or body condition, and (3) covaried with each other and whether the covariance differed with geographic region. We found that crown and throat coloration followed a latitudinal gradient, with the more southern birds showing lower ornamentation. Moreover, after-second-year birds had tails with a greater extent of white than second-year, suggesting tail color may reliably signal age that conspecifics could assess. Males with more-ornamented crown color had more-ornamented throat coloration, suggesting that this species demonstrates some potential for both redundant (facial coloration) and independent (tail white) signaling. We found no evidence, however, that covariation between traits differed across the breeding range or that the plumage traits varied with body condition. Additional research investigating the signaling function of multiple plumage ornaments in Golden-winged Warblers across their breeding range could shed light on habitat preferences and communication. *Received 28 October 2016. Accepted 4 January 2018.*

Key words: animal signals, carotenoid, geographic variation, melanin ornamentation, structural coloration, *Vermivora chrysoptera*.

Geografía y edad están relacionados con la coloración del plumaje de los machos de *Vermivora chrysoptera*

RESUMEN (Spanish)—El plumaje muestra, en ocasiones de manera confiable, una señal de la condición y edad de los individuos. La forma en la que estas características, sujetas a selección sexual, varían según la región geográfica aún no es bien entendido. En las montañas Apalaches, las poblaciones de *Vermivora chrysoptera* están fragmentadas y en declive precipitado. La poca investigación existente sugiere que los ornamentos del plumaje facial de *V. chrysoptera* podrían estar sometidos a selección sexual: la coloración negra de la garganta (basada en melanina) está asociada a la capacidad de conseguir pareja, mientras que la coloración amarilla de la corona (basada en carotenoides) está asociada con agresión y calidad del hábitat. Sometimos a prueba múltiples características del plumaje (la coloración de la corona, garganta y cola) para saber si (1) variaba a lo largo de el rango reproductivo en los Apalaches, (2) variaba según la clase de edad y condición corporal y (3) covariaba respecto a las otras características además de dilucidar si esta covarianza difería con la región geográfica. Encontramos que la corona y la coloración de la garganta siguen un gradiente latitudinal en la que los pájaros más sureños muestran una menor ornamentación. Además, los pájaros mayores a dos años tenían colas con una mayor cantidad de blanco que las aves del segundo año, lo que sugiere que el color de la cola podría ser una señal confiable para sus conespecíficos. Los machos con coronas de colores más ornamentados tenían también una coloración más ornamentada en la garganta, lo que sugiere que esta especie podría en potencia exhibir ambos tipos de señales, una redundante (la coloración facial) y una independiente (el blanco de la cola). Sin embargo, no encontramos evidencia de covarianza entre diferentes características a lo largo del rango reproductivo o de que las características del plumaje variaran con la condición corporal. Futuras investigaciones que estudien la función de enviar señales, a través de múltiples ornamentos del plumaje de *V. chrysoptera* en su rango reproductivo, podrían ilustrarnos sobre sus preferencias de hábitat y comunicación.

Palabras clave: Carotenoides, coloración estructural, ornamentación por melanina, señales animales, variación geográfica, *Vermivora chrysoptera*.

Many species of birds have striking and dimorphic plumage, and plumage coloration is often considered a classic sexually selected trait (reviewed in Hill and McGraw 2006). West-Eberhard (2014) argued that an investigation into whether sexual selection drives traits is warranted when traits show one or more of the following: (1) extreme development or marked complexity, sometimes leading to sexual dimorphism; (2) use in contests or socially competitive displays; and/or (3) marked geographic variation, suggesting rapid divergence of genetically isolated populations. Numerous studies have shown that plumage

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coloration is a target of female choice (reviewed in Hill 2006a) and can influence the outcome of intrasexual contests for mates or high-quality territories (reviewed in Senar 2006, Santos et al. 2011). Because feather ornamentation is often energetically expensive (reviewed in Dale 2006), the high-condition individuals are expected to produce and maintain elaborate plumage and therefore can honestly signal condition (Higham 2013, Biernaskie et al. 2014). Indicator models argue that traits should honestly signal individual condition (the capacity of individuals to maintain optimal functionality of vital cellular systems) or individual quality, more broadly defined as individual fitness or correlates of individual fitness (Hill 2011). Plumage may also vary with age; older males typically have the most elaborate ornaments (reviewed in Dale 2006), which may result from differences in condition and foraging ability between age classes (e.g., Griffith and Pryke 2006).

Sexually selected plumage can be characterized in multiple ways, including color (e.g., brightness, hue, and chroma) and patch size (Badyaev et al. 2001). Moreover, many taxa express multiple plumage traits. Different plumage traits and different qualities 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). Redundant ornaments might serve to amplify or reinforce another signal to allow more accurate assessment of potential mates or rivals (Møller and Pomiankowski 1993, Johnstone 1996). Alternatively, when the traits are not redundant, each may signal different information to conspecifics (Møller and Pomiankowski 1993). Traits not associated with individual quality could trigger arbitrary preferences or facilitate signal detection and assessment and benefit the receiver if they facilitate detection or signal reception (Møller and Pomiankowski 1993, Caldolin 2003). Finally, sexual signals may influence species recognition, conspecific assessment, or both (reviewed in Andersson 1994).

Two primary mechanisms that produce plumage color are pigments and feather microstructure. For pigment-based coloration, carotenoids produce yellow to red plumage, and melanins produce chestnut brown to black plumage (McGraw 2006a, 2006b). When birds ingest carotenoid pigments from plants or insect herbivores of those plants, carotenoids are metabolized and deposited into the keratin during feather growth (McGraw 2006a). Carotenoid-based plumages reveal information about individual condition in many species (Hill 2006a). Melanin pigments are produced de novo (reviewed in McGraw 2006b) but can be sensitive to oxidative stress (Galván and Alonso-Alvarez 2008, 2009), and thus they have the potential to function as an honest signal of antioxidant levels. Structural coloration, however, is produced by microstructures in the reflective keratin of the feather that scatter light and, when highly organized, reflect specific wavelengths, whereas the nonorganized microstructure produces white plumage (reviewed in Prum 2006). Although less studied than vibrant structural colors, some evidence suggests that white plumage may signal individual condition (McGlothlin et al. 2007) and territorial defense ability (Jones et al. 2017).

Although theoretical models and empirical data suggest a great diversity of variation in the strength of sexual selection among conspecifics or closely related species (reviewed in Wiens 2001), surprisingly little research addresses how sexually selected plumage ornaments vary geographically. For example, the male Common Yellowthroat (*Geothlypis trichas*) displays prominent conspicuous coloration selected for by females; however, whether the melanin-based black facial mask or the carotenoid-based yellow throat acts as the honest signal of individual condition depends on the geographic region of the population, suggesting ecological resources play a key role in shaping color evolution in these populations (Dunn et al. 2008, 2010). The well-studied Barn Swallow (*Hirundo rustica*) also exhibits great geographic variation in body size, length of outer tail feathers, and ventral color (Dor et al. 2011, Hasegawa and Arai 2013, Scordato and Safran 2014); the latter 2 traits have been the subject of sexual selection research in several populations. Recent evidence suggests that localized sexual selection is the principal driver of phenotypic divergence between closely related swallow subspecies that vary geographically (Wilkins et al. 2016). In addition, rufous coloration in Barn Swallows seems to be, in-part, based on timing of molt; higher-quality individuals that delay molting until after migrating toward their wintering grounds produce more-ornamented feathers (Norris et al. 2009). Similarly, American Redstarts (*Setophaga ruticilla*) with higher reproductive output tend to delay molting until they reach the wintering grounds and produce less-ornamented orange color than birds that molted on the breeding grounds, likely because of lowered carotenoid availability (Norris et al. 2004). Together, these results suggest that geographic variation in mating preferences and resources (in particular, at the location of molt) between populations plays an important role in shaping color variation.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Nearctic-Neotropical migratory songbird that exhibits sexual dichromatism. Males have a bright yellow crown patch, black auriculars and throat patches, and white on their outer 2–3 rectrices. Although females share the male's white patches on the rectrices and contour plumage, black facial ornamentation (auriculars, throat) is replaced by gray, and the yellow crown plumage is noticeably duller (Confer et al. 2011). Some prior research focused on variation and signaling function of Golden-winged Warbler plumage within a geographic region. In Ontario, McKinnon and Robertson (2008) found that males with greater UV chroma in the black throat patch mated with females that laid eggs earlier in the season. In Minnesota, Leichty and Grier (2006) manipulated male throat plumage and found that males without black throat coloration were less likely to retain territories and obtain mates. Finally, there is evidence for a North Carolina population in which yellow crown color and tail white area correlates with male territorial aggression and habitat quality but not any metric of reproductive success (Jones et al. 2017). These studies, however, lack a broader geographic scope to investigate variation in color and to explore what may explain such variation.

Here, we focused on coloration of the carotenoid-based yellow crown and melanin-based black throat (Fig. 1) and size of the structurally derived white patches on the outer tail feathers of breeding male Golden-winged Warblers along a latitudinal gradient in the Appalachian Mountains, USA. The objectives of our study were 3-fold. First, we characterized plumage variation across 3 breeding populations in the Appalachian Mountains to describe geographical variation in plumage. Second, we tested whether plumage traits are associated with male age and body condition. Third, we investigated whether multiple plumage traits covary and if the covariance differs with geographic region.

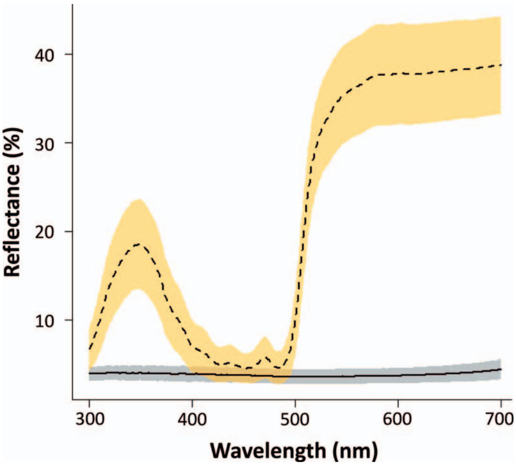

Figure 1. Mean (SD) reflectance spectra of Golden-winged Warbler crown (dashed line) and throat (solid line) feathers.

Methods

From 27 April to 23 June 2014, we sampled male Golden-winged Warblers across their Appalachian breeding range, which we separated into 3 geographic regions along the Appalachian Mountains (here, defined by each US State that the field site is in): 10 breeding sites in northwestern North Carolina (NC; southern-most field site; approximate center latitude and longitude: 36.348, –81.709), 8 sites in eastern West Virginia (WV; middle field site; ~240 km from NC; latitude: 38.353, –80.086), and 6 sites in northeastern Pennsylvania (PA; northern-most field site; ~790 km from NC and ~540 km from WV; 41.234, –75.074). Additionally, we collected a subset of North Carolina crown samples during a preliminary field season in 2013 (during the same time of year). After territory establishment, we captured birds via mist net and conspecific audio playback, tagged them with a numbered US Geographical Survey (USGS) aluminum band, and measured wing length (0.5 mm) and mass (0.01 g). We estimated the age of birds as second-year (SY) or after-second-year (ASY) based on molt limits and other plumage characteristics, but not plumage coloration (Pyle 1997).

We quantified extent of tail white (0.01 mm^2) using photographs from 12 megapixel cameras. We took photographs at a perpendicular angle with the right side of the tail flat against a background and with the feathers spread such that tail white was visible (each photograph included a size standard). Poor quality photos that could not reliably be used to measure extent of patch were excluded.

We quantified yellow coloration from crown and black coloration from the throat feathers because feathers from these regions can be easily collected. We collected 6 feathers per plumage patch and stored them in envelopes in a dark, climate-controlled environment until we measured color. All feathers were collected from approximately the center of each patch (i.e., yellow crown and black throat feathers). For spectral analyses, we taped feathers to black nonreflective paper, similar to how feathers lie flat naturally on the bird. We recorded spectral data with an Ocean Optics S2000 spectrometer (range 250–880 nm: Dunedin, FL) illuminated with both UV (deuterium bulb) and visible (tungsten-halogen bulb) light sources, measured at a 90° angle to the feather surface following methods detailed in Siefferman and Hill (2003). Reflectance measures were generated relative to a white standard (Labsphere, Inc.) that reflects 100% of light from 300 to 700 nm. We took 3 measures of plumage reflectance from each (crown and throat) sample. To reduce spectral noise, each measure consisted of the average of 20 rapid sequential spectral readings. We quantified color using 2 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 to 700 nm (Montgomerie 2006). Because calculated carotenoid chroma values are negative, we multiplied each value by –1 to ease interpretation, such that the individuals with the greatest carotenoid content are those with the highest carotenoid chroma value and thus are considered the most ornamented. Conversely, birds with the lowest throat brightness scores should have the greatest melanin pigmentation and are considered the most ornamented.

Statistical analyses

We used the standardized residuals of a linear regression of body mass on wing length to create a body condition index (Jakob et al. 1996). When constructing residuals separately for each region, however, we found no evidence that animals with longer wings were heavier (all linear regression $P > 0.10$); thus, we used the simpler method of body mass as the index of condition. Moreover, mass (mean [SD]) varied with region (NC: 8.54 [0.50] g; WV: 9.01 [0.47] g; PA: 8.88 [0.61] g). We tested for geographic differences of each color measurement using general linear models with region and age as categorical factors and body mass as a covariate. We tested for significant interactions between (1) geographic region and age on plumage color, (2) geographic region and body condition on plumage color, and (3) age and body condition on plumage color. In all models, all interaction terms were not significant ($P > 0.20$), and thus interaction terms were removed from the final models.

Next, to explore how color varied with region, we reported results of Tukey's post hoc tests from simple ANOVAs. Finally, we used Pearson correlations to evaluate covariation between multiple measures of plumage. We used SPSS software 22 (IBM 2013) for statistical analyses.

Results

We sampled 133 territorial Golden-winged Warbler males across 24 sites in North Carolina, West Virginia, and Pennsylvania (NC: 21 SY, 28 ASY, 13 unknown age; WV: 10 SY and 18 ASY; PA: 10 SY, 32 ASY, 1 unknown age). In North Carolina, we found no year effect (2013 [$n = 27$] vs. 2014 [$n = 34$]) on crown carotenoid chroma (all $P > 0.18$) and thus pooled data for further analyses. After splitting the data into 3 broad geographic regions (i.e., states sampled), color did not vary with breeding site within each geographic region (all $P > 0.18$); thus, we excluded site from all subsequent analyses.

Yellow crown color varied significantly with region (Fig. 2a) but not by age class or with body mass (Table 1). Tukey's post hoc tests demonstrated that birds in North Carolina had yellow crown feathers that were significantly less saturated with carotenoids (lower carotenoid chroma and

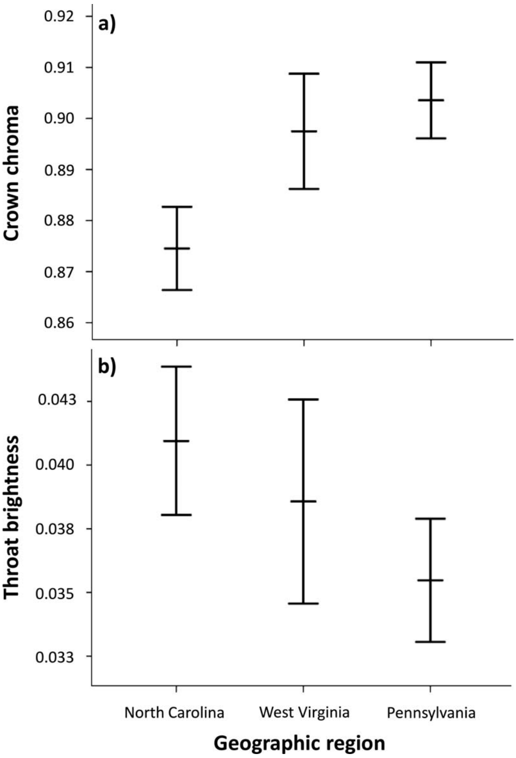

Figure 2. Comparison of (a) crown chroma and (b) throat brightness (mean reflectance of light from 300 to 700 nm) between male Golden-winged Warblers from North Carolina, West Virginia, and Pennsylvania. More-ornamented birds are represented by (a) higher reflectance values in crown feathers and (b) lower reflectance values in throat feathers. Positive values indicate heavier birds relative to their size and negative values indicate lighter birds relative to their size. Bars depict the 95% confidence interval for mean of sampled sites within each state.

thus theoretically less ornamented) than birds in West Virginia ($P = 0.001$) and Pennsylvania ($P < 0.001$); however, West Virginia and Pennsylvania birds were not significantly different in color ($P = 0.67$).

Black throat color varied significantly with region (Fig. 2a) but not by age class or with body mass (Table 1). Tukey's post hoc tests demonstrated that birds in North Carolina also had significantly less-ornamented throats (i.e., higher throat brightness, duller [grayer] black) compared to those from Pennsylvania ($P = 0.02$; Fig. 2b). No significant difference was found in throat coloration between North Carolina and West Virginia birds ($P = 0.53$) or between West Virginia and Pennsylvania birds ($P = 0.33$). These results should be cautiously interpreted, however, because the overall model was only marginally significant ($P = 0.07$; Table 1).

No significant regional differences were found in extent of tail white, and tail white did not vary with body mass (Table 1); however, older (ASY) birds exhibited significantly more extensive area of white tail plumage than younger (SY) birds (Fig. 3, Table 1).

To correct for the regional differences when testing for covariance between morphological measures, crown chroma and throat brightness were standardized to region (*z*-score). Birds with more-ornamented crown coloration also exhibited more-ornamented throat coloration (i.e., birds with more saturated crowns had darker throats; Fig. 4), whereas no other plumage traits covaried significantly (Table 2).

Discussion

We found that male Golden-winged Warblers have considerable variation in plumage ornaments throughout their Appalachian breeding range. North Carolina warblers had the least ornamented crowns and throats compared to individuals in more northern populations. Across all regions, age was related to tail white but not crown or throat coloration, and no ornaments were significantly related to body condition. However, crown and throat ornaments covaried; males with more-ornamented yellow crowns had more-ornamented black throat coloration, suggesting signal redundancy. These results suggest that plumage traits of male Golden-winged Warblers may potentially signal reliable information about age to mates or rivals and that facial ornamentation follows a latitudinal gradient. Because the interaction terms demonstrated that associations between body condition and plumage traits did not vary with region, it seems unlikely that the signaling function of traits varies with geographic region.

Older males exhibited tails with greater extent of white than younger males, consistent with extensive repeated measurements of banded Golden-winged Warblers (Pyle 1997) and a likely consequence of the adult versus juvenile prebasic molt pattern. Adult Golden-winged Warblers undergo a complete prebasic molt on or near their

Table 1. Results of general linear models testing for effects of region (NC, WV, and PA), age (SY vs. ASY), and body mass on measures of plumage ornamentation in male Golden-winged Warblers.

Plumage trait	Source	SS	*F*	*P*
Crown chroma	Model	0.18	5.69	<0.001
	Region	0.013	7.94	<0.001
	Age	0.002	2.01	0.16
	Mass	6.43E^{-5}	0.08	0.778
Throat brightness (%)	Model	0.001	2.25	0.07
	Region	0.00	3.69	0.03
	Age	6.978E^{-5}	0.87	0.35
	Mass	2.010E^{-5}	0.03	0.87
Tail white area (mm^2)	Model	90150.52	4.05	0.005
	Region	16797.63	1.51	0.23
	Age	46409.49	8.35	0.005
	Mass	4518.64	0.81	0.37

breeding grounds after breeding activities cease while the hatch-year birds undergo a partial molt of the body and head, but not of 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). Many wood-warbler species 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).

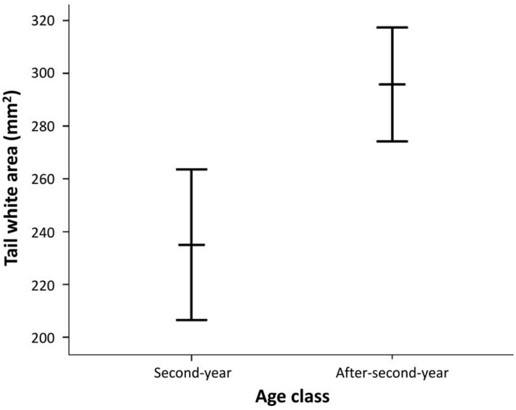

Figure 3. Comparison of tail white area of outer right rectrices of second year and after-second-year male Golden-winged Warblers from North Carolina, West Virginia, and Pennsylvania. Older Golden-winged Warbler males have a fuller extent of white plumage in their tails. Bars depict the 95% confidence interval for mean of each age class.

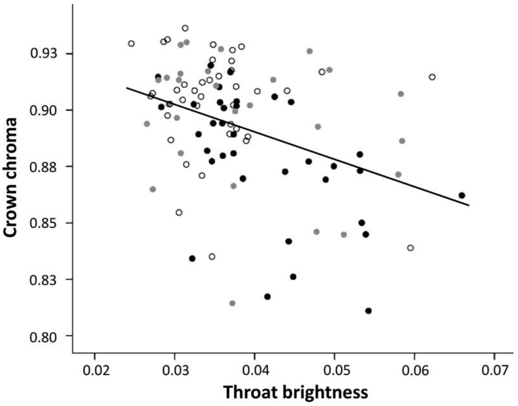

Figure 4. Relationship between crown ornamentation and throat ornamentation of male Golden-winged Warblers sampled in North Carolina (black), West Virginia (gray), and Pennsylvania (white). Plumage scores are standardized to regional means to account for regional variation in ornamentation. Higher crown chroma values and lower throat brightness values are considered more ornamented, and birds more ornamented in one head plumage trait also tended to be more ornamented in the other trait.

The regional differences in coloration show that degree of ornamentation followed a latitudinal gradient whereby more southern birds exhibited the least ornamentation and were in lower body condition compared to northern populations. These differences in ornamentation could result from either genetic or environmental (McGraw 2006a, 2006b) differences between the populations. For example, variation in ornamentation of House Finches (*Haemorhous mexicanus*) may be influenced by regional differences in food quality, particularly in carotenoid availability (Hill 1992). If regional differences in food quality exist during the time of molt, birds in some regions may have better access to the resources necessary to produce highly ornamented plumage (Hill 2006b). Golden-winged Warblers preferentially forage in tree species with abundant caterpillars (Lepidoptera; Bellush et al. 2016), but availability of high quality (or high-carotenoid content) food resources may vary among regions. Regional differences in plant community may thus impact the carotenoid intake of Golden-winged Warblers across our study area, particularly considering this species is believed to

Table 2. Results of Pearson's correlation analyses between multiple plumage traits of male Golden-winged Warblers after controlling for regional variation. Bolded text represents significance.

	Crown chroma (z)	Throat brightness (z)
Throat brightness (z)	**-0.38^{**} ($n = 102$)**	
Tail white area (z)	0.08 ($n = 78$)	0.01 ($n = 79$)

** <0.01.

rely heavily on caterpillars as a prey base (Streby et al. 2014, Bellush et al. 2016).

Regional variation in plumage ornamentation has also been proposed to result from regional differences in levels of physiological stress associated with overlap in timing of breeding and molting. For example, American Redstarts that breed later in the summer (and thus have higher within-year reproductive success) experience tradeoffs because they undergo prebasic molt during migration or in the wintering grounds, resulting in reduced carotenoid content within plumage (Norris et al. 2004). Timing of breeding onset seems to vary between these populations of Golden-winged Warblers (figure 2 in Aldinger et al. 2015), but we do not know the extent to which latitude might influence timing of molt or the extent to which birds from each population experience overlap in fall molt. To date, researchers assume that Golden-winged Warblers experience only one molt per year (a prebasic molt in fall; Confer et al. 2011), suggesting that the habitat on or near the breeding grounds plays the larger role in environmentally derived ornaments possessed the following breeding season. Although anecdotal evidence suggests that some Golden-winged Warblers undergo a prealternate molt of some head feathers on the wintering grounds prior to spring migration (March), further research is needed to assess whether this is a common occurrence (Pyle 1997; L. Chavarría-Duriaux, El Jaguar Reserve, pers. comm.).

Alternatively, the history of natural and sexual selection could vary between warbler populations across the latitudinal gradient (e.g., Barn Swallow; Wilkens et al. 2016), potentially resulting in regional differences of crown and throat coloration. Because associations between plumage coloration and body condition did not vary with region in this study, however, we believe it is unlikely that the signaling function of traits varies with geographic region. Unfortunately, limited data exist to test the strength or direction of sexual selection among populations of Golden-winged Warblers. To date, our previous efforts have suggested that crown and tail coloration are related to resource holding potential and territorial aggression (Jones et al. 2017) and thus could be signals that mediate male–male contests. Our same efforts have not revealed what color characteristics are preferred by females, however, because none of the 3 body regions are related to within-season reproductive output (Jones et al. 2017). Finally, in Golden-winged Warblers, variation in black coloration per se is not likely a signal because variation between individuals is so minimal it should not be discernable to the avian eye (Jones et al. 2017), but variation in the size of the throat patch has not been fully explored (sensu House Sparrow, *Passer domesticus*; Møller 1988). Limited evidence suggests that this patch may be relevant in female mate choice in Minnesota; Leichty and Grier (2006) found that removing the throat patch of breeding warblers influenced their ability to obtain and hold territories that attracted a female.

Selection to avoid hybridization may also explain regional variation in plumage coloration of Golden-winged Warblers. When found in sympatry, Golden-winged Warblers often hybridize with Blue-winged Warblers (*V. cyanoptera*; Gill 2004); indeed, hybridization was a motivation of the Leichty and Greer's (2006) study because Blue-winged Warblers (and Brewster's hybrids) lack the black throat and facial mask. The character states of Golden-winged Warblers that are more divergent from Blue-winged Warblers are darker throat and facial coloration (Blue-winged Warblers lack this trait) while the yellow coloration is nearly identical, and spectral differences between the 2 species (and the resulting hybrids) are likely not discernable to birds (JAJ unpubl. spectral data). Thus, in the northern portion of the Appalachian breeding population where hybrid zones are more prevalent (Vallender et al. 2007, Confer et al. 2011), interspecific competition for access to females and hybrid avoidance may have driven the selection of black throat coloration. In the southern Appalachian field sites, selection should be weaker for elaborate throat ornamentation because Blue-winged Warblers are rarer (Sauer et al. 2014, CGS unpubl. data), which is supported by our results indicating male throats are less ornamented in this population. Additionally, variation in yellow coloration between species is not discernable between Golden-winged and Blue-winged Warblers (JAJ unpubl. data), which may explain why Jones et al. (2017) were unable to find a relationship between yellow crown coloration and measures of reproductive success (or female mate choice) and yellow crown coloration.

We found no evidence that any measure of plumage coloration was significantly associated with the index of body condition. For melanin-based ornaments, this trend is not unexpected. Although some species have demonstrated condition-dependent melanin ornamentation (e.g., Pied Flycatcher [*Ficedula hypoleuca*]: Slagsvold and Lifjeld 1985; House Sparrow: Veiga and Puerta 1996), in many cases melanin ornaments are dependent on the social environment during time of molt rather than intrinsic condition (Møller 1988, McGraw et al. 2003). We expected the yellow carotenoid-based crown coloration to vary with condition however, because carotenoids often act as condition indicators (reviewed in McGraw 2006a). Carotenoids serve other important (mainly immunoenhancing) physiological functions; thus, tradeoffs may exist between pigment production and other metabolic pathways necessary for survival (McGraw 2006a). Finally, the mechanism behind honest signaling of age by white plumage remains ambiguous, despite the frequent and obvious importance of white plumage in an array of ritualized avian displays (Galván 2008). White plumage is related to body condition in some passerine species (e.g., Griggio et al. 2011). For example, healthy Dark-eyed Junco (*Junco hyemalis*) individuals have larger and brighter white patches, and birds fed supplemented diets produced more-ornamented tails (McGlothlin et al. 2007). Because we found no evidence of association between condition and tail white in male Golden-winged Warblers, tail white may be a reliable indicator of age rather than individual condition among conspecifics. Age-dependent ornamentation is common in birds and is most commonly thought to benefit younger breeders by reducing the likelihood that older individuals will initiate agonistic interactions (Lyon and Montgomerie 1986, Hawkins et al. 2012).

Alternatively, our failure to detect a relationship between plumage ornaments and body condition may be a product of our coarse index of body condition. Methods of measuring body condition that use mass indices attempt to estimate an individual's energy reserves with the assumption that more mass equates to more energy (e.g., fat) reserves (Jakob et al. 1996, Green 2001). However, morphometric approaches are often not well correlated with body fat (reviewed in Labocha and Hayes 2012), particularly in the summer breeding months when birds do not deposit fat as readily, and overall condition is likely affected by multiple physiological variables, each of which may or may not affect energy reserves (reviewed in Hill 2011). 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). Such invasive approaches, however, are not feasible with studies of imperiled species such as the Golden-winged Warbler.

The covariation of crown and throat ornamentation observed in our study suggests 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). If individual ornaments reflect different aspects of quality, however, females could better assess male quality via multiple (nonredundant) signals. For example, facial coloration may signal resource-holding potential while tail white signals male age and parental investment. In North Carolina, male Golden-winged Warblers with a greater extent of tail white provisioned nestlings more often while those with less-ornamented yellow crowns defended territories more aggressively (Tisdale 2015). By contrast, these traits are possibly not honest indicators of condition but rather are attractive to females and an evolutionary product of female aesthetic preference (Møller and Pomiankowski 1993, Prum 2013).

This is the first study to comprehensively characterize the plumage variation in male Golden-winged Warblers across a geographic gradient. First, we found clear evidence of geographic variation in plumage traits but no evidence that covariation between traits varied with region. We also found that tail white was a reliable predictor of age. We found some evidence of redundancy in signaling; males with more-ornamented yellow crowns also had more-ornamented black throat patches. Although we 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 (Jones et al. 2017). To understand the evolution of these ornaments both within and between species, future research should focus on (1) the strength of sexual selection with respect to Blue-winged Warbler hybridization and (2) the signaling function of multiple plumage ornaments across both the Appalachian and upper Great Lakes portion of the Golden-winged Warbler breeding range.

Acknowledgments

This research would not have been possible without the dedication of our field crews: C.K. Avery, C. Campbell, A.S. Dawson, C. Fiss, B. Eddinger, N. Glover, E.H. Heetderks, J. Kreiser, S. Malinich, J. Saborse, B.P. Taylor, J.L. Tucker, and L.E. Williams. We thank Mary Bomberger Brown and 2 anonymous referees for comments on earlier versions of our manuscript. Finally, we are grateful for the following individuals and agencies for their support and land access: B. Cochran, S. Wright, J. Rice, L. Campbell, L. Moretz, Southern Appalachian Highlands Conservancy (J. Leutze, C. Coxen, M. Crockett), NC Wildlife Resource Commission, TN Natural Heritage Program (L. Huff), Pisgah National Forest, Elk Knob State Park, Grandfather Mountain State Park, and Monongahela National Forest. Funding was provided by Appalachian State University through the Office of Student Research, Audubon North Carolina, as well as the United States Natural Resources Conservation Service through the Conservation Effects Assessment Project. Funders of our project had no influence on the content of the submitted manuscript and do not require approval of the final manuscript to be published.

Every bird captured was handled minimally to reduce physical stress and harm. This study was conducted in strict accordance to the guidelines of the Institutional Animal Care and Use Committee of Appalachian State University (#14-004.0), Indiana University of Pennsylvania (#14-1314), and West Virginia University (#07-0303, #10-0201). Birds were captured under US Fish and Wildlife master banding permits #23563 (L.S.), #23218 (C.G.S.), #23412 (Gregory George), and #23277B (J.L.L.).

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