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Say what? Bivalent singing in *Vermivora* warblers

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Birdsong has captivated humans throughout recorded history. Birdsong is incredibly diverse as is the process of song learning (Kroodsma 2004, Beecher and Brenowitz 2005). Songbirds (Order: Passeriformes) are categorized into two broad groups based on whether they learn their songs (oscine) or whether the development of species-appropriate songs is innate (suboscine; Kroodsma 2004) although there are exceptions like suboscine bellbirds (*Procnias* spp.) that learn and can change their songs over time (Kroodsma et al. 2013). Over the past ~100 yr, the singing behaviors of oscine species (i.e., songbirds that learn their songs) have been of significant research interest (Kroodsma 2004). Generally, song acquisition in juvenile oscine songbirds is a form of motor learning involving three distinct periods: memorization, practice, and crystallization (Beecher and Brenowitz 2005).

Memorization involves learning song characteristics and practice involves attempting and becoming more proficient at producing a song that matches or closely imitates a memorized song. Song crystallization typically occurs before an individual's first breeding season in many oscine songbirds at which point individuals lose the ability to learn new songs (i.e., close-ended song learning; Beecher and Brenowitz 2005). Some species of oscine songbirds exhibit open-ended song learning and retain the ability to learn and crystallize the songs of many species throughout their life (i.e., mimics). However, bivalent singing, or the ability to sing songs typical of two species, is rarely observed in oscine songbirds that exhibit a close-ended song-learning process (Kroodsma 2004).

Golden-winged Warblers (*Vermivora chrysoptera*) and Blue-winged Warblers (*Vermivora cyanoptera*; hereafter *Vermivora* warblers) are two Nearctic-Neotropical migrant songbirds that exhibit close-ended song learning and are extremely closely related (Kroodsma 1988, Toews et al. 2016). Their breeding distributions overlap and they regularly hybridize to produce viable young (Vallender et al. 2007). Early generation hybrids are readily identifiable by distinct plumage characteristics and later generation hybrids can typically be identified with careful examination of multiple plumage traits (Toews et al. 2016). The plumages of phenotypically pure Golden-winged Warblers and Blue-winged Warblers are strikingly dissimilar and easily differentiable (Parkes 1951; Fig. 1). Similarly, the primary songs (i.e., Type I, generally used for mate attraction) of each species are visually distinct on sonograms and audibly distinct to the human ear (Ficken and Ficken 1967; Fig. 2a, b). *Vermivora* warblers' repertoires also include a secondary song (i.e., Type II, often used during agonistic interactions with other males) that is more similar between species (Gill and Lanyon 1964, Ficken and Ficken 1967). Primary song and plumage phenotype are typically congruent within an individual (i.e., individuals sing the primary song that matches their plumage phenotype). Occasionally, individuals with phenotypically pure plumage traits sing the primary song of the other species (i.e., phenotypic mismatch; Ficken and Ficken 1967) and hybrid individuals tend to sing a primary song that is typical of one parent species despite having intermediate plumage traits (although there are anecdotal observations of hybrid *Vermivora* warblers singing the songs of both parent species; Carter 1944). To date, there have been no confirmed observations of phenotypically pure *Vermivora* warblers that sing the primary songs of both species (Ficken and Ficken 1967, Russell 1976). Furthermore, it is a common perception that individual *Vermivora* warblers (and individuals of many other New World warbler species) sing only one primary song throughout their lifetime

and do not switch between distinct song types (Kroodsma 1988).

We monitored individually marked *Vermivora* warblers and recorded their songs and singing behavior at sites across their breeding distribution as part of a study of the migratory connectivity of this species complex from 2013 to 2017 (Kramer et al. 2018; Fig. 1). During our field efforts, we observed individual *Vermivora* warblers singing the primary songs of both Golden-winged Warblers and Blue-winged Warblers in separate years ($n = 3$ individuals) and even switching back and forth between the songs of each species in the same singing bout ($n = 1$ individual). We first observed inter-annual song-switching in Anderson County, Tennessee, USA (36.21° N, 84.36° W) when a Golden-winged Warbler that sang a typical Golden-winged Warbler song in May 2013 occupied the same breeding territory in May 2014 singing a typical Blue-winged Warbler song. We did not obtain an audio recording of this bird in either year, but four of us (G. Kramer, S. Peterson, D. Buehler, H. Streby) observed the bird singing in both years and it was uniquely marked with colored leg-bands. We observed similar inter-annual song-switching behavior from May to June in 2015–2016 in two *Vermivora* warblers from different sites in the Appalachian Mountains region. First, we observed and recorded (Appendix S1: Table S1) audio of a Blue-winged Warbler in Centre County, Pennsylvania, USA (40.99° N, 77.70° W) that switched from singing a typical Blue-winged Warbler song in May 2015 to singing a monotonic Golden-winged Warbler song in May 2016 (Fig. 2c). Similarly, we observed and recorded audio of a Golden-winged Warbler in Leeds and Grenville United Counties, Ontario,

Canada (44.64° N, 76.34° W) singing a Blue-winged Warbler song in May 2015 and singing a typical Golden-winged Warbler song in June 2016 (Fig. 2d). In all three of these cases, we observed individuals singing only one primary song type in each year during the duration our field efforts (typically totaling several hours of observation on different days and at different times over the course of ~1–2 weeks at each study site). Last, we observed and recorded audio of a Golden-winged Warbler in Frontenac County, Ontario, Canada (44.53° N, 76.37° W) singing both Golden-winged Warbler songs and Blue-winged Warbler songs during the same singing bout (~10 min) in May 2015 (Fig. 2e). All individuals we observed switching songs between subsequent breeding seasons were birds that we marked with unique combinations of color bands and with uniquely numbered aluminum bands (U.S. Geological Survey and Canadian Wildlife Service bands in the U.S. and Canada, respectfully), and we captured each of these birds in each year of the study (i.e., 100% identification confidence). During our observations of the individual Golden-winged Warbler that switched between the primary songs of both species in the same bout, there were no other *Vermivora* warblers in the vicinity (~500 m) and one of us (G. Kramer) maintained uninterrupted visual contact with the individual and recorded audio of the song-switching.

Our observations of bivalent singing in *Vermivora* warblers raise questions about the role of song in these and other species. Songbirds like *Vermivora* warblers typically sing only one type of primary song throughout their lives (Gill and Murray 1972, Kroodsma 1988). Our observations suggest that singing behavior may be more variable

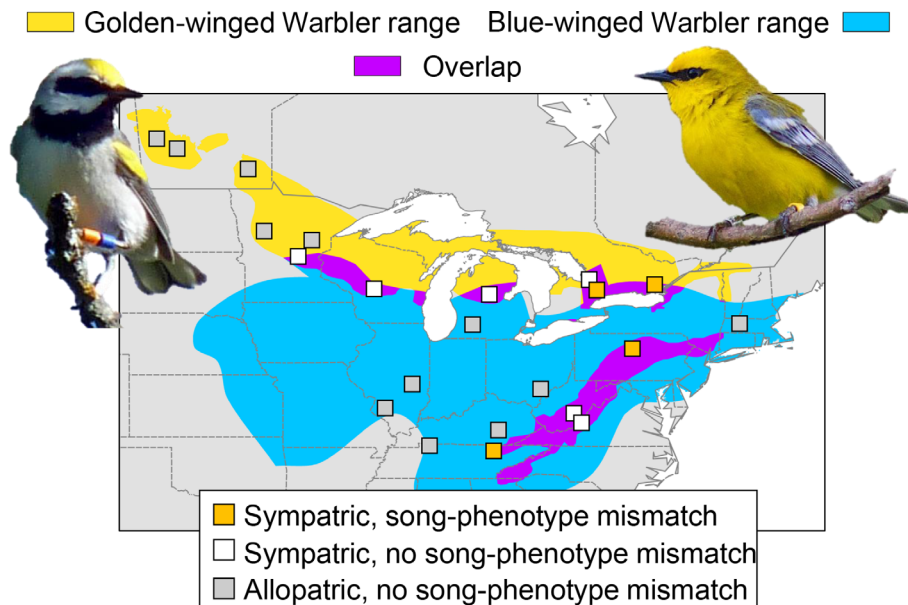


FIG. 1. Breeding distribution map of Golden-winged Warblers (left) and Blue-winged Warblers (right) and sites where we recorded the songs of one or both species from 2013 to 2017.

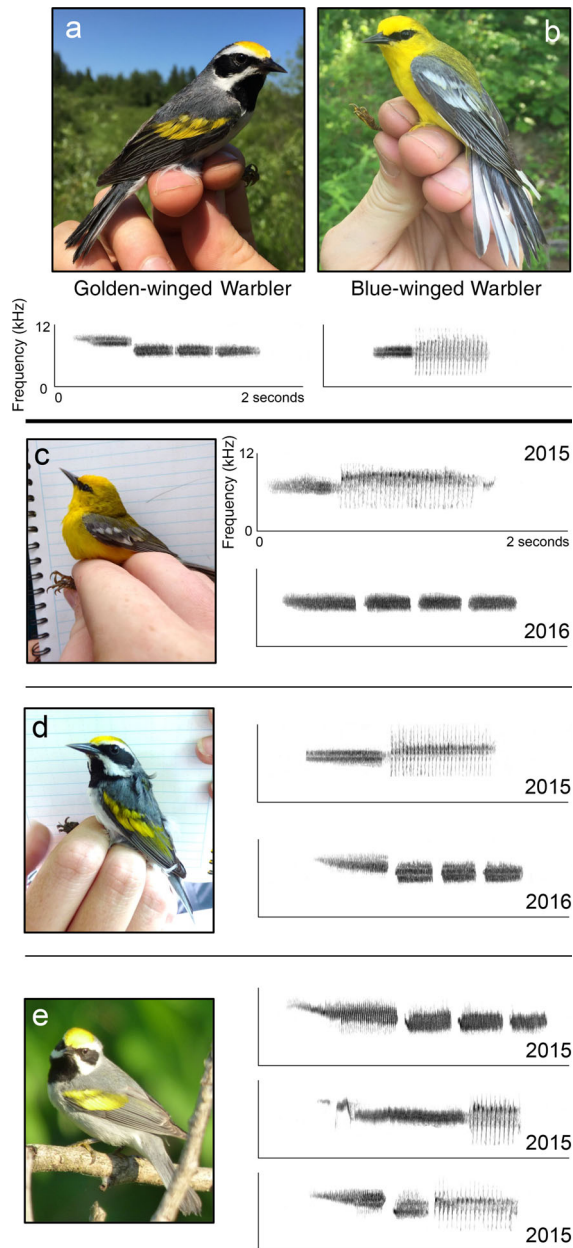


FIG. 2. Typical plumage and sonograms of an exemplar primary song of (a) Golden-winged Warblers and (b) Blue-winged Warblers. (c) Photo of adult male Blue-winged Warbler in Pennsylvania, USA that sang a typical Blue-winged Warbler song in 2015 but switched to singing a monotonous Golden-winged Warbler song in 2016. (d) Photo of adult male Golden-winged Warbler in Ontario, Canada that sang a typical Blue-winged Warbler song in 2015 but exclusively sang a Golden-winged Warbler song in 2016. (e) Photo of a Golden-winged Warbler in Ontario, Canada that was observed switching between Golden-winged Warbler songs and Blue-winged Warbler songs in the same singing bout in 2015. Scale of all sonograms is consistent across panels.

(or plastic) in *Vermivora* warblers than previously thought. Is it possible that all male *Vermivora* warblers are capable of singing both species' songs or does this only occur in areas of sympatry where young males hear both songs during development? Either way, what factors drive some individuals to switch songs within a single bout or between subsequent breeding seasons whereas others apparently sing the same song year after year? Throughout the course of our breeding-distribution-wide study, we observed the singing behaviors of thousands of *Vermivora* warblers and hundreds of individuals during two or more years. However, we only observed plumage phenotype-song mismatches, inter-annual song switching, and within-bout bivalent singing in areas of sympatry in the eastern portion of both species' breeding distributions (Vallender et al. 2007; Fig. 1). Abundance of *Vermivora* warblers has decreased significantly due to the loss of 98% of breeding population of Golden-winged Warblers in the Appalachian region since the 1960s (Rosenberg et al. 2016). Therefore, we speculate that male *Vermivora* warblers in this region may be responding to the decreased abundance of female *Vermivora* warblers (driven by the loss of female Golden-winged Warblers) by singing both species' songs in an attempt to attract any female *Vermivora* warbler as a mate.

Our observations have implications for understanding the role of song in the complicated hybridization dynamics of these species. Is bivalency a result of extensive historical hybridization (Toews et al. 2016), or a factor that is facilitating modern hybridization? There is no evidence of any fitness penalty for hybrid *Vermivora* warblers (Vallender et al. 2007). Therefore, being able to sing both species' songs and secure mating opportunities with females of both species may be adaptive for present-day male *Vermivora* warblers in the eastern portion of their breeding distribution.

These observations raise complicated questions about the species status of *Vermivora* warblers. Birdsong is thought to be a potentially isolating trait that may lead to speciation (Mason et al. 2017). However, our observations suggest that song type may not be a reliable indicator of genetic ancestry during mate selection in *Vermivora* warblers, at least in the eastern portion of both species' breeding distributions. So, what, if anything, does bivalent singing indicate to potential mates? And how will the prevalence of bivalent singing by *Vermivora* warblers change across space and time? If *Vermivora* warblers were considered a single polymorphic species, our observations would still raise questions about the role of song in assortative mating and the plasticity of song in an oscine songbird. Whether the genus *Vermivora* is comprised of a single, polymorphic species instead of two closely related species may be further elucidated by genomic studies, additional monitoring of *Vermivora* warbler

singing behavior, and investigations into the role of song in female mate choice and the fitness consequences of bivalent singing and hybridization across the *Vermivora* breeding distribution.

Last, that an individual *Vermivora* warbler may sing the songs of two putative species could complicate survey efforts (e.g., Breeding Bird Survey) if surveyors are unable to establish and maintain visual contact with singing individuals or if they assume individual warblers are only capable of singing one primary song type. Though our observations of bivalency and song-switching were relatively uncommon, they occurred exclusively in the eastern portion of both species' breeding distributions where Golden-winged Warbler abundance is relatively low (Rosenberg et al. 2016). Therefore, the erroneous identification of *Vermivora* warblers (based solely on singing behavior) during Breeding Bird Survey efforts may be more likely to bias estimates of abundance and distribution of Golden-winged Warblers in the Appalachian region.

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DATA AVAILABILITY

Audio recordings of individuals with relevant metadata are deposited at Xeno-Canto (www.xeno-canto.org; see Appendix S1: Table S1).

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2791/supinfo>