MORPHOLOGICAL AND ECOLOGICAL CAUSES OF INTERSPECIFIC AGGRESSION
BETWEEN GOLDEN-WINGED AND CHESTNUT-SIDED WARBLERS

A Thesis
by
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Abstract

MORPHOLOGICAL AND ECOLOGICAL CAUSES OF INTERSPECIFIC AGGRESSION
BETWEEN GOLDEN-WINGED AND CHESTNUT-SIDED WARBLERS

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Interspecific aggression is widespread throughout the animal kingdom, yet research
that documents the evolutionary and ecological consequences remains limited and unclear.
Aggressive behaviors are often indicative of an ecological niche overlap between
morphologically and ecologically similar species, which can cause interference competition
between animals. Competition between interspecifics has the potential to significantly
influence community structure, particularly if a competitively dominant species excludes the
subordinate species from resources required for their reproductive success. Thus, for species
of conservation concern, research focusing on interspecific behavioral interactions is critical.
Golden-winged warblers (*Vermivora chrysoptera*) frequently engage in agonistic interactions
with chestnut-sided warblers (*Setophaga pensylvanica*) in the southern Appalachian
Mountains, yet these aggression between warblers has been undocumented to date. Although
morphologically distinct in many regions, these species share a similar signaling space (i.e.,
yellow crown coloration). Here, I explore two potential explanations of interspecific
aggression between these wood warblers (Aves: Parulidae): mistaken identity and

interspecific competition. I used museum and field data and used both ecological modeling and experimental field methods to investigate the cause of interspecific aggression. First, using museum specimens, I found that the crown plumages of both warblers are two distinct shades of yellow that both warbler species should theoretically be able to distinguish. Next, I studied these warblers for two field seasons. First, I investigated whether golden-winged warblers suffered fitness consequences of sympatry with high densities of chestnut-sided warblers (summer 2014). Second, I investigated whether each species was misidentifying heterospecific models as conspecific intruders (summer 2015). I found that golden-winged warblers were more aggressive when settling in areas of high chestnut-sided warbler density, but heterospecifics did not have a negative influence on their overall reproductive success. Instead, I found that the structure of territory habitat best predicted reproductive success. These results suggest that interspecific competition for limited resources is unlikely to be the cause of agonism between the two species. Next, using models of birds presented to territorial birds in the field, I found that both warblers were equally likely to attack the 'correct' (conspecific) and 'incorrect' (heterospecific) model and that the individuals that were more likely to attack the heterospecific model displayed more aggressive phenotypes. These results suggest that, from the perspective of the golden-winged warbler, competition is unlikely to occur and interspecific aggression is a function of mistaken identity. Yet, without net gains from behaving as such, these behavioral traits between warblers may drive crown morphology to become more distinctive to reduce species recognition errors.

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I first have to thank my parents, Jennifer and Michael Garzo, for their never-ending love and support. Although my three brothers and I grew up in a relatively low-income household, they never stopped pushing me to be the best I could in terms of education. I am not sure if I would have pursued an academic career without them supporting me every step along the way. I am sorry I did not visit home as often as I would have liked to, but I hope that I have made you proud. I am also grateful for the family that I have adopted since I've spent my time at Appalachian State University. I wouldn't be the biologist I am today without the guidance from my graduate advisor, Dr. Lynn Siefferman. Although initially hesitant to accepting me into her lab, she has been instrumental in helping me become an ecologist. She never stopped helping me write grants and write up my research, no matter how rough (and numerous) the drafts were. Most importantly, I thank her for trusting me to design and carry out my own research. The ability to think about the design, its flaws and significance, and carry it out with a mostly laissez-faire attitude has allowed me to be confident in my own ability as a student, writer, and biologist. She had high expectations of me and challenged the way that I thought about the natural world in numerous ways. Thank you for always being there when I needed it. I also thank my committee members, Drs. Susan Lappan and Barbara Ballentine, for their support and fantastic advice and guidance in areas of expertise that I am not as well versed in. And, although not technically not on my committee, I am grateful for the advice I have received from Dr. Mike Gangloff on study design and writing critiques. I also thank Dr. Jeffery Larkin and Curtis Smalling for their financial and intellectual support throughout my research. The members of the Siefferman-Gangloff lab at Appalachian State University have been instrumental in keeping my sanity

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Foreword

Chapter 2 of this thesis has been submitted and published in *The Wilson Journal of Ornithology*, a peer-reviewed journal published by The Wilson Ornithological Society. Chapter 3 has been submitted for publication in *Animal Behaviour*, a peer-reviewed journal published by Elsevier. Both chapters have been formatted according to the style guide for their respective journal.

CHAPTER 1

General Introduction

Some of the greatest challenges facing modern conservation biologists are how to mitigate losses of biodiversity and prevent further population declines of at-risk species (reviewed in Cardinale et al. 2012). To effectively manage these species, examinations of how individuals interact with both biotic and abiotic factors within an ecosystem and potential behavioral interactions between heterospecific species are often warranted. Indeed, it has become increasingly clear that, for many animal conservation problems, behavioral research is imperative (reviewed in Linklater 2004). Although such research can better explain how animals persist in rapidly changing ecosystems, behavioral ecologists are often hesitant to combine their research agendas with that of conservation biologists (reviewed in Caro and Sherman 2013). Yet, when animal species are threatened with extinction, failure to examine their behavioral ecology may result in inadequate management practices that may be inadvertently detrimental to the recovery of that species (Anthony and Blumstein 2000). In particular, a better understanding of how behavioral characteristics influence community structure and the outcome of interspecific interactions could aid conservation efforts for species at-risk.

In biological systems, three broad types of interactions can occur between species: competition, predation/parasitism, and mutualism (reviewed in Dhondt 2012). While the importance of predation, parasitism, and mutualism are generally accepted as major drivers of community structure, the evolutionary significance of interspecific competition is often debated and understudied (reviewed in Dhondt 2012, Grether et al. 2013). Yet, failure to

examine the ecological consequences of sympatry between threatened and abundant species may result in inadequate management practices, and ultimately, failure to restore or maintain populations. When interspecific aggression is common between sympatric animals, competition is often inferred; aggression is thought of as a product of intense competition for shared and limited resources (reviewed in Dhondt 2012; e.g., Martin and Martin 2001a, b). Indeed, aggressive behaviors (i.e., physical bouts comprised of dives, bites, etc.) associated with access to limited resources is the predominant mode of interference competition between animals (reviewed in Grether et al. 2013).

Interspecific aggression is widespread in nature and is often as costly and intense as intraspecific aggression (Ords and Stamps 2009, Peiman and Robinson 2010). Thus, although not as widely studied as other interspecific interactions (e.g., mutualism), it is intuitive that interspecific aggression should yield important proximate and ultimate consequences (reviewed in Grether et al. 2013). For example, intense interspecific aggression exerted by competitively dominant taxa may result in the exclusion of subordinate taxa from required resources (e.g., Miller 1964, Murray 1981). As such, interference may drive selection of sympatric species such that (1) resource overlap is reduced (e.g., differences in temporal scale and/or habitat preference) or (2) traits associated with competitor recognition diverge (e.g., ornamentation, song; Peiman and Robinson 2007, Grether et al. 2009). Until recently, traits associated with species recognition and the ecological consequences of interspecific aggression have been largely understudied (but see Grether et al. 2009, Grether et al. 2013).

Interspecific aggression may be a product of misdirected conspecific competition, such that animals mistakenly interact aggressively with heterospecifics because those individuals have similar cues used in conspecific interactions. However, because the costs

and benefits of appropriately responding with aggression towards heterospecifics are often species-specific, the adaptive nature of mistaken identity is unclear (Ord et al. 2011). For example, if two species are ecological competitors, then selection should act on sympatric animals to converge in characteristics associated with competitor recognition because it may be beneficial to more easily spot heterospecific competitors (Cody 1969, Grether et al. 2009), as seen in meadowlarks (*Sturnella* spp.; Rohwer 1973) and southern Appalachian *Plethodon* salamanders (Nishikawa 1985, 1987). In contrast, if species do not compete, but interact aggressively, the associated costs of mistaken identity may select for recognition traits to diverge (Lorenz 1962, Grether et al. 2009, 2013). Here, agonistic character displacement explains morphological divergence: to costs of intense interspecific aggression should result in selection for divergence in traits that influence the rate of mistaken identity (Grether et al. 2009). This is analogous to ecological character displacement (Brown and Wilson 1956), but differs in the mechanism. Brown and Wilson (1956) suggested that ecological character displacement is a result of exploitative (indirect) competition, but that interference may evolve as an alternative to displacement. That is, they did not consider that selection would act to reduce the occurrence of agonism directly to accentuate species differences (reviewed in Grether et al. 2013).

Understanding the stimulus of aggression is imperative for species that are of conservation concern. For example, the golden-winged warbler (*Vermivora chrysoptera*) is a songbird that is rapidly declining throughout eastern North America, and it often engages in physical confrontations with the morphologically similar (and comparatively abundant) chestnut-sided warbler (*Setophaga pensylvanica*). Both wood warblers initiate agonistic interactions, but these behaviors occur inconsistently; the two species are often observed

singing from adjacent perches (pers. obs.). Nonetheless, to date, behavioral interactions between these wood warblers have yet to be studied in a systematic function. This is perplexing because both warblers occupy nearly identical breeding ranges (Sauer et al. 2014) and have similar habitat requirements (Collins et al. 1982, Confer et al. 2011, Richardson and Brauning 2013). If interspecific aggression occurs because of competition for limited resources, then the failure to investigate these behavioral traits may hinder golden-winged warbler conservation efforts.

Golden-winged warbler populations have declined significantly throughout most of the breeding range, but the Appalachian populations are experiencing the most precipitous declines (>40% decline since 1966; Sauer et al. 2014). In North Carolina, populations have declined by ~10.5% year^{-1}. Thus, the golden-winged warbler is one of the most rapidly declining, non-federally endangered birds in eastern North America (Buehler et al. 2007). The majority of breeding populations (~90%) occur between southeastern Canada and the Great Lake regions, whereas fewer populations occur in the Appalachian Mountains, generally occurring at ≥900 m in the southern Appalachians (Confer et al. 2011, Roth et al. 2012). The decline of the golden-winged warbler is largely attributed to habitat loss throughout their breeding and wintering range (Confer et al. 2011, Roth et al. 2012). Their nesting habitat is dependent on disturbance, but onset of forest regeneration and active fire suppression has limited such habitat types (Klaus and Buehler 2001). As early successional habitats are increasingly lost, aggressive behaviors may be increasingly to secure limited territories – assuming that warblers are competing for access to higher quality habitat types.

Like the golden-winged warbler, chestnut-sided warblers nest in early successional habitats (Richardson and Brauning 2013). However, preliminary observations suggest that

chestnut-sided warblers are not as limited to specific patches of shrub as golden-winged warblers and may be more of a successional habitat generalist, although requirements for habitat selection in both species are suggested to be nearly identical (at the individual territory scale; Collins et al. 1982). Although chestnut-sided warblers are experiencing slight, but statistically significant, declines range-wide (annual declines: -1.4% year^{-1} from 1966-2012; Sauer et al. 2014), they are an abundant species in the southern Appalachian Mountains, outnumbering golden-winged warblers by ≥5:1 (pers. obs.).

Both species have markedly distinct song and plumage characteristics, with obvious color and pattern differences occurring across their backs, wings, faces, chins and the underside of their wings. However, to humans, the yellow coloration of the crown plumage of golden-winged and chestnut-sided warblers appears identical. It may be that the crown coloration is not obviously different from the bird's perspective and causes these heterospecifics to misidentify each other as conspecifics. However, if plumage-based misidentification were to occur between birds, the colors would likely reflect light similarly across the avian visual spectrum. Yet, morphometrics alone may not be the only criteria for species discrimination; 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 hetero-specifics.

Here, I focus on determining the stimulus of aggression between golden-winged and chestnut-sided warblers in the southern Appalachian Mountains of western NC and eastern TN. To answer this, I investigated whether aggression could be a product of mistaken identity based on crown plumage coloration (Chapter 2, 3) or interspecific competition (Chapter 3). I used a combination of reflectance spectrometry, avian vision models, and

model (i.e., dummy) birds to investigate the likelihood of mistaken identity. In the field, I monitored golden-winged warbler populations to determine if they suffered from sympatry with high densities of chestnut-sided warblers. Because aggression is a costly behavior (Moyer 1968), golden-winged warblers should experience selection to avoid aggression if there is no net benefit conveyed in behaving aggressively. However, if these species are competing, then my research could help develop management strategies to reduce sympatry and promote higher quality golden-winged warbler habitat.

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CHAPTER 2

Agonistic Behaviors between Chestnut-sided Warblers (*Setophaga pensylvanica*) and Golden-winged Warblers (*Vermivora chrysoptera*) are Unlikely a Result of Plumage Misidentification[1]

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

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[1] Jones, JA and L Siefferman. 2014. Agonistic behaviors between chestnut-sided (*Setophaga pensylvanica*) and golden-winged warblers (*Vermivora chrysoptera*) are unlikely a result of plumage misidentification. Wilson Journal of Ornithology, 126(4):708-716.

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 phylogenic 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.

INTRODUCTION

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 human retinas (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 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 also 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.). Indeed, 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 not 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) with 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% year^{-1} from 1966–2011, $P <0.05$), while Chestnut-sided Warbler declines are less extreme (-1.4% year^{-1} 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 logical first step in

understanding whether plumage-based misidentification is likely to occur between warblers

or whether there is an underlying niche overlap. As Golden-winged Warbler populations 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), and thus, are appropriate for this

study. 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 (i.e., in the United States). 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. Thus, 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 shipped from 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. Moreover, because plumage color often varies with geography (Hill 1993, Johnston 1996, 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 to North Carolina, 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 both 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; Labsphere, Inc.). To reduce electrical noise, 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 ith 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 Core Team 2013).

However, 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 yet

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 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. Additionally, 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) wherein

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: `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

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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 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 the oldest era, in all eras, Golden-winged and Chestnut-sided warblers were distinguishable to birds. 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. However, 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.). Additionally, 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 quantitatively 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.

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TABLES

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

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

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**

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.

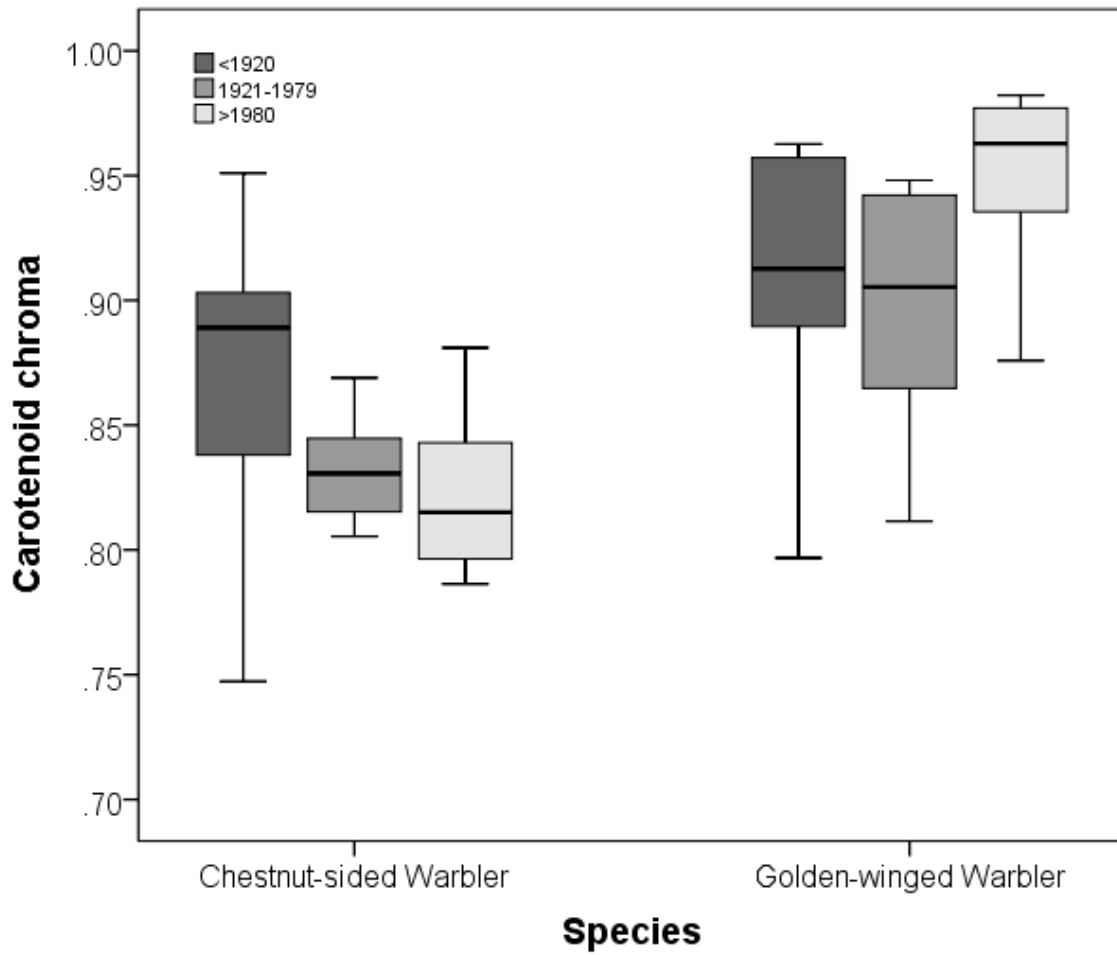| Era	Mean %reflectance (SD): GWWA	Mean %reflectance (SD): CSWA	df	t	P
<1920	0.914(0.05)	0.872(0.05)	67	3.09	0.003
1921– 1979	0.896(0.05)	0.832(0.02)	19	3.59	0.002
>1980	0.952(0.03)	0.823(0.03)	31	9.04	<0.001

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 ($P < 0.01$).
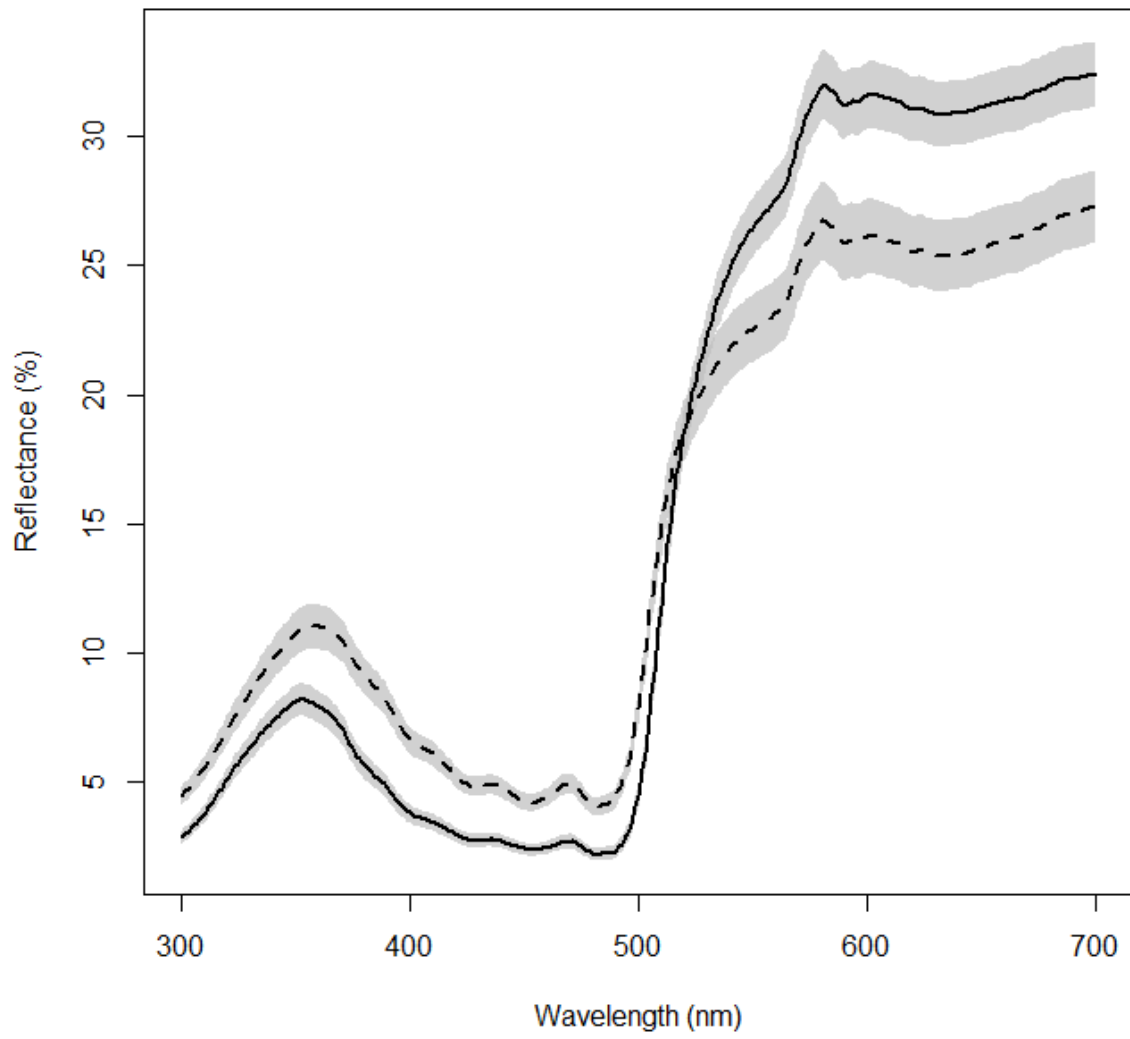
FIG. 2. Mean ($\pm$ SE) reflectance spectra of crown plumage of Golden-winged (solid line) and Chestnut-sided (dashed line) warblers.
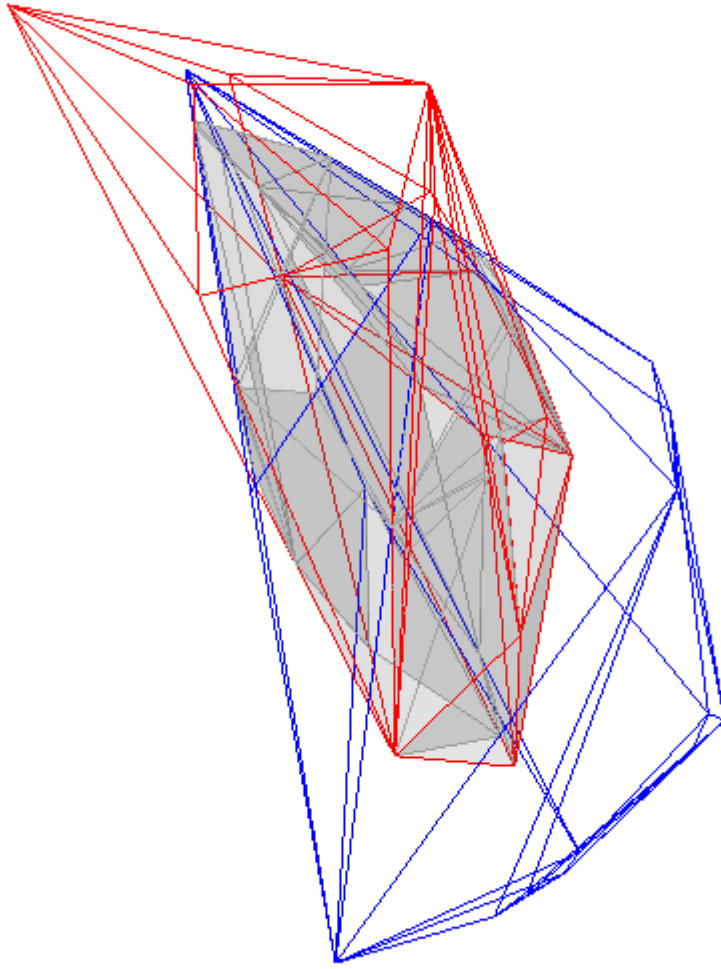
FIG. 3. Volume of overlapping colorspace between Golden-winged Warblers (red, top) and Chestnut-sided Warblers (blue, bottom). Both warblers overlap ~32.2% in tetrahedral colorspace; grey regions indicate overlapping regions.

CHAPTER 3

A Case of Mistaken Identity: Understanding the Stimulus of Agonism between Two Wood Warblers

ABSTRACT

When multiple species occur sympatrically, divergence in morphological and behavioral traits associated with species recognition and resource use are expected. Individuals that engage in interspecific aggression often suffer fitness consequences if the benefits of securing resources do not outweigh the risks associated with agonism. In the southern Appalachians, interspecific aggression frequently occurs between chestnut-sided (*Setophaga pensylvanica*) and golden-winged (*Vermivora chrysoptera*) warblers, a species that is experiencing sharp declines in population numbers. Using a combination of correlative and experimental approaches, we explored two potential explanations for interspecific aggression: interspecific competition and mistaken identity. It is commonly inferred that aggressive interactions are the product of competition due to an ecological niche overlap. However, because these warblers have similar crown coloration and aggressive interactions appear stochastic, aggression may be a result of mistaken identity. First, in 2014, we documented spatial overlap of the two species and measured reproductive success and habitat preference (using remote sensing) of golden-winged warblers. We found that golden-winged warblers that settled among high densities of chestnut-sided warblers were more aggressive, but chestnut-sided warbler density did not negatively influence their reproductive success; rather, habitat structure best predicted reproductive success. Next, in 2015, we tested for misidentification using models of con- and hetero-specifics in simulated territorial intrusions. We found that the warbler species were equally likely to attack the con- and hetero-specific

models, and that the most aggressive individuals were more likely to attack models. Our data suggest that, from the golden-winged warbler's perspective, sympatry is not detrimental and aggression is likely a function of mistaken identity. Yet, these behavioral interactions should be maladaptive, which may lead to the segregation of habitat types or divergence in crown morphology between species.

INTRODUCTION

When sympatric species interact aggressively, underlying resource overlap is often inferred and aggression is thought to be a product of interference competition for limited resources (e.g. Rice 1978, Catchpole and Leisler 1986, Martin and Martin 2001a, Peiman and Robinson 2010, Grether et al. 2013). Heterospecifics can compete over food (e.g. Minot 1981, Pimm et al. 1985) and nesting locations (e.g. Harris and Siefferman 2014), and sympatry can lead to increased nest predation rates (e.g. Martin 1993, Martin and Martin 2001b). Despite the assumption that the intensity of intraspecific aggression is typically greater, aggression between species often yields equally intense and costly consequences (Duckworth 2006, Ord and Stamps 2009, Peiman and Robinson 2010, Grether et al. 2013). Aggressive interspecific competition for limited resources may undermine the realized habitat quality of a particular territory (Johnson 2007); selection may act on individuals to choose between territories that are either higher physical quality (e.g. more preferred vegetative structure) with high densities of interspecific competitors or areas with fewer competitors but in suboptimal habitat (e.g. Martin and Martin 2001b, Jones et al. 2014). Agonistic interactions resulting from interference competition should drive character displacement (reviewed in Grether et al. 2009). That is, selection should drive divergence of traits associated with species recognition

until interspecific aggression is reduced (Orians and Wilson 1964, Grether et al. 2009). Indeed, a global analysis of avian plumage characteristics found that species that breed in sympatrically tend to show high levels of color divergence that follow patterns of character displacement (Martin et al. 2015).

As the costs and benefits of aggression are context dependent (Moyer 1968, Andersson et al. 1980, Duckworth 2006), interspecific aggression is expected to be maladaptive when the aggressor gains no net benefit (reviewed in Ord and Stamps 2009, Grether et al. 2009). An alternate hypothesis to explain interspecific aggression is mistaken identity: (reviewed in Tinbergen 1936, Murray 1971, 1981): the lack of discriminatory ability promotes misdirected conspecific aggression (i.e. misidentification) between heterospecifics. Mistaken identity may be viewed as exaptive (Gould and Vrba 1981) or maladaptive; the benefits of misdirected aggression are dependent upon whether similar species are ecological competitors (Murray 1981, Nishikawa 1987). That is, if morphologically similar species behave similarly as well as use ecologically similar resources, misdirected aggression towards heterospecifics may convey a net benefit as if they were conspecific competitors. For example, Nishikawa (1985, 1987) documents evidence for both hypotheses in two salamanders (*Plethodon jordani* and *P. glutinosus*) of the southern Appalachian Mountains, suggesting that misidentification may be exaptive. Contrarily, Korner et al. (2000) found that Waterberg flat lizards (*Platysaurus minor*) misidentify orange-throated flat lizards (*P. monotropis*) as competing conspecifics despite the absence of competitive exclusion. However, mistaken identity should be maladaptive for submissive Waterberg flat lizards because orange-throated flat lizards are likely to win aggressive confrontations.

With their high visual acuity (reviewed in Cuthill 2006), it seems perplexing that misidentification may be possible in bird taxa. Yet, Petrusková et al. (2008) document that meadow pipits (*Anthus pratensis*) misidentify tree pipits (*A. trivialis*), but only after excitation via conspecific song stimuli. That is, under normal circumstances (i.e. no apparent conspecific intruder), pipits do not appear to suffer from mistaken identity. Yet, when meadow pipits were experimentally stimulated with conspecific song, they attacked tree pipits, despite the absence of an ecological niche overlap. Their study suggests that species recognition is a product of both auditory and visual cues (Petrusková et al. 2008). Moreover, these results indicate that if interspecific aggression occurs under normal conditions between two morphologically and ecologically similar species despite the absence of competition, misidentification may be the stimulus.

In the southern Appalachian Mountains of western North Carolina (NC), agonistic interactions occur between golden-winged (*Vermivora chrysoptera*) and chestnut-sided warblers (*Setophaga pensylvanica*) and can be initiated by either species. Like many Neotropic migrants, both species are experiencing declines in overall population sizes (Homes 2007, Sauer et al. 2014). Yet, golden-winged warblers that breed in the Appalachian Mountains are experiencing particularly extreme declines (Buehler et al. 2007, Sauer et al. 2014), and thus are a species of significant conservation concern (Roth et al. 2012). For example, in NC, Breeding Bird Survey data suggest that golden-wings have declined >45% over the past decade (Sauer et al. 2014). Despite recent restoration efforts, there has been little research, to date, that focuses on how golden-winged warbler behavioral characteristics influence reproductive success, habitat selection, and community structure (Confer and Larkin 1998, Confer et al. 2011). Several factors have been identified as potential

contributors to their decline, including habitat loss (Klaus and Buehler 2001, Buehler et al.

2007) and hybridization with blue-winged warblers (*V. cyanoptera*; Vallender et al. 2009,

Confer et al. 2011). However, an overlooked potential contributor to the decline of golden-

winged warblers may be interspecific competition with non-*Vermivora* species. For example,

Martin and Martin (2001a, b) documented agonistic interactions between orange-crowned

(*Oreothlypis celata*) and Virginia's warblers (*O. virginiae*) and found fitness costs of

coexistence that extend beyond competition solely for food resources. Interspecific

competition may have similar consequences for golden-winged warbler populations when

coexisting with an aggressive congener and it has not been considered a potential contributor

of declines in this species (reviewed in Confer et al. 2011).

Because interspecific aggression is inherently risky (reviewed in Moyer 1968, Ord

and Stamps 2009, Ord et al. 2011), it is logical that aggressive interactions between golden-

winged and chestnut-sided warblers may result from competition for limited resources (e.g.

Martin and Martin 2001a), and may thus exacerbate golden-wing declines. Indeed, there is

extensive overlap in the breeding ranges of these two species (Sauer et al. 2014) and both

warbler species use early-to-mid successional habitat (Confer et al. 2011, Richardson and

Brauning 2013). At the territory-level, habitat characteristics (e.g. percent ground, shrub, and

canopy cover) appear similar (Collins et al. 1982), but these species have different nesting

requirements (i.e. substrate as well as height of nest placement) and food preferences at our

field sites (JAJ unpubl data). Thus, assessments of territory-level habitat structure should

help determine whether these warblers compete for limited resources or differ in habitat

preference (i.e. niche partitioning). If these two warbler species compete for spatial habitat

resources, then they may be increasingly limited to sympatry due to the loss of available

habitat in the southern Appalachian Mountains (Klaus and Buehler 2001). Increased

sympatry could promote negative ecological and behavioral interactions (Martin and Martin

2001a, b) and inform warbler management practices.

The underlying cause of interspecific aggression between these warblers is not clear.

First, whether these warblers compete for resources has not been tested. Second, the yellow

crown coloration of these two species should be distinguishable by birds (Jones and

Siefferman 2014; Supplemental Material, Fig. S1) but may still theoretically be the stimulus

of misidentification. One limitation to the avian vision model (Maia et al. 2013) used by

Jones and Siefferman (2014) is that it does not incorporate brief glimpses. Indeed, without an

appropriate acoustic stimuli associated with the visual observation, field researchers

frequently misidentify one species for the other when the focal bird is viewed briefly.

Although humans have trichromatic vision (whereas birds have tetrachromatic vision) and

lack the visual acuity that is found in many birds (reviewed in Cuthill 2006), it seems

plausible that the same phenomena may occur between wood warblers.

Here, we test whether aggressive behaviors between golden-winged and chestnut-

sided warblers are a product of competition for shared resources or misdirected conspecific

aggression. In 2014, using a correlative approach, we investigated whether chestnut-sided

warblers exert interspecific competition on golden-winged warblers by addressing three

questions: (1) does aggression vary with interspecific density, (2) do chestnut-sided warblers

influence reproductive success, and (3) do chestnut-sided warblers or habitat play a larger

role in reproductive success? If competition occurs between warbler species, we predict that

golden-wings would be more aggressive and suffer fitness consequences of sympatry when

their territories encompassed high densities of chestnut-sided warblers. We also predicted

that heterospecific density and habitat characteristics would jointly play a significant role in reproductive success if competition occurs. Next, we experimentally tested for misidentification in 2015 by using a combination of conspecific simulated territorial intrusions and model (i.e. dummy) birds. We further investigated whether birds with more aggressive phenotypes would be more likely to attack the opposite species.

METHODS

Study Locations and General Field Methods

From April to July 2014 and 2015, we investigated the potential for competition between both warblers in the Amphibolite and Roan ranges of the Appalachian Mountains (elevation: 850-1,645 m) of northwestern NC (Watauga, Avery, and Ashe Co.) and eastern Tennessee (Carter Co.) across seven field sites that encompass a variety of early-to-mid successional habitats (e.g. grassland, shrubland, bog) adjacent to mature hardwood forests within field sites. Most fields are adjacent to each other; we found no statistical difference in behavioral response between all sites for both species and for both years of study (one way ANOVA; all $P > 0.05$). Thus, we combined data from all field sites for statistical analyses. Males of both species were captured via mist-nets and were marked with a numbered USGS band and a unique combination of color bands for remote identification.

Assessment of Competition: 2014 Correlational Study

Estimating Chestnut-sided Warbler Density

In 2014, we focused on individual territory mapping to calculate mean heterospecific density per golden-winged territory (mean mapped points bird-1: 43 ± 21.5). We followed golden-

41

winged warbler males and recorded GPS location data of perches. We obtained ≥30 mapped

points per bird across ≥30 days to reliably estimate their territory size (Seaman et al. 1999,

Barg et al. 2004). Spatial boundaries of each male's territory was generated using the

'genmcp' command in Geospatial Modelling Environment (Beyer 2009) and imported into

ArcMap 10.1 (ERSI, Redlands, CA, USA).

We conducted avian census surveys (hereafter: point counts) of chestnut-sided

warblers while golden-winged warbler territory mapping was ongoing (May 9 – May 16,

2014). In ArcMap 10.1, we delineated locations of our field sites that were classified as

'nesting habitat' for golden-winged warblers (Roth et al. 2012); nesting habitat was defined

as shrubby areas that were adjacent to forest cover throughout our field sites with *a priori*

knowledge of vegetation structures in which golden-wings were likely to nest. To prioritize

our efforts, we conducted point counts throughout the delineated nesting habitat because

these areas were the most likely to have golden-winged warblers.

We overlaid the nesting habitat layer with a 0.4 ha grid and assigned one random

point count location per grid (points were set to be >30 m apart). At these locations, one

researcher (JAJ) conducted 3 min passive point counts (i.e. no playback) and enumerated the

number of chestnut-sided warblers heard from the point center. All point counts occurred

between 0530-1130 EDT during fair weather conditions (i.e. no precipitation or substantial

winds that would inhibit our ability to detect the birds). We used a natural neighbor spatial

interpolation to create a mean chestnut-sided warbler density layer using the number of

chestnut-sided warblers heard at each point count. Using the zonal statistics toolset in

ArcMap, we calculated the mean number of chestnut-sided warblers (as defined by our

spatial interpolation) per polygon that represented an individual golden-wing territory.

Using this approach, we were not attempting to quantify the total number of chestnut-sided warblers within individual golden-winged warbler territories. Rather, our goal was to approximate mean chestnut-sided warbler density for any particular location within the mapped golden-winged warbler territory. That is, we were attempting to estimate how many chestnut-sided warblers a golden-wing would encounter at any particular location within his territory. Moreover, we stress that our aim with this methodology was not to make any management recommendations, as would be expected with traditional avian census measures (reviewed in Thompson 2002, McCallum 2005). Although it is possible that individuals were double-counted, because interpolation averages the number of chestnut-sided warblers within a golden-winged warbler territory, our mean density measures were unlikely to over- or under-estimating the number of chestnut-sided warblers. Golden-winged warbler territories are often adjacent to each other throughout our field site. Thus, given the small spatial scale of these questions, high density point counts necessary to tease apart fine differences in chestnut-sided warbler density.

Aggressive Response towards Song Playback

To estimate aggressive behaviors, we conducted simulated territorial intrusions (STIs) in which we recorded behavioral responses of male golden-winged warblers toward conspecific playbacks, under the assumption that the response to a conspecific STI will mirror that of an interspecific competitor similarly (e.g. Duckworth 2006); our preliminary field work showed that both warblers do not respond aggressively towards heterospecific playback. All STIs took place from May 4 to June 3, 2014, between 0530-1130 EDT. First, we located each territorial male the morning of the experiment and set up a speaker ~2 m high, adjacent to a

known (i.e. mapped) perch in the center of the territory. We flagged 5 m and 10 m from the speaker in each cardinal direction to visually estimate the distance between the focal bird and the speaker (Martin and Martin 2001a). We retreated to a distance of ≥40 m, initiated our playback sequence and observed the bird for 1 min of white noise (wind and local bird songs from a distance at a lower decibel than conspecific or control playbacks) and recorded initial behaviors. Next, we administered 10 min of conspecific playback, consisting of a mixture of the two song types in the bird's repertoire (Confer et al. 2011, Richardson and Brauning 2013). During each type of playback, we noted the following behaviors: latency to respond (attentiveness of their territory) to the song playback and latency to approach the playback source (<15 m); minimum distance to the playback source to the nearest meter; attack (dive) rate; number of songs the target species sang, distinguishing between type-1 (mate attraction) and type-2 (aggressive territorial defense) song types in golden-winged warblers (Ficken and Ficken 1967, Murray and Gill 1976). All song playbacks were obtained from "xeno-canto" (www.xeno-canto.org).

Territory-Level Habitat Structure

We used EarthExplorer (earthexplorer.usgs.gov) to download June 2012 National Agriculture Imagery Program (NAIP) imagery to classify habitat structure of individual golden-winged warbler territories; NAIP imagery is high resolution (1 m) and is georeferenced. Although higher resolution spatial data is available (e.g. LiDAR), NAIP imagery offers the highest resolution obtainable that also occurs within two years of our field study; despite that plant communities have changed since 2012, field assessment confirmed that the habitat structure depicted in the imagery is consistent with 2014 vegetation structure

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(pers. obs.). We used five separate NAIP images to classify our seven field sites (Supplemental Material Table S1).

Using the Image Classification toolbar in ArcGIS 10.1, we performed a supervised classification with maximum likelihood analysis to distinguish between four habitat characteristics based on a priori knowledge of vegetation structure for our field sites: (1) abiotic factors (e.g. roads, boulders); (2) grassland (defined as predominantly grassy, homogenous habitat without any woody vegetation); (3) forested/canopy cover, with no herbaceous vegetation; (4) shrubland (i.e. nesting habitat: defined as shrubs and saplings clumped with herbaceous vegetation). Next, using the 'Extract by Mask' tool, we calculated the percent cover of each habitat-cover type per individual golden-winged warbler territory (Supplemental Material Fig. S2) and used the total number of pixels per structure class to create a percent cover estimate of each class per bird territory.

Golden-winged Warbler Reproductive Success
Females generally arrive at our field sites ~1-2 weeks after the males arrive and typically begin nest building almost immediately (Buehler et al. 2007). We monitored and focused only on measures of golden-winged warbler reproductive success relative to chestnut-sided warbler abundance. Despite limiting our interpretation of the costs of sympatry between both warblers, we feel that an analysis of golden-wing fitness relative to chestnut-sided warbler density is relevant and is the most pressing conservation concern.

Because of numerous stochastic events that may influence golden-winged warbler fitness during the breeding season (e.g. predation, inclement weather that destroyed the nest; pers. obs.), we used multiple proxies of reproductive success. We monitored golden-winged

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warbler nests every three days and measured first egg date and clutch size. We used the laying date of the first egg (of the first nesting attempt) as a proxy of fitness, considering that reproductive success typically declines with later first egg dates in most migratory passerines (e.g. Alatalo et al.1984, Verhulst et al. 1995, Daunt et al. 1999). To ensure we used laying date of the first clutch, we limited nests used in analysis to dates prior to June 7, as this is the earliest date with which we could confirm a second nesting attempt had its first egg. Finally, we recorded the success/fail rate of each nest as well as enumerating offspring successfully fledged from the nest.

Assessment of Mistaken Identity: 2015 Experimental Setup

Golden-winged Warbler Behavioral Assays

In our 2015 experiment, we prioritized conducting STIs of golden-winged over chestnut-sided warblers for two reasons. First, although the two species of warblers arrive on the breeding grounds at approximately the same time, golden-winged warblers tend to exhibit territorial behaviors for a shorter timeframe than chestnut-sided warblers (pers. obs.) Secondly, there are far fewer breeding golden-winged compared to chestnut-sided warblers, so we aimed for the largest possible sample of territorial golden-wings. From May 10 to 23, one researcher (JAJ) conducted conspecific simulated territorial intrusions of golden-winged warblers between 0600-1200 EDT following the protocol outlined in 2014. However, we analyzed each STI in two 5 min segments: (1) 5 min of broadcasted conspecific song without a visual stimulus and (2) 5 min of conspecific song coupled with either a model of a golden-winged or chestnut-sided warbler. During the first playback segment, the model bird was covered and then remotely revealed after 5 min. Each focal bird was presented with a model

of each species on separate dates (2-4 days separation) and in random order (responses were not influenced by order of trial). During each 5 min interval, we noted the following behaviors: (1) time to approach the playback source, (2) the number of dives/attacks, (3) the number of fly-throughs (defined as flying around the speaker/model, but not directly attacking it), (4) counter-singing (distinguishing between type-1 and type-2 songs), and (5) chipping rate. Golden-winged warblers often aggressively chip when stimulated by conspecific STI (JAJ pers. obs.) and we interpreted this behavior as a potential acoustic signal of aggressive intent. Mistaken identity was determined if the focal warbler attacked the model of the opposite species directly at least once during the 5 min behavioral assay.

Chestnut-sided Warbler Behavioral Assays

From May 19 to June 10 at between 0600–1200 EDT, we conducted STIs with focal chestnut-sided warblers. Because the population size of chestnut-sided warblers far exceeds golden-winged warblers in our field sites, each chestnut-sided warbler was only presented with one bird model (conspecific, heterospecific, or control (American goldfinch, *Carduelis tristis*)) to maximize sample size during the limited window of opportunity. Chestnut-sided warblers were presented with either a conspecific, heterospecific, or control bird following the 5 min behavioral analysis; models were selected randomly for individual birds. For chestnut-sided warblers, we recorded the same behavioral variables as golden-wings, excluding chipping rate. On occasion, we did observe female chestnut-sided warblers participating in attacking both heterospecific and conspecific models. However, these were often sporadic and unquantifiable, and for consistency between warblers, we only focus on male birds in this study.

Visual Stimuli

Wooden models of golden-winged and chestnut-sided warblers were hand-carved to be the approximate shape of a warbler and were colored modeling real birds using colored pencils. We found that colored pencils represented spectra that more closely resembled that of natural plumage. In addition, we also taped crown, bib (golden-wings only), and chestnut flank (chestnut-sided warblers only) feathers from birds captured in 2014 to the appropriate (i.e. conspecific) model bird to provide a more realistic model; spectral readings of the crown feathers fell within the natural range of crown plumage found by carotenoid-based pigments in these wood warblers (Jones and Siefferman 2014). The use of dummy birds also ensures each bird encounters a near-identical stimulus. Feathers we re-taped as the season progressed to ensure a full crown of feathers. The American goldfinch model was not hand-carved; rather, was made of Styrofoam and painted to resemble goldfinch coloration; however, there were no spectral abnormalities with this model. Although taxidermic mounts of each species would be more likely to elicit a stronger aggressive response, such models were not available. Moreover, because our focal warblers attacked the conspecific dummy models that we designed for this experiment, we are confident that these models are sufficient for our questions on misidentification. Unfortunately, we were unable to investigate how golden-wings behave toward a STI with a conspecific song and an American goldfinch; after we had completed the second behavioral trial for each individual, golden-winged warblers were well into nest construction and at this time frame, golden-winged warblers tend to be significantly less territorial and aggressive at our field sites (pers. obs.).

It is important to note that we did not use a heterospecific song playback associated with the heterospecific bird model for two reasons for either focal warbler. First, our previous work shows that warblers do not aggressively respond to heterospecific song playback (unpubl. data) and their songs are quite distinct (Confer et al. 2011, Richardson and Brauning 2013). Second, the scope of our study focuses on visually based misidentification. We expect that if golden-winged warblers are stimulated during natural conditions by a conspecific intruder, misdirected conspecific aggression may cause them to attack a chestnut-sided warbler.

Statistical Analysis

All statistical analyses were performed using SPSS v.22 (IBM 2013). Using a Pearson's correlation, we investigated whether 2014 densities of chestnut-sided warblers correlated with aggressive responses of golden-winged warblers to STIs, vegetation structure upon settlement, and overall territory size. To condense our aggressive behaviors, we used a principal components analysis (PCA), which explained 70.3% of variance between two components (Supplemental Table S2). PC_1-2014aggression loaded heavily on threatening behaviors (Supplemental Table S2), such that higher PC_1-2014aggression scores were defined as greater counter-singing rates (type-1 song and total songs). PC_2-2014aggression scores were more directly related to physical aggression, such that higher scores were birds that counter-sang more with their aggressive song type (i.e. type-2) as well as dove more often (Supplemental Table S2). Whether golden-winged warblers were paired or not was not related to behavioral response (defined by PC_1-2014aggression ($t_{33} = 0.24$, $P = 0.81$) and PC_2-2014aggression ($t_{33} = 0.79$, $P = 0.44$)), thus, we analyzed all males together. We used a

second PCA (PC$_1$-habitat and PC$_2$-habitat), which explained 80.8% of the variance between two components, to explore vegetation within an individual's territory (Supplemental Table S3). Principal component 1-habitat loaded heavily on open habitat, such that high PC$_1$-habitat scores are high cover of homogenous/grassy habitat with abiotic (vegetation-less) habitat associated with it (Supplemental Table S3). Principal component 2-habitat loaded with remaining vegetation, such that high PC$_2$-habitat scores are associated with forested/canopy habitat whereas negative scores are shrubland habitats (Supplemental Table S3).

Using laying date as a proxy of fitness, we used a generalized linear model, where laying date was the dependent variable and chestnut-sided warbler density and habitat (PC$_1$-habitat and PC$_2$-habitat) were covariates. We ran an additional generalized linear model with clutch sizes as the dependent variable; because earlier laying dates are significantly related to larger clutch sizes in this population ($r_{22} = 0.33$, $P = 0.002$), we also included laying date as a covariate for this model. For each generalized linear model, we used the Finite Sample Corrected Akaike's Information Criterion (AIC$_C$) model selection procedure to determine the best-fitting model (Burnham and Anderson 2002). All models were first tested for interaction terms and then were removed if interaction terms were not significant. Next, we ran an independent samples t-test between success/failure of the nest and chestnut-sided warbler density and habitat. Finally, we ran a Pearson's correlation between the number of offspring successfully fledged from the nest and chestnut-sided warbler density and habitat.

For 2015, we ran another PCA to explain flight behavior; the models produced one principal component per species (golden-wing: PC$_1$-GWWA, variance = 58.2%; chestnut-sided: PC$_1$-CSWA, variance = 59.7%; Supplemental Table S4). In general, higher PC scores were associated with birds that were more aggressive (i.e. birds that arrive sooner and attack /

fly around the speaker more often; Supplemental Table S4). In addition, we ran a second

PCA to condense acoustic behaviors of golden-winged warblers (Supplemental Table S5).

Here, the number of type-1, type-2, soft songs, and aggressive chips created two principal

components (PC_1-accoustic and PC_2-accoustic) explaining 76.4% of the variance. High PC_1-

accoustic scores are associated with high amount of aggressive song types (i.e. type-2 and

soft songs), whereas high PC_2-accoustic scores are associated with high amounts of

aggressive chips and less type-1 songs (Supplemental Table S5). We did not quantify

differences between the chipping rate and the two chestnut-sided warbler song types; when

total song rate was combined with soft songs in a PCA, the components resulted in identical

extractions. Thus, we did not perform a PCA on chestnut-sided warbler vocal behaviors.

We categorized misidentification of the dummy birds as yes/no data, and ran a chi-

square analysis to determine the likelihood the focal warbler would attack both the correct

(conspecific) and incorrect (heterospecific) model. Additionally, we used Pearson's cross-tab

chi-squared tests to investigate whether the likelihood that the warblers attacked the model

varied (yes/no) among species-specific and heterospecific models. Finally, we ran a

generalized linear model (binary logistic regression) for both focal warblers with

misidentification likelihood (yes/no) as the dependent variable and the principal components

for flight and acoustic behaviors as covariates.

Ethical Note

We conducted this study in strict accordance to the Institutional Animal Care and Use

Committee of Appalachian State University (#14-004.0). We handled every bird minimally

and in such a fashion to reduce physical stress and harm. This study was carried out under

RESULTS

Assessment of Competition

Relationship between Heterospecific Density, Aggression, and Habitat

We conducted 343 point counts throughout seven field sites and reported chestnut-sided warblers in 94% of point counts whereas golden-winged warblers were detected in 61% of the point counts. Golden-winged warbler territory ($N = 48$) sizes were on average 2.47 ($\pm$ 1.72 SD) ha and contained on average, 1.88 ($\pm$ 0.67 SD) chestnut-sided warblers per spatial unit within a mapped golden-winged warbler's territory. We found no effect of chestnut-sided warbler density on golden-winged warbler territory size ($r_{48} = 0.15$, $P = 0.31$).

Chestnut-sided warbler densities did not significantly predict golden-wing aggressive behaviors defined by PC_1-2014aggression ($r_{35} = -0.26$, $P = 0.13$), yet did significantly relate to PC_2-2014aggression ($r_{35} = 0.39$, $P = 0.02$; Fig. 1); when golden-wings held territories in locations with high densities of chestnut-sided warblers, golden-winged warblers sang their aggressive song (type-2) and dove more often while singing their territorial song (type-1) less often.

We found that the shrubland habitats made up the bulk of territory composition in golden-winged warblers (mean $\pm$ 1 SD: 48 $\pm$ 13%), followed by forest (30 $\pm$ 16%), grassland habitats (19 $\pm$ 16%) and finally abiotic components (i.e. roads; 3.0 $\pm$ 0.6%). When the density of chestnut-sided warblers was greater within individual golden-winged warbler territories, these locations had high PC_1-habitat scores (greater percent cover of open habitat; $r_{28} = 0.32$,

$P = 0.03$). However, chestnut-sided warbler density did not correlate with PC2-habitat of

golden-winged warbler territories ($r_{28} = 0.10$ $P = 0.49$).

Golden-winged Warbler Reproductive Success

After model selection, the best-supported model of laying date included chestnut-sided

warbler density and PC2-habitat (likelihood $X^2_{2, 24} = 9.15$, $P = 0.01$, $w_i = 0.55$; Fig. 2; Table

1). However, the only main effect in the model that was significant was PC2-habitat: Golden-

winged warbler females laid eggs earlier in areas with greater shrubland cover relative to

forested cover (Wald $X^2_{1, 24} = 7.28$, $P = 0.01$), but chestnut-sided warbler density did not

contribute significantly to this model (Wald $X^2_{1, 24} = 2.27$, $P = 0.13$). In addition, PC2-habitat

alone was a strong model in predicting earlier egg dates (i.e. ΔAIC_C <2; Table 1). Next, we

found strong support for three models to best explain clutch size (i.e. ΔAIC_C <2). The best-

supported model to predict clutch size was laying date alone (likelihood $X^2_{1, 24} = 10.61$, $P = $

0.001, $w_i = 0.26$; Table 2). However, two other models were also supported: earlier egg dates

were associated with first, increases in shrubland cover (PC2-habitat; $\Delta AIC_C = 0.41$) and

second, decreases to grassland cover (PC1-habitat; $\Delta AIC_C = 1.88$; Table 2). Although

chestnut-sided warbler densities were components in the first egg date model, heterospecific

density alone was only a marginal influence on clutch size (likelihood $X^2_{1, 24} = 3.05$, $P = $

0.08). However, we found no significant effect of either chestnut-sided warbler density or

habitat PCs on nest fate (all $P > 0.39$) or fledgling number (all $P > 0.42$; Table 3).

Assessment of Mistaken Identify

Golden-winged Warblers

We found that golden-winged warblers were equally likely to (or not to) attack both the conspecific model (11 attacks of 28 trials; $X^2_{1,\,28} = 1.29$, $P = 0.26$) and the heterospecific (chestnut-sided) model (12 attacks of 25 trials; $X^2_{1,\,25} = 0.40$, $P = 0.84$) during STIs. Using the cross tab analysis, we found no statistical difference in the likelihood of attacking conspecifics over heterospecific models (Pearson $X^2_{1,\,23} = 2.54$, $P = 0.11$). After model selection, the best supported model to predict the likelihood of a golden-winged warbler attacking a heterospecific model included both acoustic PCs (likelihood $X^2_{2,\,24} = 15.97$, $P < 0.001$, $w_i = 0.50$; Fig. 3; Table 4). However, the only significant main effect in this model was PC$_2$-accoustic: Golden-winged warblers that aggressively chipped and sang their type-1 song less were more likely to attack the heterospecific model (Wald $X^2_{1,\,24} = 4.93$, $P = 0.03$), but PC$_1$-accoustic did not contribute significantly to the model (Wald $X^2_{1,\,24} = 1.88$, $P = 0.17$). Although we found support for another model (ΔAIC$_C$ <2; PC$_1$-accoustic, PC$_2$-accoustic, PC$_1$-GWWA; Table 4), PC$_2$-accoustic was again the only significant main effect in the model.

Chestnut-sided Warblers

We found that chestnut-sided warblers were significantly less likely to attack the American goldfinch model (only 1 attack of 29 trials; $X^2_{1,\,29} = 25.14$, $P < 0.001$), but were equally likely to (or not to) attack the conspecific model (15 of 32 trials; $X^2_{1,\,32} = 1.25$, $P = 0.72$) and the heterospecific (golden-winged) model (20 of 38 trials; $X^2_{1,\,38} = 0.11$, $P = 0.75$) during STIs. Moreover, we found a marginally significant relationship suggesting that chestnut-sided

warblers were more likely to attack a conspecific models rather than a heterospecific (golden-winged warbler) model (Pearson $X^2_{1, 32} = 3.14$, $P = 0.08$). After model selection, we found that counter-singing rates the best predictor of attacking the heterospecific model (likelihood $X^2_{1, 38} = 4.36$, $P = 0.04$, $w_i = 0.89$; Fig. 4a; Table 5); chestnut-sided warblers that counter sang less during STIs were more likely to attack the heterospecific model. Although not a well-supported model, flight behaviors (PC$_1$-CSWA) were nonetheless a significant predictor of heterospecific attack (likelihood $X^2_{1, 38} = 10.35$, $P = 0.001$, $w_i = 0.08$; Fig. 4b); chestnut-sided warblers that dove more often prior to exposure to the model were more likely to attack the heterospecific model.

DISCUSSION

Agonism is a costly behavior (reviewed in Moyer 1968, Grether et al. 2013) and golden-wings are rapidly declining throughout the Appalachian Mountains (Sauer et al. 2014). Consequently, we concentrated our field efforts in understanding how sympatry with varying densities of chestnut-sided warblers influences behavior and reproductive success of golden-winged warblers. Indeed, we found that when occupying areas with greater densities of chestnut-sided warblers, golden-winged warblers behaved more aggressively towards conspecific STIs (Fig. 1). Yet, it was habitat 'shrubbiness' (i.e. PC$_2$-habitat scores; Fig. 2), rather than chestnut-sided warbler density, that predicted reproductive success of golden-winged warblers. We expected shrubland cover to predict reproductive output; nesting locations for golden-winged warblers occur in our classification of shrubland (Confer et al. 2011), and thus it is intuitive that these habitat parameters would influence first egg date and clutch size. Although chestnut-sided warbler densities were a main effect in the best-

supported model for first egg dates, this parameter is likely spurious/uninformative; the difference between the two best supported models for first egg date was only one main effect (chestnut-sided warbler density), which was not significant (see Arnold 2010). In addition, we found that both species readily attacked the heterospecific model and that the most aggressive birds were the most likely to attack a heterospecific intruder. Together, these data suggest interspecific aggression is a function of misidentification rather than interspecific competition for shared resources and coexistence is likely not detrimental for golden-winged warblers.

Although golden-winged warblers are more aggressive when their territories encompass a greater density of chestnut-sided warblers, high heterospecific density does not lead to lower reproductive success. We offer several non-mutually exclusive hypotheses to explain this. First, intense intraspecific competition for higher quality habitat types may restrict lower quality golden-winged warblers to areas that are preferred by chestnut-sided warblers. Those lower quality males may use a strategy of high aggression to secure mates. For example, in house finches (*Carpodacus mexicanus*), aggressive behavior has been explained as a compensatory strategy whereby lower quality and less attractive males invest heavily in aggression to secure breeding success (Stoehr and Hill 2000, Hill 2002). Second, it is possible that high-density breeding sites increase predation risk (Martin 1988, Martin 1993) and warblers that are more aggressive to STIs may be more aggressive towards predators, as seen in dark-eyed juncos (*Junco hyemalis*; Cain et al. 2011). Third, because agonism occurs between the two species, male golden-winged warblers with territories amongst many chestnut-sided warblers are likely challenged often. Increases in testosterone associated with heighted aggressive behaviors may explain these behavioral patterns. If

aggressive individuals respond with speed (i.e. quicker response time) rather than with accuracy in aggressive encounters (reviewed in Sih and Del Giudice 2012), this could explain why the more aggressive birds were more likely to attack heterospecific models.

Nonetheless, it appears that, from the golden-wing perspective, coexistence is not detrimental towards reproductive success. An important caveat to our assessment of interspecific competition is that we did not test whether golden-winged warbler density influences chestnut-sided warbler reproductive output or behavior. More powerful tests of interspecific competition involve manipulating a resource or the presence of interspecific competitors (reviewed in Dhondt 2012; e.g. Martin and Martin 2001a). However, such removal experiments are ethically and logistically problematic, particularly for at-risk species. Because golden-wings are the more pressing conservation concern, the lack of fitness consequences of sympatry with chestnut-sided warblers is particularly relevant for their management. Throughout the southern Appalachians, golden-wings occur in much lower densities than do chestnut-sided warblers. Thus, if competition were to occur between these two species, golden-wings would likely suffer greater negative effects than would chestnut-sided warblers.

We found that both warbler species were equally likely to attack the hetero- and con-specific models (~50% of individuals of both warbler species incorrectly attacked the heterospecific model), showing support for the misidentification hypothesis (Murray 1971, 1981), In addition, because chestnut-sided warblers tended to attack conspecific models more often than heterospecifics, they should be able to discern species. Only one chestnut-sided warbler attacked the goldfinch model; suggesting the warblers do not readily attack any interspecific species in the area. Rather, it seems likely that the yellow crown coloration is

the visual cue that triggers attack behavior. Indeed, golden-winged and chestnut-sided warblers are the only species with similar crown patches at our study sites. Models of avian vision (Maia et al. 2013) indicate that the shared signaling space (i.e. crown) should be visually distinctive (Jones and Siefferman 2014), but it may be that brief views do not allow for enough cognitive processing time to discriminate the colors that otherwise would be distinctive visually upon close examination. To our knowledge, neurological processing time has not been incorporated into models of avian color vision.

Misidentification should be selected against. Individuals that are mistakenly identified as conspecifics should suffer; however, making identification mistakes should also be maladaptive, as there is likely no benefit to risky behaviors (Moyer 1968, King 1973). It is possible that selection pressures to avoid interspecific aggression may drive divergence of crown color (i.e. agonistic character displacement; Grether et al. 2009). Agonism associated with color driven misidentification could influence the evolution of plumage coloration in birds; closely related bird species tend to show greater divergence in color patterns when existing sympatrically (i.e. character displacement; reviewed in Martin et al. 2015). Importantly, as these warblers appear to peacefully coexist for the majority of the time, our findings do not suggest that warblers are entirely incapable of recognizing interspecifics. Indeed, we promoted aggression and likely triggered misidentification by using a conspecific playback accompanied by a heterospecific model. Because neither warbler species responds aggressively to heterospecific playback, it may be that the normal circumstances that promote misidentification are complex. This idea is supported by the findings of Petrusková et al. (2008); individuals behave aggressively towards neutral heterospecifics only after exposure to conspecific playback.

The aggressiveness with which individuals of both warbler species responded to conspecific playback predicted the likelihood of attacking the heterospecific model. Yet, we were surprised that both species were equally likely to attack either the con- or hetero-specific model when we expected species to attack the conspecific model more frequently. It may be that only certain individuals are stimulated by models or that aggressive individuals did not take adequate time to investigate and identify the models. Indeed, we observed that focal birds often ceased attacking after closer inspection of the model. There are two important limitations to our misidentification study however. First, we only used a control (goldfinch) model during chestnut-sided warbler STIs because of time constraints on fieldwork. Yet, our data demonstrate that both warblers responded behaviorally similar to heterospecific warbler models, suggesting that it seems likely that both species were misidentifying one another based on morphological similarity rather than attacking birds of any species in the area. Second, we do not have data to evaluation whether interspecific aggression is adaptive for chestnut-sided warblers. We suspect that golden-wings do not negatively influence their fitness, but further research is needed to verify this assumption. Nonetheless, because golden-wings do not suffer any fitness consequences, misidentification is the likely explanation, at least, from their perspective.

In this study, we document the importance of integrating behavioral research with conservation biology and of studying how at-risk species interact with their community (Anthony and Blumstein 2000, Linklater 2004, Caro and Sherman 2013). Although we lack data from the chestnut-sided warbler perspective, we focused on addressing how interspecific interactions influence golden-winged warbler fitness because their declines are particularly extreme throughout the Appalachians (Sauer et al. 2014). Agonism does not appear to be a

product of interspecific competition, which may be viewed as good news for the future of golden-winged warblers. However, interspecific aggression with chestnut-sided warblers may still be a risky behavior for golden-winged warblers if no net benefit is conveyed (reviewed in Grether et al. 2013). Our study suggests that aggressive fighting between species is not always indicative of interspecific competition as is often assumed (and is often the case; e.g. Heller 1971, Morse 1974, Martin and Martin 2001a, b). Further research on the interactions between these warblers is needed if any management decisions are to be considered that may inadvertently harm one or the other (Anthony and Blumstein 2000).

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TABLES

Table 1. Model selection for variables that influenced egg laying dates of golden-winged Warblers. Laying commenced earlier when golden-winged warblers had territories in areas of lower chestnut-sided warbler densities (CSWA) and had greater shrubland cover relative to canopy cover (PC$_2$-habitat). Models are organized based on Akaike weights (w_i); the best fitting model is in bolded print.

Model	AIC$_C$	ΔAIC$_C$	w_i	Likelihood X^2	Model P
CSWA, PC$_2$-habitat	**162.62**	**0.00**	**0.55**	**9.15**	**0.01**
PC$_2$-habitat	163.99	1.37	0.28	6.98	0.01
PC$_1$-habitat, PC$_2$-habitat	166.81	4.19	0.07	7.07	0.03
CSWA, PC$_1$-habitat, PC$_2$-habitat	167.95	5.33	0.04	9.16	0.03
CSWA	168.18	5.56	0.03	2.80	0.10
PC$_1$-habitat	169.15	6.53	0.02	0.62	0.43
CSWA, PC$_1$-habitat	170.94	8.32	0.01	2.94	0.23

Table 2. Model selection for variables that influenced golden-winged warbler first-attempt

clutch sizes. Clutch sizes were larger when warblers commenced laying earlier in the season.

Models are organized based on Akaike weights (w_i); the best fitting model is in bolded print.

Model	AIC_C	ΔAIC_C	w_i	Likelihood X^2	Model P
FED	**47.73**	**0.00**	**0.26**	**10.61**	**0.001**
FED, PC_2-habitat	48.13	0.41	0.21	13.11	0.001
FED, PC_1-habitat	49.61	1.88	0.10	11.64	0.003
FED, CSWA	49.83	2.10	0.09	11.42	0.003
FED, CSWA, PC_2-habitat	50.44	2.72	0.07	14.03	0.003
FED, PC_1-habitat, PC_2-habitat	50.70	2.98	0.06	13.77	0.003
PC_2-habitat	50.83	3.11	0.06	7.51	0.01
CSWA, PC_1-habitat, PC_2-habitat	51.11	3.38	0.05	10.03	0.18
CSWA, PC_2-habitat	51.49	3.77	0.04	9.75	0.01
FED, CSWA, PC_1-habitat	52.36	4.63	0.03	12.12	0.007
PC_1-habitat, PC_2-habitat	53.01	5.28	0.02	8.24	0.02
CSWA	55.47	7.75	0.01	2.89	0.09
PC_1-habitat	56.69	8.97	0.00	1.65	0.20
CSWA, PC_1-habitat	57.56	9.83	0.00	3.69	0.16

FED = first egg date, CSWA = chestnut-sided warbler density

Table 3. Relationship between nest fate and fledgling numbers relative to Chestnut-sided

Warbler density (CSWA) and habitat variables (PC_1-habitat and PC_2-habitat).

	Nest fate			Fledgling numbers		
	t	P	df	r	P	N
CSWA	0.25	0.80	22	-0.19	0.93	24
PC_1-habitat	0.79	0.44	22	-0.17	0.42	24
PC_2-habitat	0.88	0.39	22	-0.11	0.62	24

Table 4. Model selection for variables that best predicted whether or not golden-winged warblers would attack a heterospecific bird model. Golden-winged warblers that chipped more aggressively while singing fewer type-1 songs were more likely to attack the model chestnut-sided warbler. However, flight behaviors (PC_1-GWWA) contributed little to their likelihood of attacking a heterospecific model. Models are organized based on Akaike weights (w_i); the best fitting model is in bolded print.

Model	AIC_C	ΔAIC_C	w_i	Likelihood X^2	Model P
PC_1-accoustic, PC_2-accoustic	**24.50**	**0.00**	**0.50**	**15.97**	**<0.001**
PC_1-accoustic, PC_2-accoustic, PC_1-GWWA	25.93	1.43	0.24	17.45	0.001
PC_2-accoustic	26.98	2.48	0.14	10.86	0.001
PC_2-accoustic, PC_1-GWWA	27.46	2.97	0.11	13.01	0.001
PC_1-GWWA	34.48	9.98	0.00	1.17	0.28
PC_1-accoustic	37.99	13.50	0.00	1.63	0.20
PC_1-accoustic, PC_1-GWWA	38.10	13.60	0.00	2.37	0.31

Table 5. Model selection for variables that best predicted whether or not chestnut-sided

warblers would attack a heterospecific bird model. Chestnut-sided warblers that sang less

were more likely to attack the model golden-winged warbler. Although not the most

supported model, chestnut-sided warblers that displayed more aggressive flight behaviors

(PC$_1$-CSWA) were more likely to attack the heterospecific model. Models are organized

based on Akaike weights (w_i); the best fitting model is in bolded print.

Model	AIC$_C$	ΔAIC$_C$	w_i	Likelihood	X^2	Model P
Counter-sing rate	**41.80**	**0.00**	**0.89**	**4.36**		**0.04**
PC$_1$-CSWA	46.57	4.77	0.08	10.35		0.001
PC$_1$-CSWA, counter-sing rate	48.65	6.85	0.03	10.63		0.005
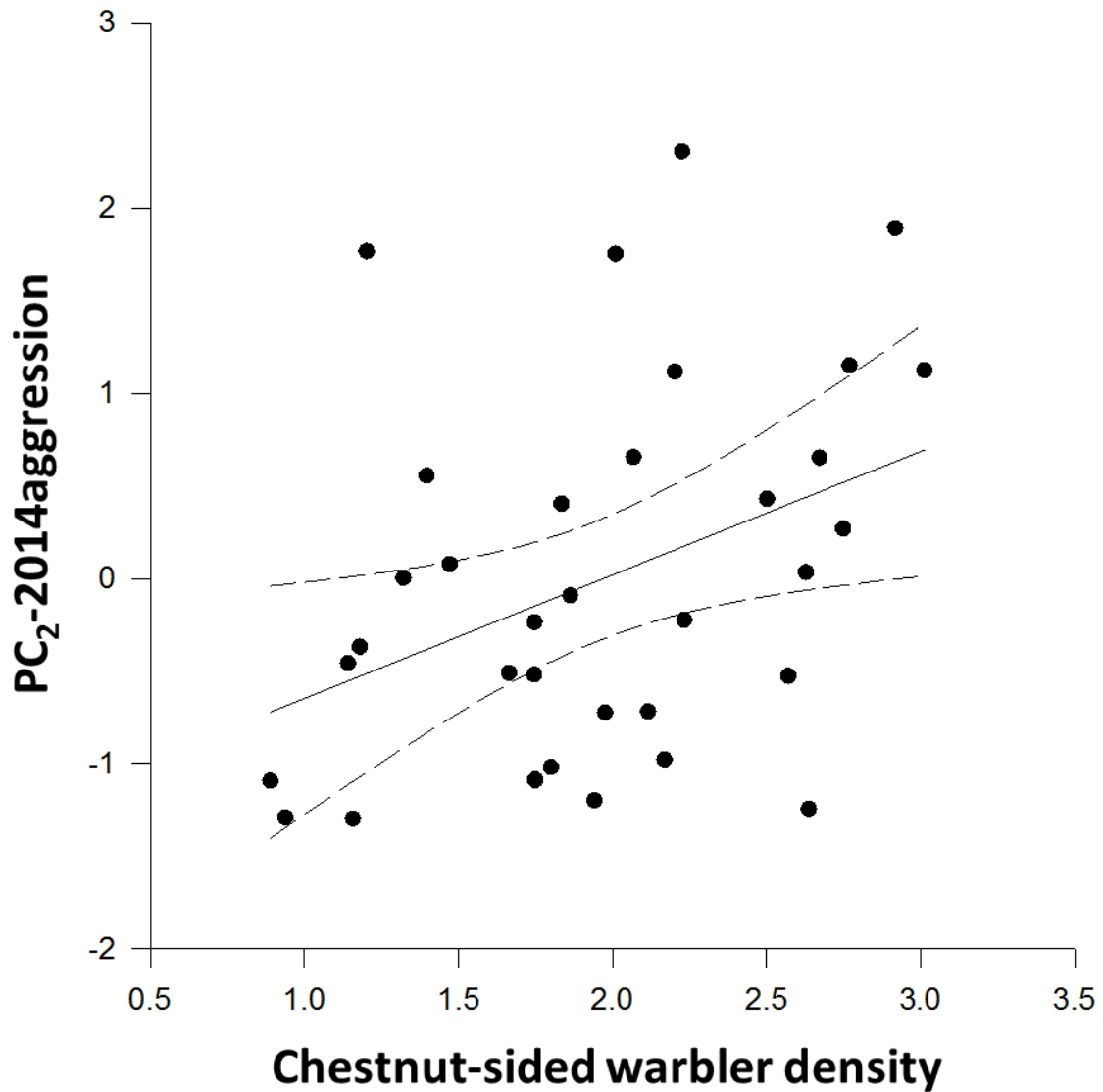
Figure 1. Golden-winged warbler aggressive behaviors (PC$_2$-2014aggression) relative to densities of chestnut-sided warblers. Golden-winged warblers tend to be significantly more aggressive (increased diving rates and type-2 song calls) when territories occur with greater densities of chestnut-sided warblers.
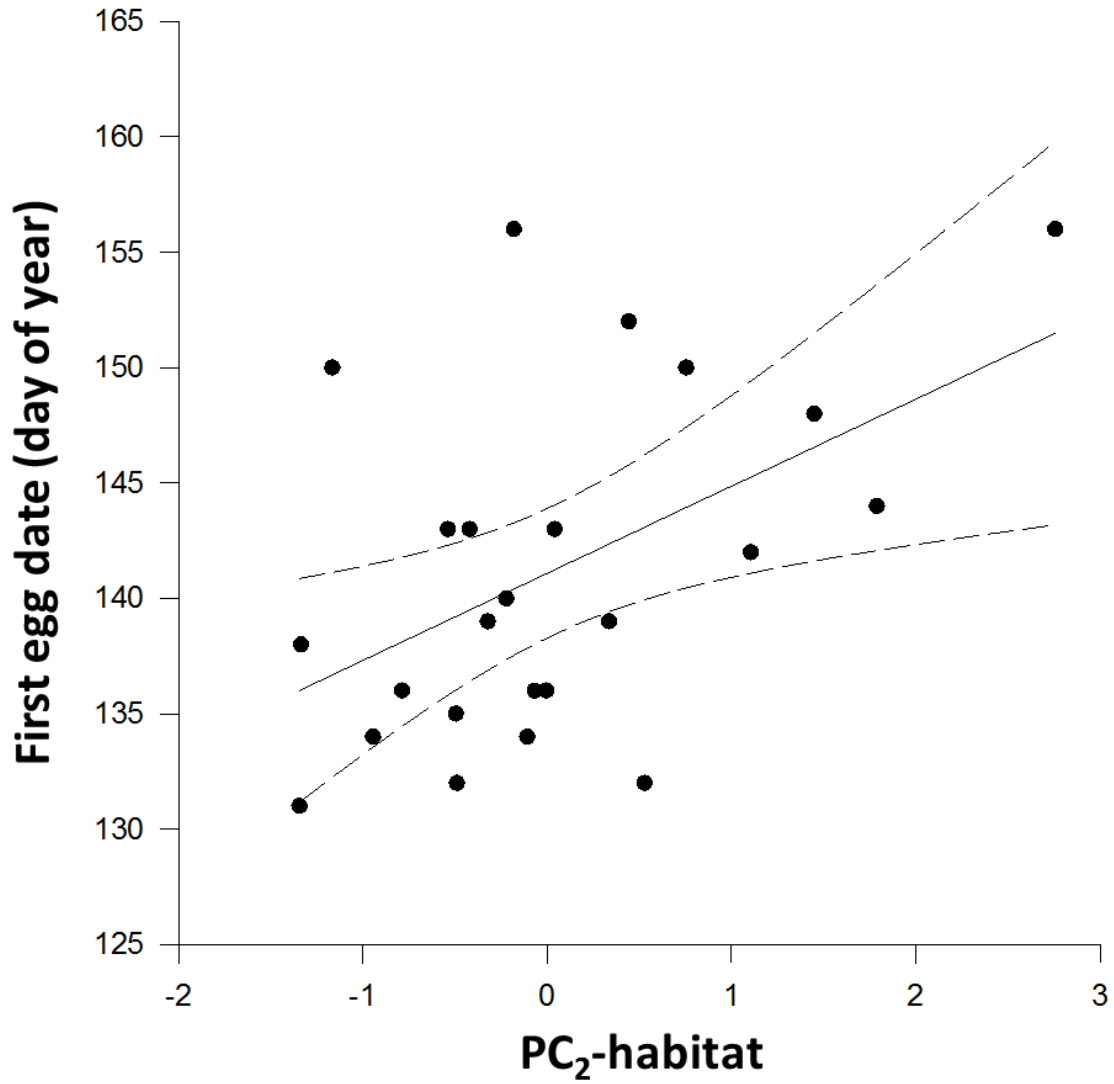
Figure 2. Nest commencement date for female golden-winged warblers relative to PC_2-habitat. Females that settled in territories with a greater proportion of shrubland habitat cover to forest cover lay their eggs earlier in the season.
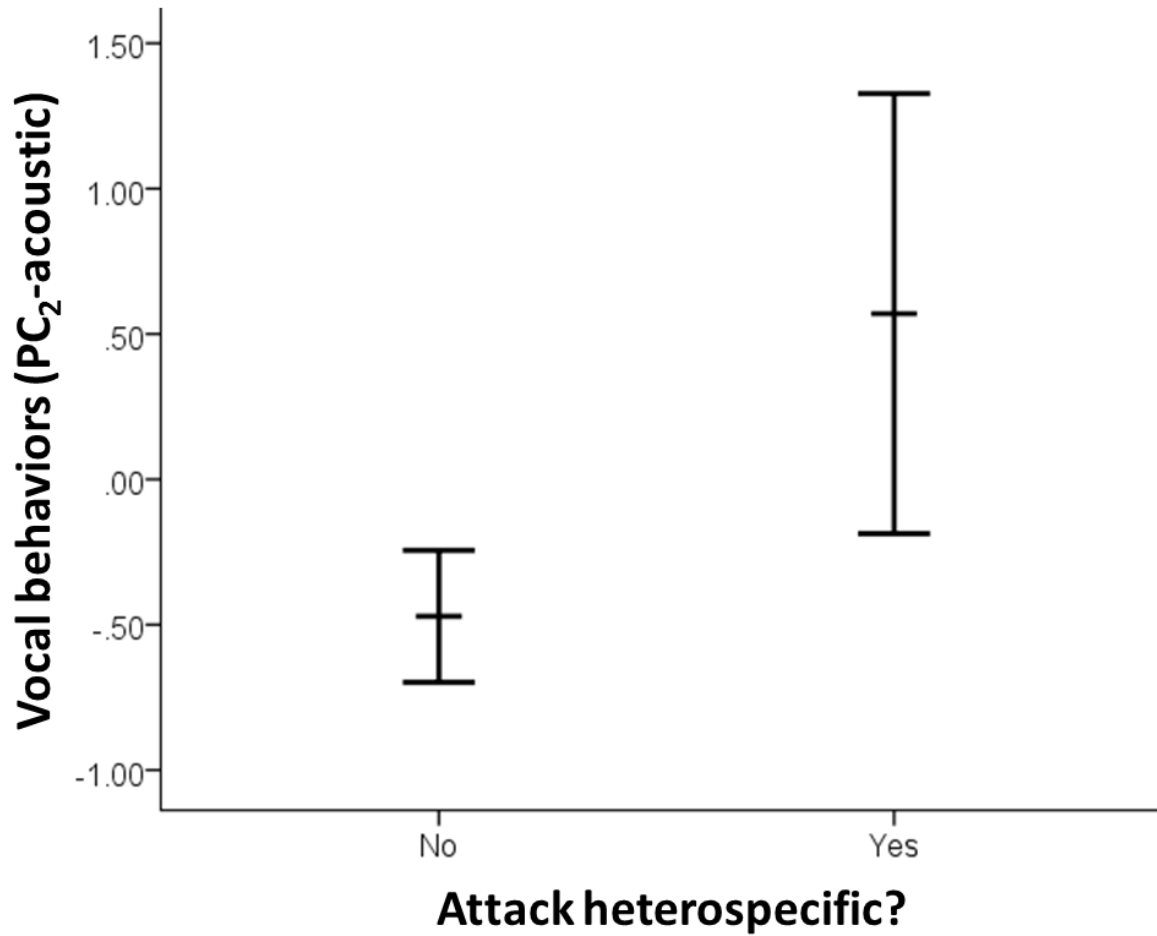
Figure 3. Conspecific aggression in response to acoustic stimuli in golden-winged warblers that did or did not attack the heterospecific model after the playback trial.
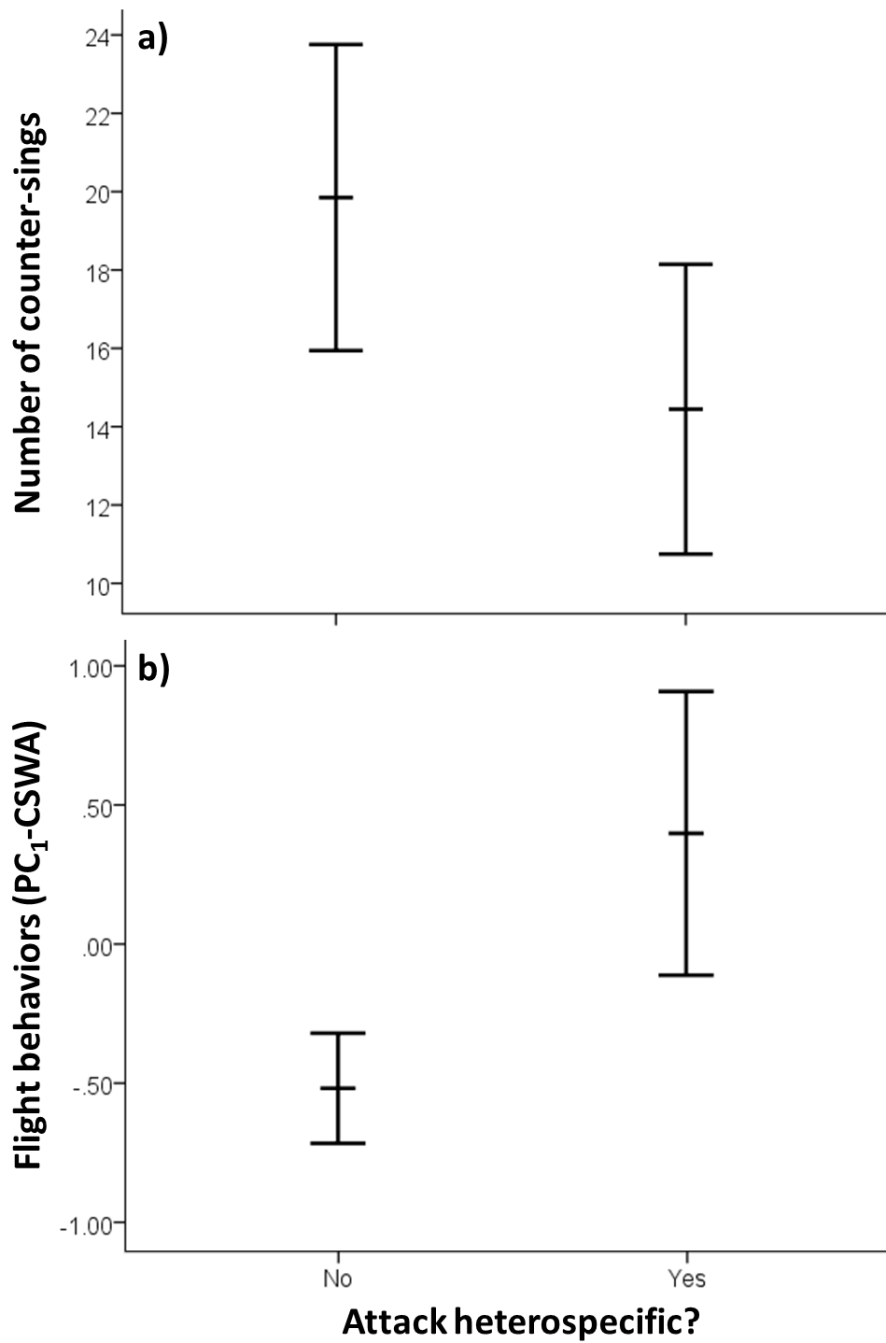
Figure 4. Conspecific aggression in response to acoustic stimuli in chestnut-sided warblers that did or did not attack the heterospecific model after the playback trial.

APPENDIX

Supplemental Tables

Table S1. NAIP imagery reference data for each field site. Entity ID refers to the imagery ID for EarthExplorer (earthexplorer.usgs.gov); coordinate locations represent the center point of the image; date refers to the date the image was captured.

Location	Entity ID:	Coordinates	Date
Watauga, NC	M_3608143_NW_17_1_20120627_2012 1018	36.3437471 N -81.7187554 W	6/27/2012
Watauga, NC	M_3608142_SE_17_1_20120627_20121 018	36.2812499 N -81.7812554 W	6/27/2012
Ashe, NC	M_3608135_SE_17_1_20120627_20121 018	36.40625 N -81.6562583 W	6/27/2012
Avery, NC	M_3608264_NW_17_1_20120629_2012 1018	36.0937444 N -82.0937527 W	6/29/2012
Carter, TN	M_3608256_SE_17_1_20120629_20121 018	36.15625 N -82.0312554 W	6/29/2012

Table S2. Principal component loading factors for each behavioral trait.

Behavioral response	Component	
	PC_1-2014aggression	PC_2-2014aggression
Respond latency	-0.69	0.07
Dive rate	0.36	0.57
Total song rate	0.93	-0.07
Type-1 song rate	0.61	-0.75
Type-2 song rate	0.49	0.74

Table S3. Principal component loading factors for each vegetation class.

Vegetation class	Component	
	PC$_1$-habitat	PC$_2$-habitat
Percent cover: Abiotic factors	0.521	0.495
Percent cover: Grassland	0.920	-0.190
Percent cover: Forested	-0.726	0.661
Percent cover: Shrubland	-0.509	-0.780

Table S4. Principal component loading factors for individual flight behavioral assays for golden-winged (GWWA) and chestnut-sided (CSWA) warblers.

Flight behaviors	Component	
	PC$_1$-GWWA	PC$_1$-CSWA
Latency to respond	-0.62	-0.64
# Fly-throughs	0.79	0.83
# Dives	0.85	0.84

Table S5. Principal component loading factors for golden-winged warbler vocal behaviors.

Vocal behaviors	Component	
	PC$_1$-accoustic	PC$_2$-accoustic
Type-1 song	0.32	-0.72
Type-2 song	0.87	0.35
Aggressive chips	0.03	0.85
Soft songs	0.91	-0.11

Supplemental Figures

Figure S1. Photograph demonstrating the plumage characteristics of the dorsal sides of

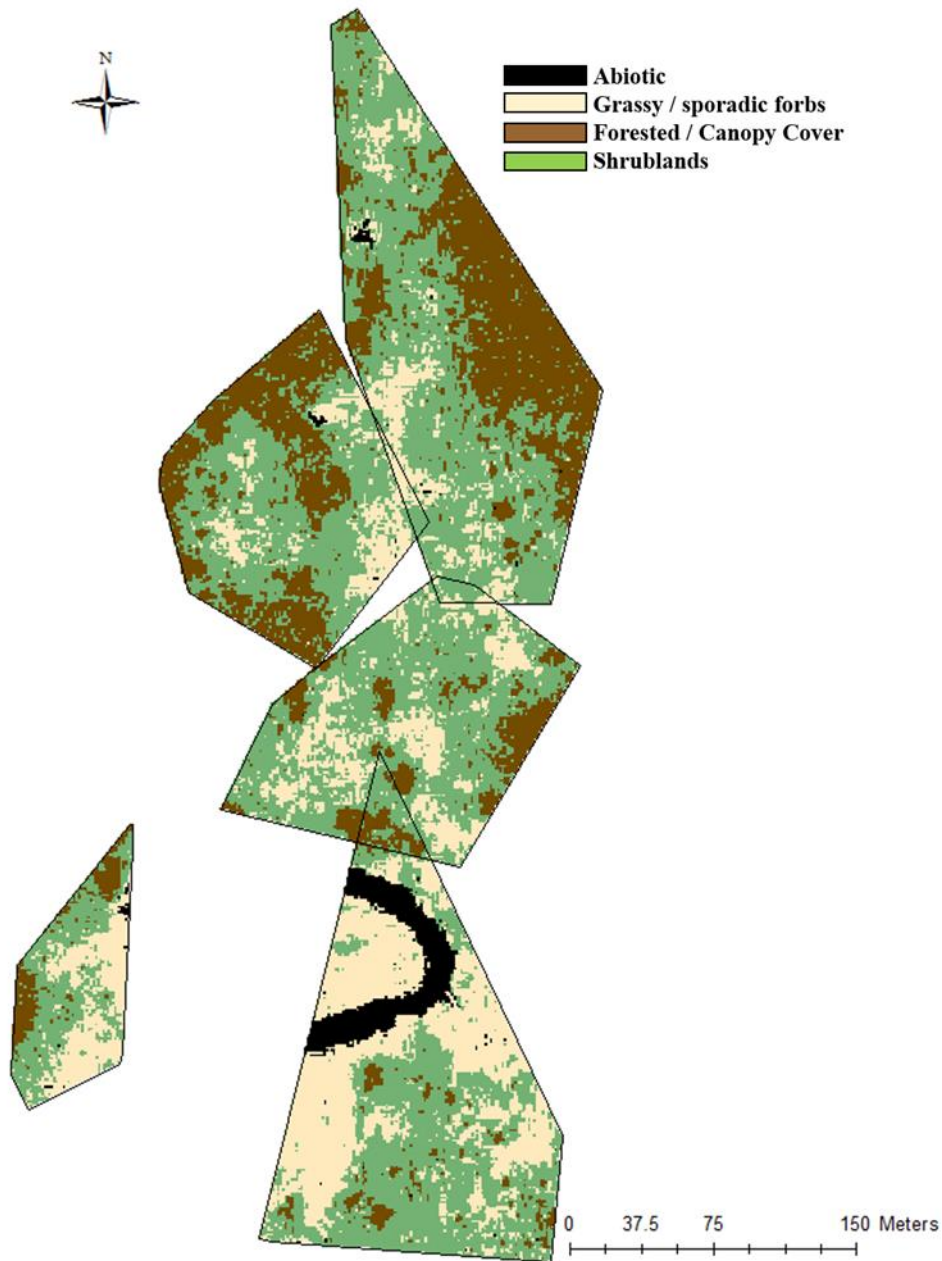golden-winged (top) and chestnut-sided warblers (bottom).

Figure S2. Examples of habitat classification of five territories of golden-winged warbler

pairs. These territories were located on Snake Mountain, Watauga Co., NC.

Vita

John Anthony Jones was born in Atlantic City, New Jersey in 1991. He attended elementary school in Atlantic County before moving to North Carolina in 1999. He then attended elementary, middle, and high school in Moore County and graduated from Union Pines High School in 2009. In August 2009, he enrolled at Sandhills Community College and finished his Associates in Science in May 2011. He then moved to Boone, NC to attend Appalachian State University, where he was awarded his Bachelor of Science degree in Biology, with a concentration in Ecology, Evolution, and Environmental biology in May 2013. In August 2013, he began his Master's program at Appalachian State University after finishing his pilot study while working for Audubon North Carolina. He was awarded his Masters of Science degree in Ecology and Evolutionary Biology in December 2015. John is now searching for a suitable lab to begin his PhD to continue his research interest in behavior, communication, and interspecific interactions.