

AGONISTIC BEHAVIORS BETWEEN CHESTNUT-SIDED (*SETOPHAGA PENNSYLVANICA*) AND GOLDEN-WINGED (*VERMIVORA CHRYSOPTERA*) WARBLERS ARE UNLIKELY A RESULT OF PLUMAGE MISIDENTIFICATION

JOHN A. JONES^{1,2} AND LYNN SIEFFERMAN¹

ABSTRACT.—Plumage coloration within species is often a signal of competitive ability and can influence territorial aggression between males. Agonistic interactions among males of different co-occurring species could result from misidentification (misdirected conspecific aggression). Reflectance spectrometry of plumage coupled with models of avian vision can be used to infer whether plumage color differences can be distinguished by birds. Here we investigate crown coloration similarity as a potential explanation for aggression between the imperiled Golden-winged Warbler (*Vermivora chrysoptera*) and the comparatively abundant Chestnut-sided Warbler (*Setophaga pensylvanica*). Because the yellow crown coloration of the two species appears identical to humans, we hypothesized that misidentification of heterospecifics as conspecifics could escalate agonistic interactions. Using museum study skins, we tested whether the yellow crown coloration of the two species should be distinguishable to the birds. Spectral reflectance data demonstrate that plumage color differs between the two species and avian vision models suggest these color differences should be easily discriminated. Thus, we conclude that plumage coloration similarity between these wood warblers is unlikely to cause misidentification of heterospecifics as conspecifics and may just be a result of phylogenetic constraint. As populations of Golden-winged Warblers are experiencing accelerating declines, research focusing on the role interspecific competition plays on reduced productivity and survival is warranted. Received 20 February 2014. Accepted 4 June 2014.

Key words: animal communication, avian vision model, carotenoid, pavo, reflectance spectrometry, *Vermivora chrysoptera*, wood warblers.

Plumage coloration often mediates agonistic interactions among conspecific males (Rohwer 1982, reviewed in Senar 2006). However, aggressive interactions among heterospecifics are more difficult to explain from an evolutionary perspective. Aggressive behaviors between two species are frequently used to infer ecological niche overlap (e.g., Heller 1971, Martin and Martin 2001). However, if males misidentify heterospecifics as conspecifics, occasional agonistic interactions would be expected, regardless of niche requirements between species. Indeed, two reviews suggest that some degree of heterospecific aggression may occur because of misdirected conspecific aggression across taxa (reviewed in Murray 1971, 1981). Morphometrics alone are not the only criteria for discriminating one species from another; Ord et al. (2011) found that discrimination is dependent on context, and is guided by the cost-benefit ratio of responding aggressively towards either con- or heterospecifics. Thus, if two species occupy similar habitats, use nearly identical resources, and

display similar plumage colors, misdirected aggression may occur often.

If plumage-based misidentification were to occur between birds, the colors would likely reflect light similarly across the avian visual spectrum. Although humans are trichromatic and can perceive and discriminate colors better than most eutherian mammals (reviewed in Cuthill 2006), our color perception is not as acute and does not encompass as wide of a spectral range as birds. Indeed, there are three important distinctions between human and avian vision. First, birds have four types of single cones and one type of double-cone that is not found in mammals (Cuthill et al. 2000, Hart 2001). Second, birds have lens, corneas, and aqueous and vitreous humors that are transparent to UV-A wavelengths (~315 nm), and thus, see ultraviolet light (Burkhardt 1989, Cuthill 2006), while humans do not perceive wavelengths below 400 nm because of absorbance by the ocular media preceding the retina (Douglas and Marshall 1999). Finally, at the expense of poor color vision in low levels of light (Vorobyev 2003), carotenoid-containing oil droplets in avian cones are responsible for increased color distinguishability between close wavelengths if optimal lighting is provided (Govardovskii 1983, Vorobyev 2003). Thus, the acuity of bird color vision is

¹Biology Department, 572 Rivers Street, Appalachian State University, Boone, NC 28608-2027, USA.

²Corresponding author; e-mail: Jonesja2@appstate.edu

much higher than humans (reviewed in Cuthill 2006). To determine whether colors are distinguishable to birds, objective measures of plumage reflectance (Bennett et al. 1994, Cuthill et al. 1999) coupled with models of avian vision (Maia et al. 2013) are necessary.

Focal observations have revealed complex interaction patterns between Golden-winged Warblers (*Vermivora chrysoptera*) and morphologically similar Chestnut-sided Warblers (*Setophaga pensylvanica*) in the southern Appalachians. In 2013, we observed agonistic behaviors between Golden-winged and Chestnut-sided warblers, but these behaviors were not consistent. For example, we have noted aggressive altercations while the focal species were singing from adjacent perches, during targeted mist-netting attempts of both species, and after releasing an animal from banding. However, we have also noted no apparent aggressive behaviors between males of both species during each of these situations. Further, other warbler species occur in sympatry at our field site, yet we recorded no aggressive interactions among males of other species. Although Chestnut-sided Warblers exhibit markedly distinct plumage and song characteristics from Golden-winged Warblers, the yellow crown plumage of both warbler species appears identical to human observers, even when held in hand (JAJ and LS, pers. obs.). The foraging and flight behaviors of both warblers are similar enough to fool researchers at our field site; at first glance, we often mistake one species for the other. Thus, the combination of similar morphology as well as behaviors may promote misidentification between species. We hypothesize that there are no differences in the coloration of crown feathers between species or that the warblers fail to perceive these differences in crown coloration.

It is also possible, however, that interspecific competition over shared resources is the cause of aggressive interactions. Golden-winged and Chestnut-sided warblers defend territories and nest in early-to-mid successional habitats (Confer et al. 2011, Richardson and Brauning 2013) and have nearly identical habitat requirements (Collins et al. 1982). Territories generally include mature hardwood forest adjacent to successional habitat (Confer et al. 2011, Richardson and Brauning 2013), thus interspecific interactions likely occur in variable lighting conditions. Populations of Golden-winged Warblers are experiencing drastic declines (annual declines:

–2.6% per year from 1966–2011, $P < 0.05$), while Chestnut-sided Warbler declines are less extreme (–1.4% per year from 1966–2011; $P < 0.05$; Sauer et al. 2012). In the southern Appalachian Mountains, Chestnut-sided Warblers outnumber Golden-winged Warblers by $\geq 5:1$ (JAJ and LS, pers. obs.).

Here, we use reflectance spectrometry coupled with models of avian vision to test whether birds should be able to discern color differences in the crown plumage of Golden-winged and Chestnut-sided warblers. To date, no study has quantitatively assessed aggressive behaviors between these warblers or their causes. This study represents a first step in understanding whether plumage-based misidentification is likely to occur between warblers or whether there is an underlying niche overlap. As populations of Golden-winged Warblers are experiencing accelerating declines, increased research on species sympatry is needed to better understand potential causes of reduced productivity and survival.

METHODS

Data Collection.—Museum specimens are a valuable tool for researchers (Winker 2004); reflectance spectra measured from plumage of museum specimens display similar variation to that found in wild birds (Doucet and Hill 2009). From October–December 2013, we measured plumage reflectance of museum study skins of 59 after-hatch-year male Golden-winged and 70 after-hatch-year male Chestnut-sided warblers collected during the breeding season. We choose males that were collected during April–June, to ensure that we did not use hatch-year males in our study, as aggressive interactions between species has only been observed with birds that have survived at least one migration attempt to the breeding grounds; our final sample likely included second-year and after-second-year birds.

The measurements were taken at the North Carolina Museum of Natural Sciences and additional study skins were provided by the Field Museum of Natural History, American Museum of Natural Science, Academy of Natural Sciences, and Carnegie Museum. We avoided study skins that were noticeably dirty, likely because of collection in areas with increased coal production. Because museum specimens are subject to degradation over long periods of time (Armenta et al. 2008, Doucet and Hill 2009), we recorded collection year. Because plumage color often

TABLE 1. Sample sizes of study skins of Golden-winged and Chestnut-sided warblers across geographic range and time.

	Golden-winged Warbler			Chestnut-sided Warbler		
	North App	South App	Great Lakes	North App	South App	Great Lakes
<1920	18	1	2	43	6	1
1921–1980	10	1	0	10	2	1
>1980	21	6	0	2	4	1

varies with geography (Johnston 1966, Hill 1993, Doucet and Hill 2009), we recorded geographic region of collection and grouped the data into three categories: northern Appalachian Mountains (PA and North), southern Appalachian Mountains (WV and South) and the Great Lakes regions (west of PA). Because of the scattered availability of study skins for loan, the sample sizes per geographic region and era are varied (Table 1).

Spectral Measurements.—We measured crown plumage reflectance with an Ocean Optics reflectance spectrometer (S2000: Range 250–880 nm: Dunedin, FL, USA) equipped with a deuterium bulb (UV light source) and a tungsten-halogen light source (visible light source), using SpectraSuite software (Ocean Optics). We used a micron fiber-optic probe held from the sample at a 90° angle to the birds' crown (Siefferman and Hill 2003). We generated reflectance measurements relative to a white standard (100% reflectance from 300–700 nm). To reduce variance, each reading was from an average of 20 sequential reflectance curves (Siefferman and Hill 2003). This was replicated three times, measuring a different location of the yellow crown at least 1 mm apart for each sample.

Carotenoid colors are represented often in wood warblers and these plumage patches are located in discrete regions that function in inter- and intraspecific communication (reviewed in Morse 1989, McNett and Marchetti 2005). Because we assume this yellow plumage is carotenoid based (reviewed in McGraw 2006, Owens 2006), we quantified the yellow crown color using the carotenoid chroma descriptor of reflectance spectra: carotenoid chroma = $(R_{\lambda 450} - R_{\lambda 700})/R_{\lambda 700}$, where $R_{\lambda i}$ is the percent reflectance at the i^{th} wavelength (λ_i) (Montgomerie 2006).

Vision Model Measurements.—To test whether the crown plumage is distinguishable between warblers, we ran the full-spectrum (300–700 nm) reflectance data through models of avian vision:

Perceptual, Analysis, Visualization, and Organization of Spectral Color Package (pavo) in the R v.3.0.2 statistical program (Maia et al. 2013, R Development Core Team 2013). It is important to note that pavo does not take into account the year of collection, which is important for carotenoid based colors that fade over extended periods of time (Armenta et al. 2008, Doucet and Hill 2009). Spectral sensitivity has not been measured in wood warblers. However, as most bird species have ultraviolet sensitive (UVS) cones (reviewed in Cuthill 2006), we used the default average UV visual system function (avg.uv) in pavo; the avg.uv function is based on the average peak sensitivity found in birds that have the UV type of visual system (Endler and Mielke 2005; Maia, pers. comm.).

To estimate distinguishability, we used two statistics in pavo. First, we used the voloverlap function to calculate the area of overlapping tetrahedral colorspace in both species. This function is useful for examining whether species occupy similar or different sensory systems by the amount of volume overlap exhibited (Stoddard and Prum 2008, Stoddard and Stevens 2011, Maia et al. 2013). Second, we used the color distance function, coldist, to calculate color distances with receptor noise based on the relative photoreceptor density between species (Vorobyev and Osorio 1998). To do this, we used relative cone abundances for the European Starling (*Sturnus vulgaris*; Hart et al. 1998, Maia et al. 2013) and set the Weber fraction to a value of 0.05 (Vorobyev and Osorio 1998, Vorobyev et al. 1998). The coldist function calculates chromatic differences (i.e., shape of the curve [ΔS]) and achromatic differences (overall % reflectance [ΔL]). With a threshold value of 1.0, calculated color values that exceed the threshold will be more likely to be noticeably different (see Vorobyev and Osorio 1998, Vorobyev et al. 1998 for color calculations). Achromatic differences are calculated based on the double cones

TABLE 2. Three-way analysis of variance table between Golden-winged Warblers and Chestnut-sided Warblers across era and geographic region. Bolded text represents significant relationships.

Source	df	SS	MS	F	P
Model	15	0.2489	0.0166	5.6	<0.001
Species	1	0.1614	0.1614	54.8	<0.001
Era	2	0.0279	0.0139	4.7	0.01
Species*Era	2	0.0468	0.0234	8.0	<0.001
Region	2	0.0096	0.0048	1.6	0.20
Species*Region	2	0.0007	0.0003	0.1	0.89
Era*Region	4	0.0010	0.0003	0.1	0.99
Species*Era*Region	2	0.0015	0.0007	0.3	0.78
Error	133	0.3326	0.0029	5.6	<0.001

responsible for chromatic processing (Siddiqi et al. 2004); we used the double cone abundance for European Starlings in this study (Hart et al. 1998).

This model incorporates information about ambient lighting conditions (i.e., blue-sky vs. forest shade vs. standard [D65] lighting). Because we found no significant difference between lighting, we examined all visual models under both the bluesky and forestshade light environments (Endler and Mielke 2005). Blue-sky represents a lighting condition that best mimics our field site where both warblers defend territories and aggressively interact with one another. Forest shade is a more conservative approach in this model but also represents approximately half of the field site, as territories are adjacent to mature forests (Confer et al. 2011, Richardson and Brauning 2013).

Statistical Methods.—We categorized our study skins into three eras: pre-1920, 1921–1980, and post-1980. To assess the importance of time and region on plumage coloration, we used a three-way ANOVA (proc glm, SAS Institute Inc. 2011) where species, era, and geographic region were the independent variables and carotenoid chroma was the dependent variable. Remaining statistical analysis and graphics for carotenoid chroma was performed in SPSS v.21 (IBM Corp. 2011). Vision model analyses were performed in R

v.3.0.2 (R Core Team 2013) and were graphically represented using pavo (Maia et al. 2013). We removed outliers from our analysis that were ≥ 2 standard deviations from the mean.

RESULTS

Spectral Reflectance Analysis.—We found no statistically significant interactions between the species type and geographical region of collection on carotenoid chroma ($P = 0.88$), but there was a significant interaction between species and year ($P < 0.001$; Table 2). Thus, we removed geographical region from future analyses and accounted for era in our analysis. Independent samples *t*-test revealed that carotenoid chroma varied significantly between Golden-winged and Chestnut-sided warblers across all eras ($P < 0.01$; Table 3; Fig. 1).

Vision Model Analysis.—Golden-winged Warblers have greater reflectance of carotenoid chroma (450–700 nm) than Chestnut-sided Warblers but reflect less UV (Fig. 2). Using the voloverlap function, we determined the volume of spectral overlap between both warblers to be 32.2% under bluesky illumination (Fig. 3) and 33.2% under forestshade. Using coldist, we determined the just noticeable difference values for Chestnut-sided and Golden-winged warblers:

TABLE 3. Comparison of carotenoid chroma ($(R_{\lambda 450} - R_{\lambda 700})/R_{\lambda 700}$) derived from the spectral reflectance measurements of the crown plumage of Golden-winged (GWWA) and Chestnut-sided warblers (CSWA), separated by collection era.

Era	Mean %reflectance (SD): GWWA	Mean %reflectance (SD): CSWA	df	t	P
<1920	0.914(0.05)	0.872(0.05)	67	3.09	0.003
1921–1979	0.896(0.05)	0.832(0.02)	19	3.59	0.002
>1980	0.952(0.03)	0.823(0.03)	31	9.04	<0.001

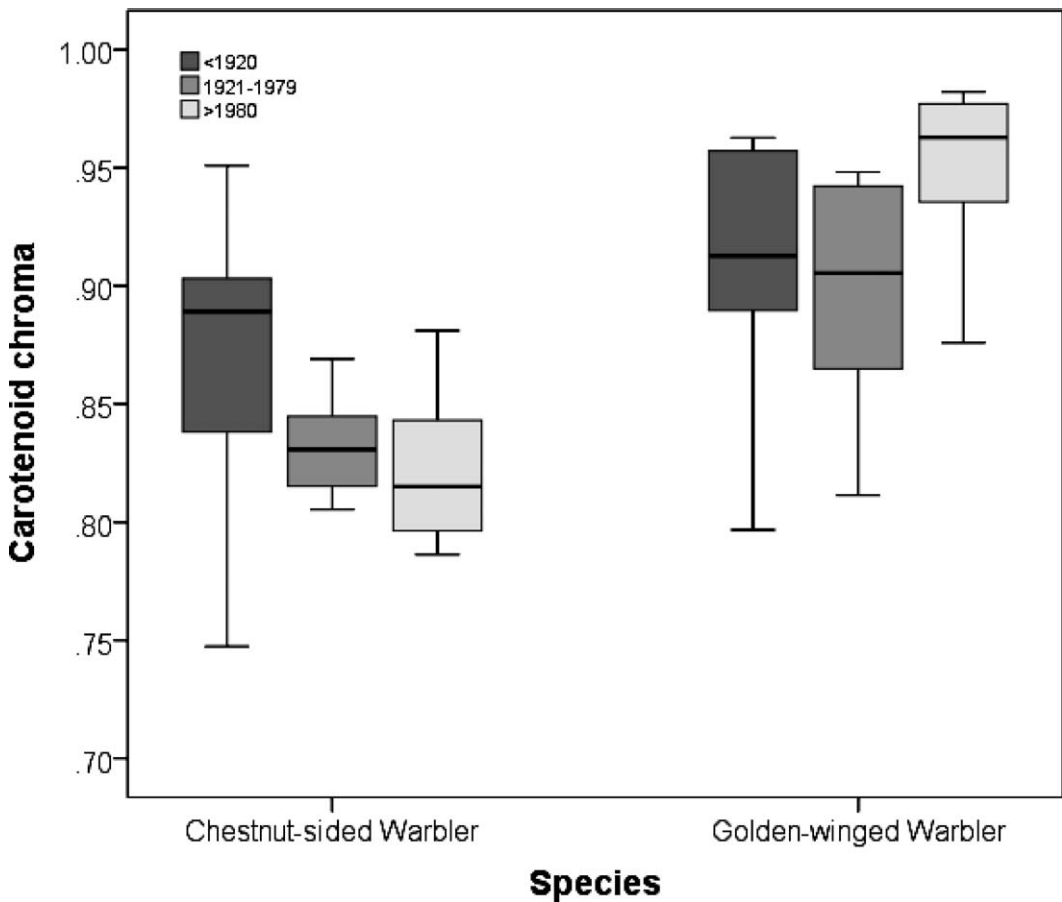


FIG. 1. Comparison of carotenoid chroma ($(R_{\lambda 450} - R_{\lambda 700})/R_{\lambda 700}$) derived from spectral reflectance of the crown coloration of Golden-winged ($n = 58$) and Chestnut-sided ($n = 68$) warblers. Samples are divided into the three most abundant time eras. Crowns belonging to Golden-winged Warblers reflect significantly more carotenoid chroma than those of Chestnut-sided Warblers across all eras ($P < 0.01$).

bluesky: $\Delta S = 8.25$ and $\Delta L = 1.73$ (Fig. 2); forestshade: $\Delta S = 7.85$ and $\Delta L = 2.49$.

DISCUSSION

Two lines of evidence suggest that plumage-based misidentification is unlikely to occur between these two wood warbler species. First, carotenoid chroma differed between the two species suggesting that the plumage coloration is not identical. Although there was an interaction between species carotenoid content and year of collection, Golden-winged Warblers reflected significantly more light across the yellow-red spectrum across all time frames, suggesting that these data will result in accurate results in pavo. Second, the results of the models of avian vision (Maia et al. 2013) suggest that species-specific

differences in plumage coloration should be distinguishable to the warblers. We found only 32.2% of the volume of the colorspace overlapped between species crown color. Color distance analysis suggests that the chromatic distances (i.e., shape of reflectance curves) far exceed the threshold (1.0) for notably different color between warbler species in illumination settings that mimic a blue sky as well as forest cover. Additionally, achromatic differences (overall % reflectance) exceed threshold for notable differences in both settings, but even more so in shaded environments, suggesting that misidentification should be even less likely when under forest cover. Together, these results suggest that carotenoid-based yellow plumage is significantly different between warblers, and the birds should be able to

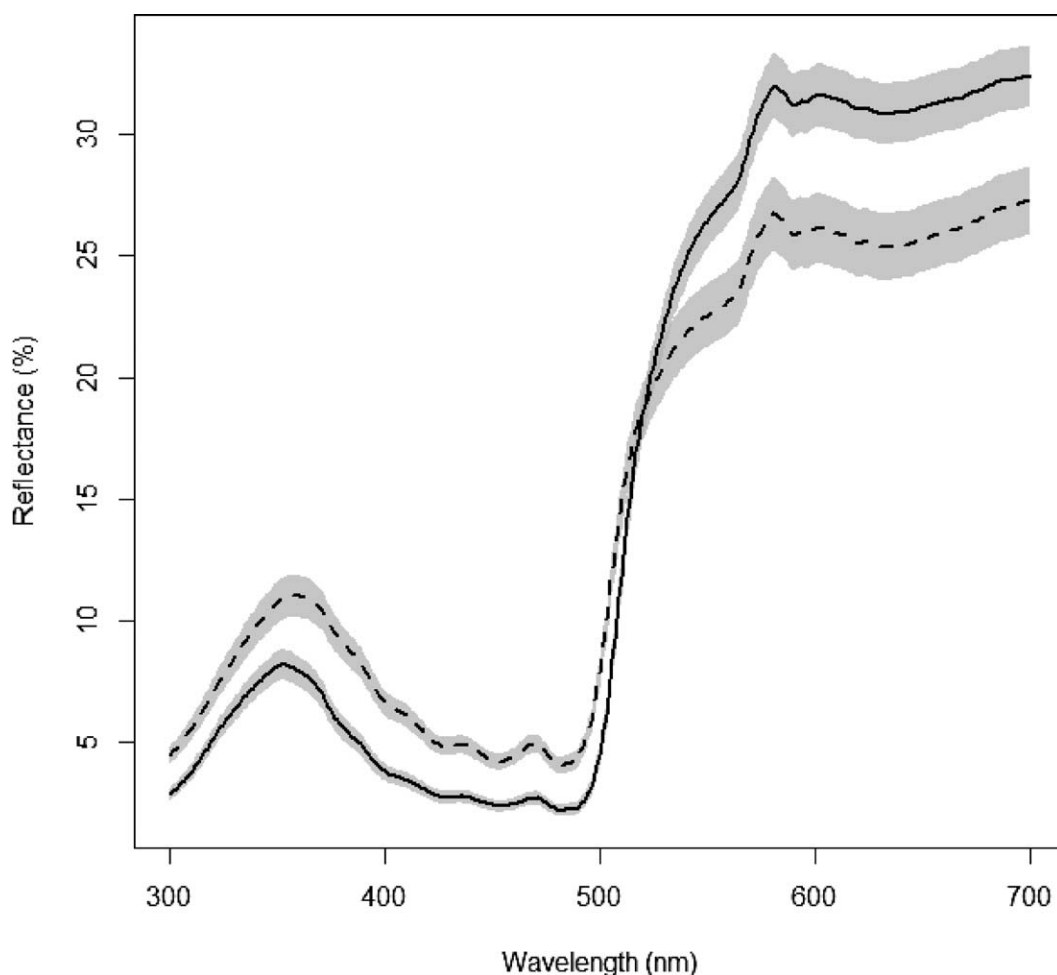


FIG. 2. Mean (\pm SE) reflectance spectra of crown plumage of Golden-winged (solid line) and Chestnut-sided (dashed line) warblers.

distinguish the chromatic and achromatic differences between Chestnut-sided and Golden-winged warblers.

Interpretation of our data necessitates that we assume that museum specimens represent color variation in wild birds. Indeed, Doucet and Hill (2009) found that differences between the plumage coloration of wild birds and museum skins are generally small. McNett and Marchetti (2005) found that wood warbler museum skins tend to be duller than wild birds, likely caused by a reduction in UV reflectance. Typical of yellow carotenoid-based plumage, the spectral reflectance of the crown of both Golden-winged and Chestnut-sided warblers reflects some UV wavelengths, but the yellow-red region reflects much more light (Fig. 2).

We attempted to account for factors that may influence our dataset, such as geographic variation, age at death, and age of the study skin; we included collection year, collection location into our analysis, and only measured after-hatch-year birds collected during the breeding season (Doucet and Hill 2009). First, there was no significant interaction between geographic region and species on reflectance across all eras, suggesting minimal geographic variation exists in these species. Second, our results are consistent with the findings of Armenta et al. (2008); less fading occurred in specimens collected within 50 years. Our oldest study skins were among the most degraded, and showed the greatest variation in carotenoid chroma. However, although we saw increased variation in plumage coloration within

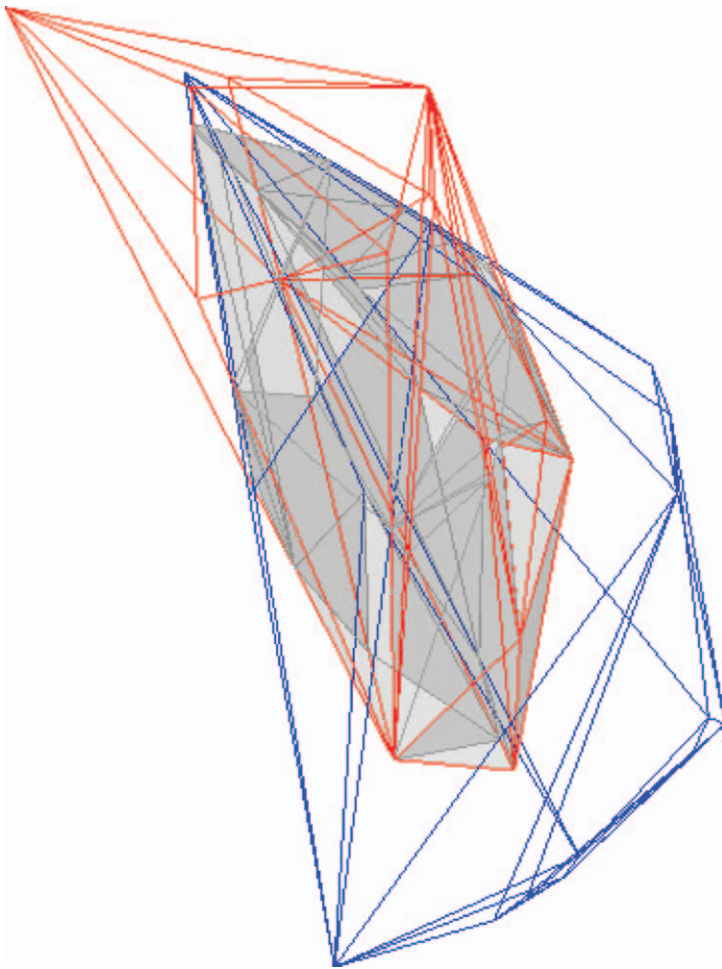


FIG. 3. Volume of overlapping colorspace between Golden-winged Warblers (red, top) and Chestnut-sided Warblers (blue, bottom). Both warblers overlap $\sim 32.2\%$ in tetrahedral colorspace; grey regions indicate overlapping regions.

the oldest era, in all eras, Golden-winged and Chestnut-sided warblers were distinguishable. Finally, although we did not split our dataset by the bird's age, we found that plumage coloration was always distinguishable between the two species. We caution that not having age data is a limitation of this study; it may be the 32.2% overlap in spectral tetrahedral colorspace found between species are representative of the oldest (and assumed brightest) Chestnut-sided Warblers and the youngest (dullest) Golden-winged Warblers.

This study represents the first attempt to understand the stimuli that promote agonistic interactions between Golden-winged and Chestnut-sided warblers. Our data suggest that agonistic

interactions between Golden-winged and Chestnut-sided warblers are unlikely to be the result of plumage misidentification. However, misidentification based on similarity of behaviors may still exist, and thus promotes the aggressive responses (Ord et al. 2011). Moreover, although the majority of plumage between species is distinct, carotenoid-based crown feathers may play an important role in animal communication in wood warblers (Morse 1989). Thus, although the plumage coloration should be distinguishable between species, these colors may play a role in competitive interactions.

Alternatively, these aggressive behaviors may derive from competition associated with overlapping ecological niches. The breeding ranges

(Sauer et al. 2012) and habitat requirements (Collins et al. 1982) of these two warblers overlap extensively. Chestnut-sided Warblers are mid-successional habitat generalists in the southern Appalachians (JAJ, pers. obs.), and occur in locations disturbed by humans as well as in areas with minimal human impact, whereas Golden-winged Warblers require specific early-to-mid successional habitat types (Confer et al. 2011) and rarely occur in areas disturbed by humans (JAJ, pers. obs.). As agonistic behaviors between these two species are not consistent throughout our field sites, there may be ecological factors that influence the likelihood of aggressive behaviors when these in these wood warblers occur in sympatry. A field-based study is warranted to examine how agonistic interactions correlate with the degree of niche overlap and to estimate the costs of coexistence. As habitats continue to change and/or decrease in abundance on breeding and wintering grounds, these wood warblers may be restricted to cohabitating identical territories, thus promoting increased aggression and potentially deleterious effects on the imperiled Golden-winged Warbler.

ACKNOWLEDGMENTS

We thank C. G. Smalling for providing the inspiration to conduct this research. We thank E. A. Berezniatskaia for aiding in data collection, R. Maia for assistance with running and interpreting results from pavo, and A. Surmacki, M. R. Harris, M. B. Brown, and two anonymous reviewers for suggestions on revisions on earlier versions of this manuscript. Additionally, we are grateful for J. Gerwin and B. O'Shea at the North Carolina Museum of Natural History for their hospitality as well as hosting additional specimens from cooperating museums. This study would not have been possible without N. Rice at the Academy of Natural Sciences, J. Kirchman at the American Museum of Natural Sciences, B. Marks from the Field Museum of Natural History, and S. Rodgers of Carnegie Museum loaning additional warbler study skins to North Carolina. Finally, we thank the Graduate Student Association of Senators as well as the Office of Student Research at Appalachian State University for providing funding.

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