

Multiple Plumage Ornaments as Signals of Intrasexual Communication in Golden-Winged Warblers

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Abstract

Avian plumage represents some of the greatest diversity in integument coloration of all animals. Plumage signals are diverse in function, including those that allow for assessing potential mates or the mitigation of agonistic interactions between rivals. Many bird species possess multiple ornamental traits that have the potential to serve as multiple or redundant signals. For example, male golden-winged warblers (*Vermivora chrysoptera*) have brilliant carotenoid-based yellow crowns, melanin-based black throats, and structurally based white patches on their outer tail feathers. Using a correlative approach, we investigated whether plumage ornaments have the potential to reliably signal ability to acquire higher quality territory, aggressive response to simulated territorial intrusions, and reproductive success. We found that both crown chroma and tail brightness were significantly related to habitat quality and aggression; more ornamented birds held territories with higher quality habitat and were less aggressive toward simulated conspecific stimuli. Older birds sang less threatening songs than younger birds and were more likely to sing their mate attraction song type (type 1) rather than songs typically reserved for agonistic interactions (type 2). Finally, despite our previous research demonstrating that habitat strongly predicts reproductive success in this warbler population, we found no evidence of a direct link between ornamentation and reproductive success. Overall, these data suggest that younger males, and those with lower quality ornaments, compensate with more aggressive behaviors. Additional research is needed to investigate the dynamics between behavioral traits and ornaments to better understand complex signaling and how golden wing signals function in conspecific interactions (male–male interactions and mate-choice).

Introduction

Animals across taxa have evolved distinctive morphological characteristics that serve functions ranging from crypsis to communication. In particular, birds are renowned for their diversity in coloration which is arguably unmatched by any extant animal group (Stoddard & Prum 2011). Within species, variation in color ornaments can convey reliable information

about individual condition, quality, dominance, or fighting ability (reviews in Hill & McGraw 2006; Santos et al. 2011). In males, sexual selected colors may arise due to female mate-choice for signals of phenotypic or genetic quality (Hill 1991; McGraw 2003; Safran & McGraw 2004) or because males use these signals to mediate same-sex interactions (Andersson 1994; Pryke & Griffith 2006). Ornaments that mediate intrasexual agonism are expected to convey reliable

information about dominance (Rohwer 1982; Senar 2006). These status signals may indicate social rank, age, or fighting ability (Fugle et al. 1984; Senar 2006; Mercadante & Hill 2014), such that subordinate individuals benefit from not challenging dominant individuals in contests they would likely lose and dominant individuals benefit from not allocating energy and time to engaging with individuals of lower quality (Rohwer 1975; Hawkins et al. 2012; Mercadante & Hill 2014; Young et al. 2015). Intuitively, for territorial species, territory acquisition is critical for within-season reproductive success and birds often vigorously defend breeding resources (Lack 1968; Ligon 1999). Yet, it is beneficial for individuals to reliably signal information to rivals about their competitive ability and resource holding potential (their likelihood of winning physical altercations; Parker 1974) to avoid risky and unnecessary confrontations in these contexts (Pryke et al. 2001; Vedder et al. 2010; Mercadante & Hill 2014). However, an alternative approach for males with less-attractive signals may be increased aggression toward highly ornamented individuals as a compensatory strategy to acquire mates (Stoehr & Hill 2000; Hill 2002).

Many birds possess multiple ornamental traits that reliably convey information that may be assessed by rivals. Plumage coloration is most commonly derived from one of three mechanisms: carotenoid pigments (red, orange, yellow), melanin pigments (black, brown, gray), and feather microstructure (blue, iridescent, white; Hill & McGraw 2006). Melanins have been well studied as a status signal in male–male interactions (Roulin 2015 and references therein), while the role of carotenoid- and structurally based (specifically unpigmented, or white, ornaments) coloration in signaling intrasexual contests have been comparatively limited. However, a growing body of research is emerging to suggest that both carotenoid-based (reviewed in Griffith et al. 2006) and unpigmented (structural) plumage ornaments (Balph et al. 1979; Ferns & Hinsley 2004; van Dongen & Mulder 2007) influence intrasexual agonism. For example, the carotenoid-based coloration of crimson finches (*Neochmia phaeton*) signals male–male dominance to familiar neighbors in this social species (Young et al. 2015). Streak-backed orioles (*Icterus pustulatus*) respond more aggressively to more ornamented rivals, and thus, it is inferred that those individuals represent more of a threat (Murphy et al. 2009). Finally, great tits (*Parus major*) with more immaculate white cheek patches have greater access to safer feeding sites and tend to breed earlier, and experimental reductions in ornamentation lead to greater numbers of agonistic

interactions among same-sex conspecifics (Ferns & Hinsley 2004).

Although each plumage color type has the potential to be a status signal, little research has addressed whether multiple ornaments simultaneously signal quality. Indeed, species with more than one ornament type have the capability to convey multiple or redundant messages (Møller & Pomiankowski 1993; Heberts & Papaj 2005) that vary across context (geographic region; Dunn et al. 2010). However, the comparative importance of one mechanism-based ornament versus that of another (carotenoid vs. melanin or pigment vs. structural) is relatively unclear. Birds that display colors derived from multiple mechanisms represent an interesting opportunity to study the relative importance and signaling function of multiple ornaments. Yet, although there has been an increase in the number of studies that investigate multiple conspicuous traits in individual species (Candolin 2003), comparatively few have focused on the signaling function for birds that possess multiple traits of different developmental mechanisms (reviewed in Hegyi et al. 2015). Fewer still are studies that investigate the two pigment classes in conjunction with structural ornaments. For example, golden whistlers (*Pachycephala pectoralis*) that display carotenoid-, melanin-, and structurally based (here, white) plumage only signal status with structurally based white plumage (van Dongen & Mulder 2007).

Golden-winged warblers (*Vermivora chrysoptera*) provide an excellent opportunity to study the comparative importance of the three common plumage color types found in passerines. Golden wings possess multiple plumage characteristics that may signal aspects of individual quality and/or competitive ability: yellow carotenoid-based crowns, black melanin-based throat patches, and white structurally based tail patches. To date, the only research focusing on the status signaling of golden wing coloration has focused on the signaling function of the black (melanin-based) throat patch. Experimental removal of the throat patch led to reduced pairing success and thus may function in female mate-choice, male–male dominance, or may indicate species identity (this species hybridizes with blue-winged warblers (*Vermivora cyanoptera*) that lack throat patches; Leitchy & Grier 2006). Further, golden-winged warblers with earlier laying dates have greater ultraviolet (UV) reflectance of this black patch (McKinnon & Robertson 2008). Finally, older males have larger patches of white on their tails (hereafter, tail-white) compared to younger males and males with more ornamented yellow crowns also express more ornamented black throats

(Tisdale 2015). Thus, it is likely that conspicuous coloration in golden-winged warblers may signal reliable messages to conspecifics, but how these multiple plumage characteristics are associated with aggression and resource holding potential has yet to be addressed.

Our objectives were to quantify multiple morphological characteristics of golden-winged warblers and investigate whether color variation (1) is distinguishable to the avian eye, (2) is related to parameters associated with resource holding potential (i.e., male competitive ability to obtain higher quality territories (based on habitat assessment) and their aggressive response to simulated conspecific intruders), and/or (3) predicts aspects of reproductive success. We predict that, if plumage color reliably signals competitive ability, more ornamented males will defend territories of greater quality (greater preferred habitat structure (less open/grassland and more shrubland; Jones et al. 2016)). Additionally, we predict that more ornamented males will react less aggressively toward simulated territorial intrusions that may pose little threat (playback trials without male models). Finally, we predict that ornaments will correlate with measures of reproductive success.

Methods

Study Species

Golden-winged warblers (Aves: Parulidae) are neotropical migrants that have received significant conservation attention recently (Roth et al. 2012). These warblers have experienced range-wide population declines for >40 yr, with the most dramatic declines occurring throughout the southern Appalachian Mountains (e.g., NC populations experience ~10.5% per year declines; Sauer et al. 2014). Remaining populations of golden wings are fragmented into two breeding populations: the Great Lakes and the Appalachians (Buehler et al. 2007; Confer et al. 2011). Several factors are likely contributing to population declines, but hybridization with blue-winged warblers and habitat loss (due to forest regeneration and fire suppression; Klaus & Buehler 2001; Buehler et al. 2007) are likely the most significant causes (Roth et al. 2012). These warblers nest in young forest and shrubland communities and during the post-fledging period use a variety of forest age classes from dense stands of saplings and pole timber to mature forest (Confer et al. 2011, Larkin unpubl. data). Golden-winged warblers broadcast territorial songs atop trees/shrubs within semi-open regenerating

forests and shrublands with abundant sunlight, which may act to increase visual signal effectiveness.

General Field Methods

We studied male golden-winged warblers at eight breeding sites in the southern Appalachian Mountains of western North Carolina (Ashe, Avery, and Watauga Cos.) and eastern Tennessee (Carter Co.) from Apr. to Jul. 2014. All field sites provide suitable nesting locations for golden wing pairs, and we have found that pairs behave similarly across field sites (Jones et al. 2016). We captured (via mist net coupled with conspecific playback) and marked males with one numbered USGS band and unique combinations of color bands for remote identification. In hand, we aged birds as second-year (SY) or after-second-year (ASY).

While birds were in the hand, we took standardized photographs of the tail-white extent using 10–12 megapixel cameras. Photographs were taken at a perpendicular angle such that the tail feathers were spread and tail white was visible. Tail-white extent was drawn manually in Adobe Photoshop[®]. Each photograph included a 10 × 10 cm size standard which was used to calibrate measurements; we calculated tail-white extent in mm² (Tisdale 2015). Photographs were not used if the quality was such that we could not reliably determine color extent. Afterward, we collected six crown and throat feathers and the outer most right tail feather for spectrometric color analysis of each plumage patch (Plumage Color Analyses).

Throughout the breeding season, we located and monitored golden-winged warbler nests to determine reproductive success. Here, we focus on laying date of the first egg of the first nesting attempt as well as first-attempt clutch sizes as proxies of reproductive success as we have previously found support for these variables in our population (Jones et al. 2016). Laying date has been found to be an important predictor of within-season reproductive success of golden-winged warblers (Aldinger et al. 2015; Jones et al. 2016). We additionally quantified fledgling numbers. Despite that 2015 was a typical year for golden-winged warblers (i.e., no apparent shortage of available habitat or female mates), we were unable to capture a sufficient sample of female birds to quantify their age or coloration ($n = 3$). Therefore, although it limits our interpretation of signaling function as it relates to female mate-choice, we focus only on male warblers in this study.

Territory Size and Composition

We mapped and determined habitat structure of individual golden-winged warbler territories (methods

and data reported in Jones et al. (2016): a study focusing on interspecific competition). Briefly, we spot-mapped the spatial location of territorial males during the breeding season using handheld GPS units. Spatial boundaries of individual territories were generated in Geospatial Modeling Environment (Beyer 2009), which were then imported into ArcMap 10.1 (ESRI, Redlands, CA, USA) for further analysis. We used remotely sensed imagery (2012, National Agriculture Imagery Program (NAIP)) from EarthExplorer (earthexplorer.usgs.gov) to classify habitat structure into four cover types: open or bare ground (road, rocky outcrops), grassland (homogenous area without any dense vegetation structure), shrubland areas (nesting habitat; higher density herbaceous areas that with young shrub/sapling cover), and forested or canopy cover (individual tree or continuous canopy cover). Percent cover of each classified cover type was generated for each individual golden-winged warbler territories (Jones et al. 2016). We found no statistically significant relationship between the proportion of each cover type and individual territory size (all $p > 0.13$). Although on-the-ground vegetative measures are likely more detailed than using remotely sensed imagery (and thus more useful for golden wing conservation), our goal was to cover the full extent of each golden wing territory, and thus, it was beyond the scope and capabilities to conduct extensive vegetation measures for each territory in this study. Moreover, we feel that territory-level analysis is more relevant for males who defend entire territories, whereas localized vegetative studies may be more useful if female quality was assessed in this study (as females likely dictate nest location).

Quantification of Aggressive Behaviors

We quantified individual aggression by conducting simulated territorial intrusions (STIs), in which we recorded the behavioral response of targeted males in response to a conspecific audio playback (see methods in Jones et al. 2016). Behavioral STIs occurred from May 4 to Jun. 3, 2014 from 0530 to 1130 EDT. We placed speakers ~2 m off the ground adjacent to a known perch. Retreating to a distance of ≥ 40 m, we broadcasted a conspecific playback for 10 min; audio playback was a mixture of the two song types of stereotypical golden-winged warblers (i.e., no blue-winged warbler or hybrid song phenotypes; Confer et al. 2011). Throughout the 10 min, we recorded diving rates and counter-singing rates (distinguishing between type-1 and type-2 song types; Ficken & Ficken 1967; Confer et al. 2011) as proxies of

aggression (Jones et al. 2016). We characterized the least aggressive males as those that dove less and sang song types typically associated with aggression (type-2) less often and song types primarily associated with mate attraction (type-1) more often.

Plumage Color Analyses

We stored feathers in envelopes in a climate-controlled dark environment until taking spectral measures. One researcher (JAJ) measured feathers using an Ocean Optics S2000 (range 250–880 nm: Dunedin, FL, USA) spectrometer using OOIBASE 32 software (Ocean Optics; detailed methods in Siefferman & Hill 2003). Briefly, we taped feathers on black, nonreflectance paper in such a fashion that it would mimic how feathers lie naturally on birds. We used a micron fiber-optic probe emitting UV-visible light. Light reflectance measures were generated relative to a white standard (Labsphere, Inc.) that reads 100% reflectance from 300 to 700 nm. Because golden-winged warbler crown feather reflectance generates a spectral curve that is typical of carotenoid-based pigments, we used the standard carotenoid chroma descriptor of reflectance spectra for this analysis: $(R_{\lambda 450} - R_{\lambda 700})/R_{\lambda 700}$ (Montgomerie 2006). Males with increased carotenoid saturation (higher chroma values) are classified as more ornamented. Next, we quantified the black coloration of the throat feathers and white coloration of the tail using average brightness (% reflectance), calculated as the mean of the summed reflectance: $\Sigma R_{\lambda 300-700}/n_{wl}$ (Montgomerie 2006). Darker (less bright) melanin-based plumage (here, throat coloration) and brighter unpigmented plumage (here, tail-white) are birds that are classified as more ornamented.

Modeling Color Distinguishability

To test whether the color of each ornament type had the potential to function as a signal to conspecifics, we tested whether the two male golden-winged warblers that were the most and least ornamented birds in our population would be distinguishable to the avian eye. We quantified avian color perception in the package 'pavo' (Maia et al. 2013) in R v.3.2.3 (R Core Team 2015) for the absolute brightest vs. dullest (achromatic scale) and most vs. least chromatic (chromatic scale) for each ornament type. To our knowledge, spectral sensitivities for wood warblers have yet to be measured. Therefore, we used a generalized model for birds that fall under the ultraviolet sensitive (UVS) classification (Endler & Mielke 2005). To model

background light environment, we used the D65 light setting: an illumination that represents average standard daylight. Following the methods of Jones & Siefferman (2014), we calculated the chromatic (shape of the curve (chroma)) and achromatic (overall percent reflectance (brightness)) contrasts between birds in units of discrimination (just noticeable differences (JNDs); Vorobyev & Osorio 1998; Vorobyev et al. 1998). JNDs have a unitless threshold value of 1.0, where values <1.0 indicate that two colors are indistinguishable, but values deviating from 1.0 indicate greater distinguishability (Siddiqi et al. 2004). Here, we interpret JND values <1.0 as indistinguishable, 1.0–2.0 as barely distinguishable, and >2.0 as easily distinguishable colors (Maia pers. comm.; Mcelroy 2015).

Statistical Analyses

All analyses were performed using *SPSS v.22* software (IBM Corp 2013) or *R v.3.2.3* (R Core Team 2015). We used the principal components analysis (PCA) used in Jones et al. (2016) to explain our habitat variables because they are intercorrelated (Table 1). The PCA explained 80.8% variance between two components with Eigenvalues >1, where Habitat-PC₁ loaded heavily on open cover (positive scores are associated with greater grassy/homogenous cover and less forested and shrubland cover) and Habitat-PC₂ loaded with remaining vegetation (positive scores are associated with greater forested/canopy cover, and negative scores are associated with shrubland cover). Open/bare ground factors loaded equally on both components, and thus, we do not consider them to be a significant factor in the analysis (Table 1). Previous analysis of these PCs has shown that Habitat-PC₂ best predicts golden-winged warbler reproductive success (Jones et al. 2016) and thus is defined as a reliable measurement of higher quality. However, we include analysis of Habitat-PC₁ because it distinguishes between grassland/homogenous habitat and more shrubland/forested habitat (potential suitable locations for nesting birds; Jones et al. 2016).

Table 1: Principal component loading factors for each vegetation class. Data taken from Jones et al. (2016)

Vegetation class	Component	
	Habitat-PC ₁	Habitat-PC ₂
Percent cover: abiotic factors	0.52	0.50
Percent cover: grassland	0.92	−0.19
Percent cover: forested/canopy	−0.73	0.66
Percent cover: shrubland	−0.51	−0.78

We used an analysis of covariance (ANCOVA) to test for interactions between age and color on habitat acquisition, aggression, and reproductive success. Although we found nonsignificant trends that older males tend to be more ornamented ($p > 0.07$), ANCOVA analysis revealed that there were no statistically significant interactions between age and color on any variable measured in this study (all $p > 0.19$). Therefore, remaining analyses are presented using color measures uncontrolled for age. Additionally, because we have previously found a significant relationship between golden-winged warbler and the density of heterospecifics (chestnut-sided warblers; Jones et al. 2016), we controlled behavioral response to STIs for the density of chestnut-sided warblers found in individual territories. Nonetheless, whether or not we controlled for age or heterospecific density, the statistical and biological trends were the same.

We investigated associations between golden-winged warbler ornamentation and their territory vegetation, aggressive behaviors, and reproductive success by using multiple regressions. We ran two models addressing parameters associated with resource holding potential (Habitat-PC₁ and Habitat-PC₂, and their aggressive behaviors) and the other associated with reproductive success and fitness (first egg date, clutch size, and numbers fledged). Additionally, we tested whether male age was correlated with aggressive intent or reproductive success with independent samples unpaired *t*-tests. Finally, we used Pearson's correlations to test for associations between aggression and measures of reproductive success.

Results

Avian vision model analyses revealed that the yellow crown ornamentation of golden-winged warblers is easily distinguishable in chromatic variation (distinguishable coloration; JND = 8.09), but not achromatic variation (indistinguishable brightness; JND = 0.42). Black throat chromatic variation was marginally above threshold (barely distinguishable; JND = 1.22), whereas overall throat brightness well exceeded threshold (JND = 16.51). Finally, tail chromatic variation is indistinguishable between males (JND = 0.10), but achromatic variation is easily distinguishable (JND = 4.34).

Multiple regression analysis yielded a significant model for crown chroma (adjusted multiple $r^2 = 0.40$, $F_{4, 15} = 3.88$, $p = 0.02$), such that golden wings with more ornamented crowns (greater crown chroma) were less aggressive (less dives per min) but maintained territories with greater forest/shrub cover

relative to open/homogenous cover (lower Habitat-PC₂ scores; Fig. 1; Table 2). We found that tail-white brightness yielded similar results ($r^2 = 0.36$, $F_{4, 13} = 3.02$, $p = 0.05$), such that birds with more ornamented tails (brighter) were less-aggressive (more type-1 songs rather than aggressive type-2 songs per min). We found a statistically nonsignificant trend ($p = 0.09$) that may be biologically relevant; birds with greater tail-white brightness held territories with higher Habitat-PC₂ scores (more early successional nesting cover relative to closed-canopy forest cover (Fig. 2; Table 2)). Neither throat brightness ($r^2 = 0.14$, $F_{4, 16} = 1.70$, $p = 0.19$) nor tail-white extent ($r^2 = 0.07$, $F_{4, 10} = 1.24$, $p = 0.36$) predicted either habitat PC or aggressive behaviors (Table 2).

There was a tendency for older males to have sung type-1 songs more often ($\bar{x} \pm SD$; ASY: 3.18 ± 1.42 songs per min; SY: 1.83 ± 1.41 songs per min; $t_{7, 19} = 2.15$, $p = 0.04$; Fig. 3) but to have sung type-2 songs less often (ASY: 0.51 ± 1.31 songs per min; SY: 1.71 ± 1.98 songs per min; $t_{7, 19} = 1.81$, $p = 0.08$; Fig. 3). We found no significant relationship between male age and diving rate ($t_{7, 19} = 1.42$, $p = 0.17$).

Finally, multiple regression analysis revealed that golden-winged warbler ornamentation was not

related to any measure of reproductive success (crown chroma: $r^2 = 0.01$, $F_{3, 13} = 0.06$, $p = 0.98$; throat brightness: $r^2 = 0.12$, $F_{3, 13} = 0.55$, $p = 0.66$; tail-white brightness: $r^2 = 0.13$, $F_{3, 13} = 0.63$, $p = 0.61$; tail-white extent: $r^2 = 0.36$, $F_{3, 9} = 0.22$, $p = 0.88$; Table 3). We also found no effect of male age on first egg dates ($t_{5, 13} = 0.23$, $p = 0.82$), clutch size ($t_{5, 13} = 0.18$, $p = 0.86$), or fledgling numbers ($t_{5, 13} = 0.20$, $p = 0.85$). No behavioral responses to conspecific stimuli were significantly associated with any measure of reproductive success (all $p > 0.18$; Table 4).

Discussion

Here, we found evidence that multiple ornaments of male golden-winged warblers may convey honest information about resource holding potential and territorial aggression. As expected, we found that crown chroma, throat brightness, and tail brightness should be easily distinguishable to birds and thus have the potential to serve a signaling function between golden-winged warblers. More ornamented birds (those with greater carotenoid chroma and those that tended to have brighter tail-white) held territories

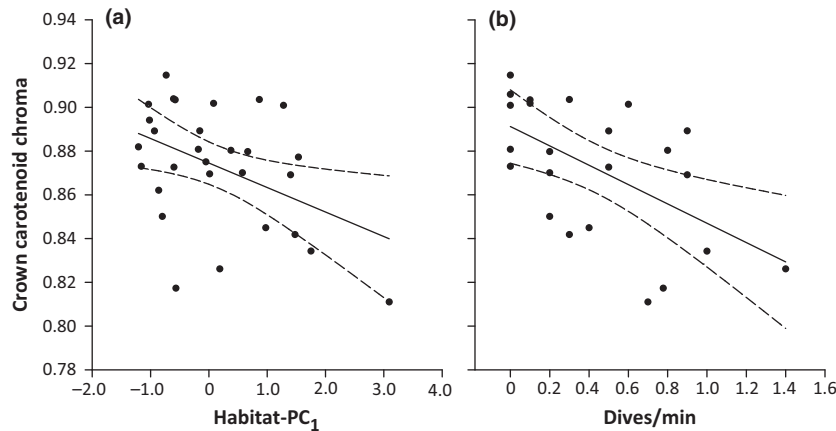


Fig. 1: Relationship between golden-winged warbler crown ornamentation, territory habitat composition, and behavioral response to conspecific playback. More ornamented (higher chroma) males have significantly (a) lower percent cover of homogenous habitat and more shrubland/canopy cover in their territories and are (b) significantly less aggressive toward conspecific playback stimuli.

Table 2: Multiple regression analysis between plumage characteristics of male golden-winged warblers and the habitat of their territory and aggressive behaviors. Each row represents an independent model.

Plumage trait	Habitat-PC1		Habitat-PC2		Dive rate		Type-1 song rate		Type-2 song rate	
	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>
Crown chroma*	-0.02 (0.005)	2.96**	-0.01 (0.004)	1.59	-0.03 (0.02)	2.96**	0.001 (0.003)	0.37	0.01 (0.004)	1.34
Bib brightness	0.002 (0.002)	1.33	0.004 (0.002)	2.23*	0.004 (0.005)	0.76	0.0001 (0.001)	0.16	0.002 (0.001)	1.23
Tail brightness*	-0.002 (0.003)	0.82	-0.005 (0.003)	1.81	-0.009 (0.008)	1.05	0.005 (0.002)	2.71*	0.001 (0.002)	0.49
Tail-white extent	-8.98 (19.3)	0.47	34.53 (20.4)	1.70	-30.79 (42.3)	0.73	-4.46 (10.7)	0.42	-11.65 (14.7)	0.79

** $p \leq 0.01$; * $p \leq 0.05$.

Fig. 2: Relationship between golden-winged warbler tail ornamentation, territory habitat composition, and behavioral response to conspecific playback. More ornamented (brighter tail-white) males (a) tend to settle in areas with higher shrubland cover relative to canopy cover ($p = 0.09$) and (b) counter-sing with their less-aggressive, type-1 song more when stimulated by conspecific playback stimuli.

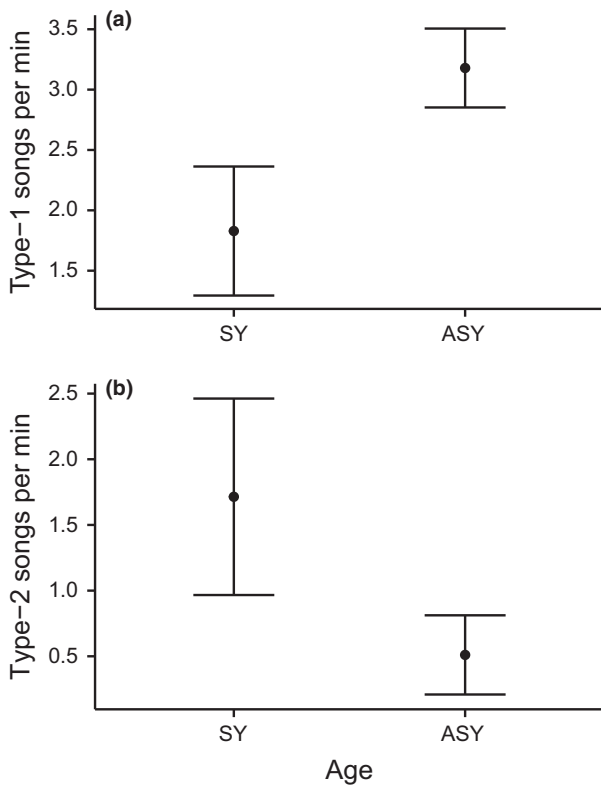
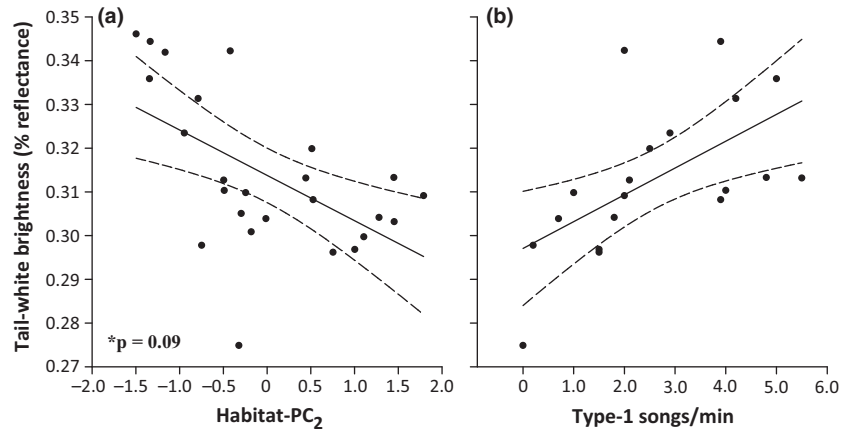


Fig. 3: Relationship between golden-wing vocal responses to conspecific stimuli and age class. Older (after-second-year (ASY); $n = 19$) golden-winged warbler males counter-sang with more type-1 songs (a) and less type-2 songs (b) compared to younger males (second-year (SY); $n = 9$). Bars represent mean \pm SD.

with higher quality vegetation parameters (Fig. 1a and 2a). Previous work within this population of golden-winged warblers demonstrated that females in territories with higher Habitat-PC₂ scores laid eggs earlier in the season (Jones et al. 2016). Additionally, higher quality males responded the least aggressively

to STIs; the least aggressive males had higher crown chroma (Fig. 1b) and brighter white tails (Fig. 2b). However, we surprisingly found no direct relationship between reproductive success and either plumage ornamentation or aggression, suggesting that habitat quality may be the most important driver of reproductive success. Overall our data suggest that, for golden-winged warblers, ornaments convey reliable information about male aggression and ability to settle on higher quality habitat. Thus, it seems more plausible that these traits influence male–male contests rather than female mate-choice.

In the context of agonistic intrasexual interactions, the relative coloration of each of the two competing males may drive the behavioral responses of both individuals; two bright males and two dull males may behave more aggressively toward each other than two males with dissimilar ornamentation (Mateos & Carranza 1997). Variation in aggressive response toward colors may be species specific (reviewed in Senar 2006). For example, in red-collared widowbirds (*Euplectes ardens*), carotenoid coloration likely functions as a badge of social status. Using models presentations, Pryke et al. (2001) found that, when male widowbirds exhibited more exaggerated plumage compared to the model, they behave more aggressively. Conversely, more ornamented males may choose not to engage in aggressive behaviors if the intruder is not perceived as a threat (Ligon 1999; Greene et al. 2000). For example, less ornamented male house finches (*Haemorhous mexicanus*) are more aggressive over food resources than more colorful males despite the fact that females show clear preferences for more colorful males (reviewed in Hill 2002). Thus, duller male house finches may be aggressive as a compensatory strategy to aid in mate acquisition (Stoehr & Hill 2000; Hill 2002). We found that more

Plumage trait	First egg date		First-attempt clutch size		Fledgling number	
	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>	β est. (SE)	<i>t</i>
Crown chroma	0.0003 (0.001)	0.26	0.007 (0.02)	0.41	-0.001 (0.004)	0.32
Bib brightness	0.0004 (0.0003)	1.27	0.004 (0.005)	0.92	-0.0005 (0.001)	0.40
Tail brightness	0.001 (0.001)	0.85	0.01 (0.01)	1.36	-0.002 (0.003)	0.81
Tail-white extent	1.23 (3.34)	0.36	31.02 (47.34)	0.66	1.12 (10.21)	0.11

Table 3: Multiple regression analysis between plumage characteristics of male golden-winged warblers and parameters of reproductive success. Each row represents an independent model. No models were statistically significant.

Behavioral response	First egg date			First-attempt clutch size			Fledgling numbers		
	<i>r</i>	<i>n</i>	<i>p</i>	<i>r</i>	<i>n</i>	<i>p</i>	<i>r</i>	<i>n</i>	<i>p</i>
Dive rate	-0.33	17	0.21	0.32	17	0.23	0.20	17	0.46
Type-1 song rate	0.13	17	0.64	-0.35	17	0.18	-0.26	17	0.34
Type-2 song rate	-0.21	17	0.42	0.28	17	0.29	-0.08	17	0.78

Table 4: Pearson's correlation between golden wing reproductive parameters and behavioral response variables to simulated conspecific intruders.

ornamented golden-winged warblers displayed less-aggressive responses to simulated conspecific intruders. It may be that older, more ornamented golden wings do not perceive our STI as a sufficient threat, potentially due to lack of a visual stimulus with the acoustic playback. Alternatively, it may be that younger, less ornamented golden wings behave aggressively to compensate for poor ornamentation (*sensu* house finches; Hill 2002). If either strategy (highly ornamented and not aggressive vs. dull but highly aggressive) are equally appealing to female warblers, then this may explain the lack of significance with respect to reproductive success in this study. This possible best-of-a-bad-job strategy displayed by duller males may allow them to achieve reproductive opportunities comparable to highly ornamented individuals (Hill 2002; McGraw et al. 2007).

We found no evidence that melanin-based throat coloration was associated with habitat quality, aggression, or reproductive parameters of male golden-winged warblers. Our results support the findings of Young et al. (2015) but contrast with previous research on golden-winged warblers that suggest a role for the black throat coloration in female mate-choice. McKinnon & Robertson (2008) found that males with greater UV chroma of the black throat patch were mated to females that laid eggs earlier in the season. However, our analyses demonstrate little variation in the UV region of this achromatic color trait and, using a comparison of the least vs. most ornamented males, we show that UV variation would be barely (if at all) discernable to birds. Moreover, this

discrimination is only feasible given optimal lighting; in our color perception analysis, we used an illumination setting that mimics average daylight. However, in unfavorable conditions (such as cloudy days), birds would unlikely be able to discern chromatic color differences (Vorobyev 2003). Thus, although variation in UV chroma may be correlated with intrinsic quality of males (McKinnon & Robertson 2008), it is unlikely to act as a signal. Variation in overall brightness (an achromatic measurement), on the other hand, is much greater, and such variation is easily discernable to warblers. Nonetheless, our field data suggest melanin throat coloration is not likely a signal *per se* as it is not associated with habitat quality, aggression, or reproductive success.

We can hypothesize two potential explanations to explain the function of melanin-based throat coloration of male golden-winged warblers. First, it may be the presence and/or size of the throat patch, rather than the coloration, that is the important signal of quality between males (Møller 1988; Doucet et al. 2005; reviewed in Senar 2006). For example, when Leichty & Grier (2006) used a manipulation that removed the black throat patch of breeding males, those males tended to lose their territories to conspecific competitors. Although this experiment could be criticized because it altered male morphology beyond the natural range of variation, it was intended to mimic a golden-winged warbler/blue-winged warbler hybrid. Their results may suggest a role of the presence of the black throat patch in social signaling (social dominance). A second, non-mutually exclusive hypothesis is that throat-based coloration may act

as an amplifier (Hansson 1991; Candolin 2003; Endler 2012): The presence of the dark coloration may increase the probability of detection and conspicuousness of another correlated signal to reduce signal receiver errors (Candolin 2003; Hebets & Papaj 2005). Golden-winged warbler males with more ornamented crowns also have darker throat patches (Tisdale 2015). Thus, the presence of the dark melanin throat may act to amplify the carotenoid signal. Alternatively, the black plumage may amplify the white coloration surrounding the throat and mask of golden wings. Endler (2012) argues that the conspicuousness of one signal may be dependent upon the contrast from adjacent signals. Unfortunately, we did not quantify the coloration or extent of white facial plumage. An experimental manipulation of the patch size and coloration of the throat ornamentation, within the natural range of variation, may help answer each proposed hypothesis.

Our previous work in this system has revealed that tail-white ornaments may signal reliable information about age and parental effort (Tisdale 2015). Here, we find that tail white may play an important role in territory acquisition and behavior (Fig. 2). First, although not statistically significant ($p = 0.09$), our data suggest there may be a biologically relevant trend whereby males with brighter tail white settled in territories with greater early successional nesting cover (Habitat-PC₂), and early successional cover predicts reproductive success in this population of golden wings (Jones et al. 2016). Second, when stimulated by conspecific intruders, males with brighter tail white sang more type-1 songs, and this song type is typically associated with mate attraction rather than intrasexual aggression (Ficken & Ficken 1967; Confer et al. 2011). Thus, tail white may serve multiple messages, conveying honest information about resource holding potential, age, or intrinsic quality that could be assessed by either sex. Indeed, unpigmented (white) plumage patches have been shown to be a status signal in several species (Hill et al. 1999; Ferns & Hinsley 2004; van Dongen & Mulder 2007), but it is unknown whether the cost of unpigmented plumage is reinforced by social status (analogous to traditional melanin-based status signals; Roulin 2015) or if there is an associated maintenance cost (Kose et al. 1999). Colors produced by unpigmented ornaments are derived from the reflectance of light off of unorganized keratin nanostructure, and as such, the physiological costs associated with maintaining these traits are unclear (Griffith et al. 2006). An alternative, non-mutually exclusive explanation of tail-white function is that it is used to benefit warblers in foraging. When

the tail white of slate-throated redstarts (*Myioborus miniatus*) was experimentally blackened, they had significantly reduced success in flush-pursuit foraging (Mumme 2002). Therefore, both natural and sexual selection may jointly play an important function in the evolution of tail white in warblers (*sensu* Balmford et al. 2000).

We also found that older birds respond to conspecific intruders less aggressively than younger birds (Fig. 3). During STIs, older males sang type-1 (mate attraction) songs more than younger birds, but sang type-2 (aggressive song types) less than the younger individuals. If females prefer older males (as would theoretically be easily recognized by tail coloration during tail displays) than younger (and presumed less attractive) males, then aggression may be a compensatory strategy; younger males may be more aggressive in response to simulated conspecific intruders because the likelihood of territory usurpation is greater.

In this study, we examined relationships between multiple signals from a single modality. Despite having found some clear trends in this study, lingering questions remain regarding the adaptive function of multiple ornaments in golden-winged warblers and the potential to convey multiple or redundant messages. It is becoming increasingly apparent that studying signals in isolation may not be sufficient to truly understand signal function; signals often involve complex behavioral routines (dynamic signals) coupled with ornaments (static signals; Hebets & Papaj 2005). In male golden wings, Tisdale (2015) found correlations between crown and throat coloration, suggesting that these signals may be redundant or may reinforce each other (Møller & Pomiankowski 1993; Johnstone 1996; Rowe 1999). Here, we find that both crown and tail ornaments predict aggressive behaviors as well as territory habitat structure, suggesting that these signals may reinforce each other to convey honest information about male–male competitive ability. However, we cannot rule out the possibility that some signals may have multiple messages. Moreover, although these signals are likely used in intrasexual contests, it is possible that females may assess these signals in the context of mate-choice. Therefore, further studies of how conspecifics react to both plumage ornaments and dynamic behavioral displays (including song) may better identify how these multiple signaling traits function and convey multiple messages within and between sexes.

In summary, we found compelling correlative evidence that male golden-winged warblers display multiple color ornaments that likely relay reliable

information regarding male–male competitive ability. We found that older males with more ornamented crowns and tails were able to secure territories with higher quality habitat. Moreover, these highly ornamented males behave significantly less aggressively to simulated conspecific intruders, which may be a product of assessing the perceived threat (which in this case was the absence of a model) before engaging in risky aggression. Thus, less ornamented individuals may use aggression as a compensatory mechanism to cope with intense competition from older, more ornamented males that allow them to achieve equal (or comparable) reproductive success for the season (Hill 2002; McGraw et al. 2007). Importantly, the signaling function of carotenoid crowns and unpigmented tails in male–male contests found here does not exclude the possibility for simultaneous signaling for female mate-choice. This study represents an initial step to understanding multiple plumage ornaments in golden-winged warblers and their function. Manipulative experiments that present mounts of varying degrees or ornamentation coupled with mate-choice and male–male competition assays may further unravel lingering questions regarding the content of these signals as well determine the potential receivers.

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