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A case of mistaken identity: understanding the stimulus of agonism between two wood warblers



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Keywords: aggression chestnut-sided warbler coexistence golden-winged warbler interspecific aggression misidentification Setophaga pensylvanica simulated territorial intrusion Vermivora chrysoptera When multiple species occur sympatrically, divergence in morphological and behavioural 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 warblers, Setophaga pensylvanica, and golden-winged warblers, Vermivora chrysoptera, 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 conspecifics and heterospecifics in simulated territorial intrusions. We found that both warbler species were equally likely to both types of models, and that the most aggressive individuals were more likely to attack models. Our results suggest that, from the goldenwinged warbler's perspective, sympatry is not detrimental and aggression is probably a function of mistaken identity. Yet, these behavioural interactions should be maladaptive, which may lead to the segregation of habitat types or divergence in crown morphology between species.

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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. Catchpole & Leisler, 1986; Grether et al., 2013; Martin & Martin, 2001a; Peiman & Robinson, 2010; Rice, 1978). Heterospecifics can compete over food (e.g. Minot, 1981; Pimm, Rosenzweig, & Mitchell, 1985) and nesting locations (e.g. Harris & Siefferman, 2014), and sympatry can lead to increased nest predation rates (e.g. Martin, 1993; Martin & 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; Grether et al., 2013; Ord & Stamps, 2009; Peiman & Robinson, 2010). 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 in 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. Jones, Harris, & Siefferman, 2014; Martin & Martin, 2001b). Agonistic interactions resulting from interference competition should drive character displacement (reviewed in Grether, Losin, Anderson, & Okamoto, 2009). That is, selection should drive divergence of traits associated with species recognition until interspecific aggression is

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reduced (Grether et al., 2009; Orians & Willson, 1964). Indeed, a global analysis of avian plumage characteristics found that species that breed sympatrically tend to show high levels of colour divergence that follow patterns of character displacement (Martin, Montgomerie, & Lougheed, 2015).

As the costs and benefits of aggression are context dependent (Andersson, Wiklund, & Rundgren, 1980; Duckworth, 2006; Mover. 1968), interspecific aggression is expected to be maladaptive when the aggressor does not benefit (reviewed in: Grether et al., 2009; Ord & Stamps, 2009). An alternative hypothesis to explain interspecific aggression is mistaken identity (reviewed in: Murray, 1971, 1981; Tinbergen, 1936): the lack of discriminatory ability promotes misdirected conspecific aggression (i.e. misidentification) between heterospecifics. Mistaken identity may be viewed as exaptive (i.e. traits that have been selected for in one function but that also function adaptively in another context; Gould & Vrba, 1982) 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 and use ecologically similar resources, misdirected aggression towards heterospecifics may convey a net benefit as if they were conspecific competitors. For example, Nishikawa (1985, 1987) documented evidence for both hypotheses in two salamanders (Plethodon jordani and Plethodon glutinosus) of the southern Appalachian Mountains, suggesting that misidentification may be exaptive. Contrarily, Korner, Whiting, Willem, and Ferguson (2000) found that Waterberg flat lizards, Platysaurus minor, misidentify orange-throated flat lizards, *Platysaurus 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, Petrusek, Pavel, and Fuchs (2008) documented that meadow pipits, *Anthus pratensis*, misidentify tree pipits, *Anthus 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. Petrusková et al.'s (2008) study suggests that species recognition is a product of both auditory and visual cues. 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, U.S.A., agonistic interactions occur between golden-winged warblers, Vermivora chrysoptera, and chestnut-sided warblers, Setophaga pensylvanica, and can be initiated by either species. Like many Neotropical migrants, both species are experiencing declines in overall population sizes (Sauer et al., 2014). Yet, golden-winged warblers that breed in the Appalachian Mountains are experiencing particularly extreme declines (Buehler, Roth, Vallender, & Will, 2007; Sauer et al., 2014), and thus are a species of significant conservation concern (Roth, Rohrbaugh, Will, & Buehler, 2012). For example, in North Carolina, 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 focusing on how golden-winged warblers' behavioural characteristics influence reproductive success, habitat selection and community structure (Confer, Hartman, & Roth, 2011; Confer & Larkin, 1998). Several factors have been identified as potential contributors to their decline, including habitat loss (Buehler et al., 2007; Klaus & Buehler, 2001) and hybridization with bluewinged warblers, *Vermivora cyanoptera* (Confer et al., 2011; Vallender et al., 2009). 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, 2001b) documented agonistic interactions between orange-crowned warblers, *Oreothlypis celata*, and Virginia's warblers, *Oreothlypis 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 aggressive heterospecifics, but it has not been considered to be a potential contributor of this species' decline (reviewed in Confer et al., 2011).

Because interspecific aggression is inherently risky (reviewed in Moyer, 1968; Ord, King, & Young, 2011; Ord & Stamps, 2009), it is logical that aggressive interactions between golden-winged and chestnut-sided warblers may result from competition for limited resources (e.g. Martin & 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 & Brauning, 2013). At the territory level, habitat characteristics (e.g. percentages of ground, shrub and canopy cover) appear similar (Collins, James, & Risser, 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 (Jones, n.d.). 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 owing to the loss of available habitat in the southern Appalachian Mountains (Klaus & Buehler, 2001). Increased sympatry could promote negative ecological and behavioural interactions (Martin & Martin, 2001a, 2001b) 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 & Siefferman, 2014; Supplementary Fig. S1) but may still theoretically be the stimulus of misidentification. One limitation to the avian vision model (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013) used by Jones and Siefferman (2014) is that it does not incorporate brief glimpses. Indeed, without an appropriate acoustic stimulus 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 phenomenon may occur between wood warblers.

Here, we tested whether aggressive behaviours 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. We addressed three questions: (1) does aggression vary with interspecific density; (2) do chestnutsided warblers influence reproductive success; and (3) do chestnut-sided warblers or habitat play a larger role in reproductive success? If competition occurs between these warbler species, we predicted 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: 850-1645 m) of northwestern North Carolina (Watauga, Avery and Ashe counties) and eastern Tennessee (Carter County) across seven field sites that encompassed a variety of early-to-mid successional habitats (e.g. grassland, shrubland, bog) adjacent to mature hardwood forests within field sites. Most fields were adjacent to each other; we found no statistical difference in behavioural response between sites for either species in either year 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 U.S. Geological Survey band and a unique combination of colour bands for remote identification.

Assessment of Competition: 2014 Correlational Study

Estimating chestnut-sided warbler density

In 2014, we followed golden-winged warbler males and recorded perches using GPS data to generate maps of individual territories (mean number of spot-mapped points per bird: 43 ± 21.5). We obtained \geq 30 mapped points per bird across \geq 30 days to reliably estimate their territory extent (Barg, Jones, & Robertson, 2004; Seaman et al., 1999). Spatial boundaries of each male's territory were generated using the 'genmcp' command in Geospatial Modelling Environment (Beyer, 2009) and imported into ArcMap 10.1 (ERSI, Redlands, CA, U.S.A.).

We conducted avian census surveys (hereafter: point counts) of chestnut-sided warblers while golden-winged warbler territory mapping was ongoing (9–16 May 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 (J.A.J.) conducted 3 min passive point counts (i.e. no playback) and counted chestnut-sided warblers heard from the point centre. All point counts occurred between 0530 and 1130 hours Eastern Daylight Time (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 neighbour spatial interpolation, a technique used when data points (here, point counts) are distributed unevenly (Sibson, 1981), 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 goldenwinged 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: McCallum, 2005; Thompson, 2002). 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 have over- or underestimated 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 were necessary to tease apart fine differences in chestnut-sided warbler density.

Aggressive response towards song playback

To estimate aggressive behaviours, we conducted simulated territorial intrusions (STIs) in which we recorded behavioural responses of male golden-winged warblers towards conspecific playbacks, under the assumption that the response to a conspecific STI would similarly reflect that of a heterospecific (e.g. Duckworth, 2006); our preliminary field work showed that neither warbler responds aggressively towards heterospecific playback. Thus, to estimate aggressive behaviours, we used conspecific playback for all STIs. Behavioural trials took place from 4 May to 3 June 2014, between 0530 and 1130 hours EDT. First, we located each territorial male the morning of the experiment and set up a speaker ca. 2 m high, adjacent to a known (i.e. mapped) perch in the centre 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 & Martin, 2001a) and retreated to a distance of at least 40 m. 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 & Brauning, 2013). During each STI, we noted the following behaviours: latency to approach the playback source (<15 m; attentiveness of their territory); attack (dive) rate; number of songs the target species sang, distinguishing between type 1 (mate attraction) and type 2 (aggressive territorial defence) song types in golden-winged warblers (Ficken & Ficken, 1967; Murray & 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 the habitat structure of individual golden-winged warbler territories; NAIP imagery is high resolution (1 m) and is georeferenced. Although higher resolution spatial data are available (e.g. LiDAR), NAIP imagery offered the highest resolution obtainable that also occurred within 2 years of our field study; although plant communities have changed since 2012, field assessment confirmed that the habitat structure depicted in the imagery is consistent with 2014 vegetation structure (J. A. Jones, personal observation). We used five separate NAIP images to classify our seven field sites (Supplementary 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, homogeneous 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 percentage cover of each habitat cover type per individual golden-winged warbler territory (Supplementary Fig. S2) and used the total number of pixels per structure class to create a percentage cover estimate of each class per bird territory.

Golden-winged warbler reproductive success

Females generally arrive at our field sites about 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 chestnutsided warbler abundance. Despite limiting our interpretation of the costs of sympatry between both warblers, we feel that an analysis of golden-wing nest success 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 reproductive success during the breeding season (e.g. predation, inclement weather that destroys the nest; J. A. Jones, personal observation), we used multiple proxies of reproductive success. We monitored golden-winged warbler nests every 3 days and recorded first egg date and clutch size. We used the laying date of the first egg (of the first nesting attempt) as a proxy of nest success, as reproductive success typically declines with later first egg dates in most migratory passerines (e.g. Alatalo, Lundberg, & Ståhlbrandt, 1984; Daunt, Wanless, Harris, & Monaghan, 1999: Verhulst, Van Balen, & Tinbergen, 1995), and specifically in golden-wings (Aldinger et al., 2015). To ensure that we used the laying date of the first clutch, we limited nests used in analysis to dates prior to 7 June, as this was the earliest date that we could confirm a second nesting attempt had its first egg. Finally, we recorded the success/fail rate of each nest as well as the number of offspring successfully fledged from the nest. Golden-winged warblers only attempt one successful nest per season, but will renest if the first attempt fails (Confer et al., 2011).

Assessment of Mistaken Identity: 2015 Experimental Set-up

Golden-winged warbler behavioural 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 behaviours for a shorter time frame than chestnut-sided warblers (personal observation) Second, there are far fewer breeding golden-winged than chestnut-sided warblers, so we aimed for the largest possible sample of territorial goldenwings. From 10 to 23 May, one researcher (J.A.J.) conducted conspecific simulated territorial intrusions of golden-winged warblers between 0600 and 1200 hours EDT following the protocol outlined in 2014. However, we analysed each STI in two 5 min segments: (1) 5 min of broadcast conspecific song without a visual stimulus and (2) 5 min of conspecific song coupled with a model of either a golden-winged or a 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 the 5 min interval prior to exposure to the model bird, we noted the following behaviours: (1) time to approach the playback source; (2) the number of dives/attacks; (3) the number of 'flythroughs' (defined as flying around the speaker/model, but not directly attacking it); (4) countersinging (distinguishing between type 1 and type 2 songs); (5) chipping rate; and (6) soft songs. Golden-winged warblers often aggressively chip when stimulated by conspecific STI (J.A. Jones, personal observation), and we interpreted this behaviour 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 second 5 min segment.

Chestnut-sided warbler behavioural assays

From 19 May to 10 June 2015 at between 0600 and 1200 hours EDT, we conducted STIs with focal chestnut-sided warblers. Because the population size of chestnut-sided warblers far exceeds that of golden-winged warblers in our field sites, each chestnutsided warbler was only presented with one bird dummy (conspecific, heterospecific or control (American goldfinch, Carduelis tris*tis*)) 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 behavioural analysis; models were selected randomly for individual birds. For chestnut-sided warblers, we recorded the same flight behaviour variables as golden-wings (latency, dive rate, 'flythroughs') and total countersinging rate for the first 5 min segment and attack (yes/no) for the second. On occasion, we observed 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 coloured to resemble real birds using coloured pencils. We found that coloured 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 carotenoid-based pigments in these wood warblers (Jones & Siefferman, 2014). The use of dummy birds also ensured that each bird encountered a near-identical stimulus. We retaped feathers as the season progressed to ensure a full crown of feathers. The American goldfinch model was not hand carved but 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 were sufficient for our questions on misidentification. Unfortunately, we were unable to investigate how golden-wings behave towards an STI with a conspecific song and an American goldfinch; after we had completed the second behavioural trial for each individual, goldenwinged warblers were well into nest construction and at this time, they tend to be significantly less territorial and aggressive at our field sites (J. A. Jones, personal observation).

There are two important caveats to our 2015 experiment. First, we did not use a heterospecific song playback associated with the heterospecific bird model for either focal warbler species because (1) our previous work showed that warblers do not respond aggressively to heterospecific song playback (Jones, n.d.) and their songs are distinct (Confer et al., 2011; Richardson & Brauning, 2013) and (2) the scope of our study focused on visually based misiden-tification. We expected 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. Second, for all STIs of both warbler species, only one song and dummy bird exemplar were used. For song exemplars, we used song to direct the attention of focal warblers to the dummy birds in order to see how the warblers would respond to the model rather than how they would respond to the song. For model exemplars, the crown plumage was created by layering feathers from multiple males (captured in 2014). However, focal birds did not view models with the same crown ornamentation; we replaced feathers as needed because feathers were displaced by birds (attacking) and environmental conditions (i.e. wind).

Statistical Analysis

All statistical analyses were performed using SPSS v.22 (IBM, 2013). Using a Pearson 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. Using laying date as a proxy of nest success, we used a generalized linear model, where laying date was the dependent variable and chestnut-sided warbler density and habitat were covariates. We ran an additional generalized linear model with clutch size 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 bestfitting model (Burnham & 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 correlation between the number of offspring successfully fledged from the nest and chestnut-sided warbler density and habitat.

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 cross-tab chi-square tests to investigate whether the likelihood that the warblers attacked the model varied (yes/no) between 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 behaviours as covariates.

Ethical Note

We conducted this study in strict accordance to the Institutional Animal Care and Use Committee of Appalachian State University (no. 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 United States Fish and Wildlife master banding permits no. 23563 (L.S.) and no. 23218 (C.G.S.) and North Carolina Wildlife Resource Commission no. 14-ES00385 (C.G.S.).

RESULTS

Assessment of Competition

Relationship between heterospecific density, aggression and habitat

Of 343 point counts conducted throughout seven field sites, we recorded chestnut-sided warblers in 94% whereas golden-winged warblers were detected in 61%. Golden-winged warbler territory

(N = 48) sizes were on average 2.47 (±1.72 SD) ha and contained, on average, 1.88 (±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).

Whether golden-winged warblers were paired or not was not related to behavioural response to conspecific playback (all $t_{34} < 1.17$, all P > 0.25). Thus, we analysed all males together. We found that golden-winged warblers in territories among high densities of chestnut-sided warblers dived at the speaker more often ($r_{35} = 0.34$, P = 0.05; Fig. 1a) and counter-sang with their type 1 song less often ($r_{35} = -0.37$, P = 0.03; Fig. 1b). Latency to arrive within 15 m of the speaker ($r_{35} = -0.12$, P = 0.49) and type 2 countersinging ($r_{35} = 0.07$, P = 0.71) were not significantly related to chestnut-sided warbler density. Golden-winged warblers that dived more often arrived more quickly ($r_{36} = 0.69$, P < 0.001), but dive rate was not significantly associted with singing rate (either type 1 or type 2 songs; P > 0.10).

We found that the shrubland habitats made up the bulk of territory composition for golden-winged warblers (mean \pm SD: $48 \pm 13\%$), followed by forest ($30 \pm 16\%$), grassland habitats $(19 \pm 16\%)$ and finally abiotic components (i.e. roads; $3.0 \pm 0.6\%$). We used a principal components analysis (PCA; PC1-habitat and PC₂-habitat), which explained 80.8% of the variance between two components, to explore vegetation within an individual's territory (Supplementary Table S2). Open habitat loaded heavily on PC1habitat, such that high PC1-habitat scores represented less forest and shrubland cover but high cover of homogeneous/grassy habitat: Supplementary Table S2). Principal component 2 habitat loaded with remaining vegetation, such that high PC₂-habitat scores were associated with forested/canopy habitat whereas negative scores were shrubland habitats (Supplementary Table S2). When the density of chestnut-sided warblers was greater within individual golden-winged warbler territories, these locations had high PC₁-habitat scores (greater percentage 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 (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 $\chi^2_{1,24} = 7.28$, P = 0.01), but chestnut-sided warbler density did not contribute significantly to this model (Wald $\chi^2_{1,24} = 2.27$, P = 0.13). In addition, PC₂-habitat alone was a strong model in predicting earlier egg dates (i.e. $\Delta AIC_C < 2$; Table 1). Next, we found strong support for three models to best explain clutch size (i.e. $\Delta AIC_C < 2$). The best-supported model to predict clutch size was laying date alone (Table 2). However, two other models were also supported: earlier egg dates were associated with (1) increases in shrubland cover (PC₂-habitat) and (2) decreases in grassland cover (PC₁-habitat; Table 2). Although chestnut-sided warbler densities were components in the first egg date model, heterospecific density alone had only a marginal influence on clutch size (likelihood $\chi^2_{1,24} = 3.05, P = 0.08$). 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 Identity

For our 2015 behavioural analysis, we ran a PCA for flight behaviours for the 5 min behavioural trial prior to exposure to the



Figure 1. Golden-winged warbler behavioural response to conspecific playback relative to densities of chestnut-sided warblers (a) rate of diving at the speaker and (b) rate of countersinging with the territorial (type 1) song.

model bird; the models produced one principal component per species (golden-wing: PC₁-GWWA, variance = 58.2%; chestnutsided: PC₁-CSWA, variance = 59.7%; Supplementary Table S3). In general, higher PC scores were associated with birds that were more aggressive (i.e. birds that arrived sooner and attacked/flew around the speaker more often; Supplementary Table S3). In addition, we ran a second PCA to condense golden-wing acoustic responses to conspecific stimuli prior to model exposure (Supplementary Table S4). Here, the number of songs (type 1, type 2, soft songs) and aggressive chips created two principal components (PC₁-acoustic and PC₂-acoustic) explaining 76.4% of the variance. High PC₁-acoustic scores were associated with producing a greater number of aggressive song types (i.e. type 2 and soft songs), whereas high PC₂-acoustic scores were associated with producing a greater number of aggressive chips and fewer type 1



Figure 2. Nest commencement date for female golden-winged warblers relative to PC_2 -habitat. High PC_2 -habitat scores are associated with forested habitat whereas negative scores represent shrubland habitats.

songs (Supplementary Table S4). We do not have a PCA for chestnut-sided warbler vocal behaviours because we only quantified total songs that were sung in response to conspecific playback.

Golden-winged warblers

We found that golden-winged warblers were equally likely to attack or not to attack both the conspecific model (11 attacks of 28 trials; $\chi^2_{1,28} = 1.29$, P = 0.26) and the heterospecific (chestnutsided) model (12 attacks of 25 trials; $\chi^2_{1,25} = 0.40$, P = 0.84) during STIs. Using the cross-tab analysis, we found no statistical difference in the likelihood of attacking conspecific over heterospecific models (Pearson $\chi^2_{1,25} = 2.54$, 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 (Fig. 3, Table 4). However, the only significant main effect in this model was PC₂-acoustic: golden-winged warblers that aggressively chipped and sang their type 1 song less were more likely to attack the heterospecific model (Wald $\chi^2_{1,24} = 4.93$, P = 0.03), but PC₁-acoustic did not contribute significantly to the model (Wald $\chi^2_{1,24} = 1.88$, P = 0.17). Although we found support for another model ($\Delta AIC_C < 2$; PC₁-acoustic, PC₂-acoustic, PC₁-GWWA; Table 4), PC₂-acoustic 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 one attack of 29 trials; $\chi^2_{1,29} = 25.14$, P < 0.001), but they were equally likely to attack or not to attack the conspecific model (15 of 32 trials; $\chi^2_{1,32} = 1.25$, P = 0.72) and the heterospecific (golden-winged) model (20 of 38 trials; $\chi^2_{1,38} = 0.11$, P = 0.75) during STIs. Moreover, we found a marginally significant relationship suggesting that chestnut-sided warblers were more likely to attack a conspecific model than a heterospecific (golden-winged warbler) model (Pearson $\chi^2_{1,32} = 3.14$, P = 0.08). After model selection, we found that countersinging rate was the best predictor of attacking the heterospecific model (Fig. 4a, Table 5); chestnut-sided warblers

Table 1			
Model selection for variables that	t influenced egg-lavin	g dates of golden-w	inged warblers

Model	AIC _C	ΔAIC _C	Wi	Likelihood χ^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. PC1-habitat	170.94	8.32	0.01	2.94	0.23

CSWA: chestnut-sided warbler density; PC₁-habitat: open homogeneous/grassy habitat; PC₂-habitat: shrubland habitat. Models are organized by Akaike weights (*w_i*); the best-fitting model is in bold.

Table 2

Model selection for variables that influenced golden-winged warbler first-attempt clutch sizes

Model	AIC _C	$\Delta \text{AIC}_{\text{C}}$	w _i	Likelihood χ^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, PC1-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, PC1-habitat, PC2-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, PC1-habitat, PC2-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, PC1-habitat	57.56	9.83	0.00	3.69	0.16

FED: first egg date; CSWA: chestnut-sided warbler density; PC₁-habitat: open homogeneous/grassy habitat; PC₂-habitat: shrubland habitat. Models are organized by Akaike weights (w_i); the best-fitting model is in bold.

that counter-sang less during STIs were more likely to attack the heterospecific model. Although not a well-supported model, flight behaviours (PC₁-CSWA) were none the less a significant predictor of heterospecific attack (Fig. 4b, Table 5); chestnut-sided warblers that dived more often prior to exposure to the model were more likely to attack the heterospecific model.

DISCUSSION

We concentrated our field efforts on understanding how sympatry with chestnut-sided warblers influences behaviour and reproductive success of golden-winged warblers because golden-wings are rapidly declining in the Appalachian Mountains (Sauer et al., 2014) and agonism is a costly behaviour (reviewed in: Grether et al., 2013; Moyer, 1968). 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. PC₂-habitat scores; Fig. 2), rather than chestnut-sided warbler density, that predicted reproductive success of golden-winged warblers (as

Table 3

Relationship between nest fate (*t* test) and fledgling numbers (Pearson correlation) relative to chestnut-sided warbler density (CSWA) and habitat variables

	Nest fate		Fledgling numbers		
	t ₂₂	Р	r ₂₃	Р	
CSWA PC ₁ -habitat	0.25 0.79	0.80 0.44	-0.19 -0.17	0.93 0.42	
PC ₂ -habitat	0.88	0.39	-0.11	0.62	

 PC_1 -habitat: open homogeneous/grassy habitat; PC_2 -habitat: shrubland habitat.

defined by first egg date and clutch size). We expected shrubland cover to predict reproductive output; nesting locations for goldenwinged 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 density of chestnut-sided warblers was a main effect in the best-supported model for first egg dates, this parameter is probably spurious/uninformative; the difference between the two best-supported models for first egg date was only one main effect (chestnutsided 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 results suggest that interspecific aggression is a function of misidentification rather than interspecific competition for shared resources, and that coexistence is probably not detrimental for golden-winged warbler reproductive success. None the less, the act of agonism is probably maladaptive and selection should act on individuals to diverge in traits associated with species recognition to reduce the occurrence of aggression.

Although golden-winged warblers were more aggressive towards conspecific stimuli when their territories encompassed a greater density of chestnut-sided warblers, high heterospecific density did not lead to lower reproductive success. We offer several nonmutually 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



Figure 3. Behavioural response of golden-winged warblers to conspecific stimuli prior to exposure to the heterospecific model that they did or did not attack. High PC_{2} -acoustic scores are associated with more of the aggressive chips and fewer type 1 songs. Error bars are 95% confidence intervals.

Table 4

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vlodel selection for variables that best p	predicted whether or not golden-v	vinged warblers would attack a	heterospecific bird model

Model	AIC _C	ΔAIC _C	w _i	Likelihood χ^2	Model P
PC ₁ -acoustic, PC ₂ -acoustic	24.50	0.00	0.50	15.97	<0.001
PC ₁ -acoustic, PC ₂ -acoustic, PC ₁ -GWWA	25.93	1.43	0.24	17.45	0.001
PC ₂ -acoustic	26.98	2.48	0.14	10.86	0.001
PC ₂ -acoustic, PC ₁ -GWWA	27.46	2.97	0.11	13.01	0.001
PC1-GWWA	34.48	9.98	0.00	1.17	0.28
PC ₁ -acoustic	37.99	13.50	0.00	1.63	0.20
PC ₁ -acoustic, PC ₁ -GWWA	38.10	13.60	0.00	2.37	0.31

PC₁-acoustic: type 2 and soft songs; PC₂-acoustic: aggressive chips and type 1 songs; PC₁-GWWA: golden-winged warbler flight behaviours. Models are organized by Akaike weights (w_i); the best-fitting model is in bold.

may use a strategy of high aggression to secure mates. For example, in house finches, *Carpodacus mexicanus*, aggressive behaviour has been explained as a compensatory strategy whereby lower-quality and less attractive males invest heavily in aggression to secure breeding success (Hill, 2002; Stoehr & Hill, 2000). Second, it is possible that high-density breeding sites increase predation risk (Martin, 1988, 1993) and warblers that are more aggressive to STIs may be more aggressive towards predators, as seen in dark-eyed juncos, *Junco hyemalis* (Cain, Rich, Ainsworth, & Ketterson, 2011). Third, because agonism occurs between the two species, male



Figure 4. Behavioural response of chestnut-sided warblers to conspecific stimuli prior to exposure to the heterospecific model that they did or did not attack. (a) Countersinging and (b) flight behaviours. High PC₁-CSWA scores represent fast response times and more frequent diving at the speaker. Error bars are 95% confidence intervals.

golden-winged warblers with territories among many chestnutsided warblers are probably challenged often. Increases in testosterone associated with heightened aggressive behaviours may explain these behavioural patterns. If aggressive individuals respond more quickly rather than with more accuracy in aggressive encounters (reviewed in Sih & Del Giudice, 2012), they may be more likely to attack heterospecific models.

None the less, it appears that, from the golden-wing perspective, coexistence is not detrimental for 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 behaviour. More powerful tests of interspecific competition involve manipulating a resource or the presence of interspecific competitors (reviewed in: Dhondt, 2012; e.g. Martin & 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 an effect of chestnut-sided warblers on golden-wing reproductive success is particularly relevant for their management. Throughout the southern Appalachians, golden-wings occur in much lower densities than chestnut-sided warblers. Thus, if competition were to occur between these two species, golden-wings would probably suffer greater negative effects than would chestnut-sided warblers.

We found that both warbler species were equally likely to attack the heterospecific and conspecific models (ca. 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. That is, chestnut-sided warblers do not appear to lack the ability to correctly identify their species, and mistaken identity may be restricted to those with more aggressive phenotypes. Only one chestnut-sided warbler attacked the goldfinch model, suggesting that the warblers do not readily attack any heterospecifics in the area. Rather, it seems likely that the yellow crown coloration is the visual cue that triggers attack behaviour. 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 signalling space (i.e. the crown) should be visually distinctive (Jones & Siefferman, 2014), but

Table 5

Model selection for variables that best predicted whether or not chestnut-sided warblers would attack a heterospecific bird model

Model	AIC _C	$\Delta \text{AIC}_{\text{C}}$	wi	Likelihood χ^2	Model P
Countersinging 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, countersinging rate	48.65	6.85	0.03	10.63	0.005

PC₁-CSWA: chestnut-sided warbler flight behaviours. Models are organized by Akaike weights (w_i); the best-fitting model is in bold.

it may be that brief views do not allow for enough cognitive processing time to discriminate the colours that otherwise would be visually distinctive upon close examination. To our knowledge, neurological processing time has not been incorporated into models of avian colour vision. None the less, because these warblers do not respond to heterospecific song playback, it is likely that mistaken identity is based on visual, rather than acoustic, signals.

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 probably no benefit to risky behaviours (King, 1973; Moyer, 1968). It is possible that selection pressures to avoid interspecific aggression may drive divergence of crown colour (i.e. agonistic character displacement; Grether et al., 2009). Agonism associated with colourdriven misidentification could influence the evolution of plumage coloration in birds; closely related bird species tend to show greater divergence in colour patterns when sympatric (i.e. character displacement; reviewed in Martin et al., 2015). Importantly, as these warblers appear to coexist peacefully most of the time, our findings do not suggest that warblers are entirely incapable of recognizing heterospecifics. Indeed, we promoted aggression and probably 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. In an anecdotal report, Ficken and Ficken (1968) found that golden-wings that behave aggressively towards chestnut-sided warblers sing their type 2 song afterwards. Thus, aggression may be a product of mistaken identity, as indicated by vocal behaviours that are usually reserved for conspecific encounters (Ficken & Ficken, 1968).

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, in both species, there was no statistical difference in the likelihood of attacking the conspecific or heterospecific model. It may be that only certain individuals are stimulated by models or that aggressive individuals did not take adequate time to investigate and identify them. Indeed, we observed that focal birds often ceased attacking after closer inspection of the model.

There are three important limitations to our misidentification study, however. First, we used only one song and one dummy exemplar, which raises concerns of pseudoreplication at the level of the exemplar. Although we used song only to direct the attention of birds to the model, it is possible that we could have inflated the number of heterospecific model attacks if our single conspecific playback song exemplar was more similar to the heterospecific song than a typical song. However, these two warbler species have markedly distinct song characteristics, so we feel that using a single song recording is unlikely to have compromised our results. Additionally, at first glance, having used a single model dummy bird per species may appear to be problematic. However, the feathers on the wooden models were (1) a combination of multiple birds and (2) replaced as needed throughout the study. Thus, the plumage ornamentation of our models varied through time. Another limitation is that we only used a control (goldfinch) model during chestnut-sided warbler STIs because of time constraints on fieldwork. Yet, our results demonstrate that, in both warbler species, individuals that were less aggressive to conspecific playback were the least likely to misidentify a heterospecific as a conspecific. Thus, it seems likely that both species misidentify one another based on morphological similarity and not that they attack any bird in the area when stimulated by conspecifics. Finally, we do not have data to evaluate

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. None the less, because we were unable to quantify the effects of chestnut-sided warblers on golden-wing warbler adult body condition or survival, we cannot rule out the possibility that fitness consequences of sympatry exist. However, it seems likely that misidentification is the explanation for interspecific aggression.

In this study, we documented the importance of integrating behavioural research with conservation biology and of studying how at-risk species interact with their community (Anthony & Blumstein, 2000; Caro & Sherman, 2013; Linklater, 2004). Although we lack data from the chestnut-sided warbler perspective, we focused on addressing how interspecific interactions influence golden-winged warbler reproductive success 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 behaviour for goldenwinged warblers if aggression does not improve their ability to secure resources (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; Martin & Martin, 2001a, 2001b; Morse, 1974). Further research on the aggressive interactions between these warblers is needed to better understand the associated costs of agonism on the physical state (e.g. physiological (stress)) of adult birds and any costs of interspecific aggression.

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Supplementary Material

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