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RESEARCH ARTICLE

Divergence in plumage, voice, and morphology indicates speciation in Rufous-capped Warblers (*Basileuterus rufifrons*)

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ABSTRACT

The biodiversity of the Neotropics is considerable, but it is likely underestimated owing to gaps in sampling effort and a focus on using morphological features of animals to determine species differences rather than divergence in their mating signals and behavior. Recent multi-trait analyses incorporating morphological, plumage, and vocal data have allowed for more accurate quantification of tropical biodiversity. We present a comprehensive study of morphological features, plumage, and vocalizations of the Neotropical resident Rufous-capped Warbler (*Basileuterus rufifrons*). This species' taxonomic status is controversial because the *B. r. salvini* subspecies is intermediate in plumage coloration between the neighboring *B. r. delattrii* and *B. r. rufifrons* subspecies. Using morphological and spectral plumage measurements of field and museum specimens, as well as analyses of vocalizations from field recordings and sound libraries, we compared phenotypes of all 8 currently recognized Rufous-capped Warbler subspecies, with an emphasis on *delattrii*, *rufifrons*, and *salvini*. We found that *delattrii* and *rufifrons* differ significantly in morphology and plumage, and that *salvini* is similar to *rufifrons* in morphology and some plumage features. Vocalizations fall into 2 distinct groups, *delattrii* and *rufifrons-salvini*, which differ in multiple spectro-temporal characteristics with no overlap between them, even among individuals in the *delattrii–rufifrons* zone of sympatry. Our results therefore suggest that Rufous-capped Warblers comprise 2 distinct groups: Rufous-capped Warblers (*B. r. rufifrons* and *salvini* as well as *B. r. caudatus*, *dugesi*, and *jouyi*) and Chestnut-capped Warblers (*B. r. delattrii* as well as *B. r. actuosus* and *mesochrysus*). Future genomic analysis of samples from multiple sites in Mexico and Central America will further refine our assessment of range-wide phenotypic and genetic divergence in this species complex.

Keywords: Basileuterus rufifrons, Chestnut-capped Warbler, multi-trait analysis, Neotropics, Rufous-capped Warbler, song, species limits, subspecies

LAY SUMMARY

- The taxonomy of Rufous-capped Warblers is controversial: 8 subspecies exhibit divergent plumage color and songs and consequently they are sometimes treated as 2 separate species.
- Using field data, museum specimens, and sound archives, we compared the body size, plumage color, and songs of all 8 Rufous-capped Warbler subspecies.
- Seven of 8 subspecies comprised 2 groups with different color, songs, and body size: the northern, white-bellied *rufifrons* group and the southern, yellow-bellied *delattrii* group.
- The eighth subspecies, *salvini*, showed similarity to the *rufifrons* group, rather than being intermediate between the 2 groups as described in previous studies.
- We found that Rufous-capped Warblers comprise 2 separate groups, which improves our knowledge of Neotropical avian biodiversity.

Las divergencias en plumaje, voz y morfología indican especiación en *Basileuterus rufifrons*

RESUMEN

La biodiversidad del Neotrópico es considerable, pero está probablemente subestimada debido a las limitaciones en los esfuerzos de muestreo y a una costumbre de usar los rasgos morfológicos de los animales para determinar las diferencias entre especies más que las divergencias en sus señales de apareamiento y comportamiento. Análisis multi-rasgos recientes que incorporan datos morfológicos, de plumaje y vocales han permitido una cuantificación más precisa de la biodiversidad tropical. Presentamos un estudio integral de los rasgos morfológicos, del plumaje y de las vocalizaciones de la especie neotropical residente *Basileuterus rufifrons*. El estatus taxonómico de esta especie es controvertido porque la subespecie *B. r. salvini* es intermedia en la coloración del plumaje entre las subespecies vecinas *B. r. delattrii* y *B. r. rufifrons*. Usando medidas morfológicas y espectrales del plumaje de especímenes de campo y de museo, así como análisis de vocalizaciones de grabaciones de campo y de librerías de sonido, comparamos los fenotipos de las ocho subespecies actualmente reconocidas de *B. rufifrons*, con un énfasis en *delattrii*, *rufifrons* y *salvini*. Encontramos que *delattrii* y *rufifrons* difieren significativamente en morfología y plumaje, y que *salvini* es similar a *rufifrons* en morfología y algunos rasgos del plumaje. Las vocalizaciones cayeron en dos grupos diferentes, *delattrii* y *rufifrons-salvini*, los cuales difirieron en múltiples características espectro-temporales sin superposición entre ellos, incluso entre individuos en la zona de simpatría *delattrii–rufifrons*. Nuestros resultados por consiguiente sugieren que *B. rufifrons* abarca dos grupos diferentes: *B. r. rufifrons, salvini, caudatus, dugesi* y *jouyi* por un lado, y *B. r. delattrii, actuosus* y *mesochrysus* por el otro. Futuros análisis genómicos, con muestras provenientes de múltiples sitios en México y América Central mejorará aún más nuestra evaluación sobre la divergencia fenotípica y genética en todo el rango de este complejo de especies.

Palabras clave: análisis multi-rasgos, *Basileuterus rufifrons*, *B. r. delattrii*, *B. r. rufifrons*, canto, límites de especies, Neotrópico, subespecies

INTRODUCTION

The Neotropics exhibit high biodiversity, with a wide variety of habitats and complex geography promoting local adaptation and reproductive isolation (Pérez-Emán 2005, Cadena et al. 2007, Smith et al. 2014). Although biodiversity remains greatly underestimated in tropical species (Milá et al. 2012, Freile et al. 2014), recent advances in the use of multi-trait phenotypic analyses in systematics research are revealing previously undocumented variation (e.g., Cadena and Cuervo 2010, González et al. 2011, Sandoval et al. 2017). The resulting taxonomic refinements allow researchers to more accurately describe tropical diversity and focus conservation efforts (e.g., Haig and D'Elia 2010).

Although birds are well studied compared with other Neotropical taxa, particularly invertebrates, many historical subspecies descriptions were based on specimens collected prior to the advent of audio recordings of vocalizations and the use of spectrometry to measure plumage color, and therefore morphology and subjective impressions of plumage coloration were the primary traits used for classification (e.g., Ridgway 1902, Monroe 1968). Birdsong is now recognized to be a sexually selected mating signal (Catchpole and Slater 2008), and there is increasing evidence that song divergence between populations may promote reproductive isolation even when morphology and plumage vary little (Toews and Irwin 2008, Dingle et al. 2010). Indeed, many cryptic species in both temperate and tropical regions have recently been described based primarily upon vocal differences (e.g., Toews and Irwin 2008, O'Neill et al. 2011, Hosner et al. 2013). However, a lack of range-wide data on vocalizations, particularly from hybrid or contact zones, means that taxonomic relationships remain unclear even for widespread species (e.g., González et al. 2011). In order to assess the degree of reproductive isolation between closely related populations, researchers should therefore compare phenotypes both within and outside of secondary contact or hybrid zones. Gradual or clinal variation in sexual signals could indicate interbreeding between groups, whereas abrupt changes could indicate reproductive isolation (e.g., the groups overlap in range but do not interbreed; Toews and Irwin 2008).

The Rufous-capped Warbler (*Basileuterus rufifrons*) is a common resident warbler species distributed from Arizona through Mexico and Central America, and into South America. This species' taxonomic status has long been disputed (Ridgway 1902, Todd 1929) because of considerable variation in plumage and vocalizations throughout its range (Curson 2010). Eight subspecies are recognized, 7 of which fall into 2 groups on the basis of their plumage features: (1) the northern, white-bellied *rufifrons* group of southern Arizona, Mexico, and western Guatemala (*B. r. caudatus*, *dugesi*, *jouyi*, and *rufifrons*); and (2) the southern, yellow-bellied *delattrii* group of southeastern Mexico, Central America, Colombia, and Venezuela (*B. r. actuosus*, *delattrii*, and *mesochrysus*; Curson 2010; Figure 1). Songs of both males and females also differ between these 2 groups; songs in the *rufifrons* group feature more repetition of syllable types, whereas songs in the *delattrii* group have more variation in syllable types (Howell and Webb 1995, Curson 2010, Demko and Mennill 2019). The eighth subspecies, *B. r. salvini*, found in the lowland Atlantic area of southern Mexico and northern Central America, is thought to be intermediate between the *delattrii* and *rufifrons* groups: it has a pale yellow or mixed white-yellow belly, although other features such as crown color resemble the *rufifrons* group (Friedmann et al. 1957, Curson 2010; Figure 2). However, comparisons of *B. r. salvini* vocalizations to those of the *delattrii* and *rufifrons* groups are contradictory (Monroe 1968, Howell and Webb 1995), and no previous analyses have quantified vocal differences between Rufous-capped Warbler subspecies. Furthermore, the *delattrii* group, *rufifrons* group,

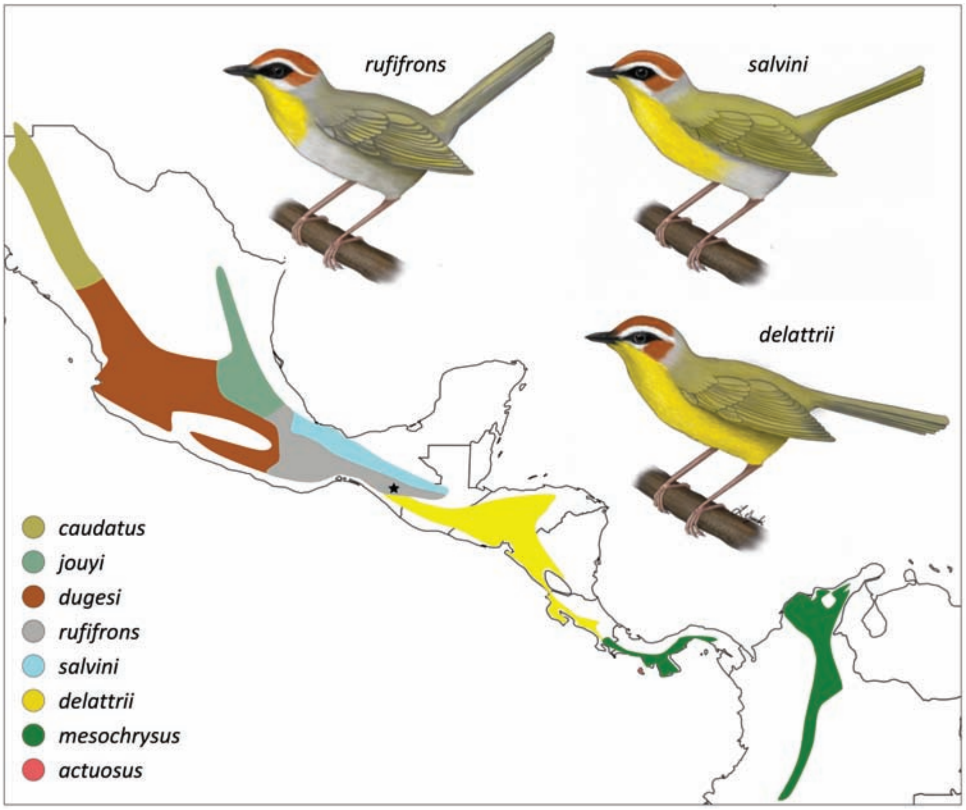

FIGURE 1. Range distributions of the 8 recognized Rufous-capped Warbler subspecies. White-bellied *B. r. rufifrons* (light gray shading) and yellow-bellied *B. r. delattrii* (yellow shading) are sympatric in southern Chiapas, Mexico (black star). The *rufifrons* group includes *B. r. caudatus*, *jouyi*, *dugesi*, and *rufifrons*, and the *delattrii* group includes *B. r. delattrii*, *mesochrysus*, and *actuosus*. The range of intermediate-plumaged *B. r. salvini* (blue shading) adjoins that of *B. r. rufifrons*, but does not overlap with that of *B. r. delattrii*.

and *B. r. salvini* differ in their habitat preferences. Whereas birds in the *delattrii* group inhabit dry to semi-humid deciduous forest (e.g., tropical dry forest) and second-growth habitat (e.g., coffee plantations) from 0 to 1,500 meters above sea level (m.a.s.l.), birds in the *rufifrons* group live in dry scrub, semi-open, and second-growth habitats from 0 to 3,000 m.a.s.l., most commonly at mid- to high-elevation above 1,000 m.a.s.l., and *B. r. salvini* live in semi-open and second-growth lowland habitats from 0 to 500 m.a.s.l. (Curson 2010). Based on the disputed status of *B. r. salvini*, some authorities have lumped all subspecies together (Ridgway 1902, Monroe 1968), whereas others have split them into the Rufous-capped Warbler *B. rufifrons* (i.e. "the *rufifrons* group" plus *B. r. salvini*) and the Chestnut-capped Warbler *B. delattrii* (i.e. "the *delattrii* group"; Todd 1929, Howell and Webb 1995).

Over the past century, the Rufous-capped Warbler taxon has been repeatedly split and lumped with the addition of new data throughout the species' range. The first range-wide classification of this clade (Ridgway 1902) considered all subspecies to comprise a single species because of the similar belly and upperpart coloration of the *delattrii* group and *B. r. salvini.* However, subsequent work classified the *delattrii* group as a separate species from the *rufifrons* group and *B. r. salvini* based on the *delattrii* group's positive wing-tail difference (wings longer than tails); all-yellow breast and belly, chestnut crown, and auricular feathers; and absence of a white lower auricular patch (Todd 1929; Figure 2). All subspecies were once again grouped together according to the work of Monroe (1968), who combined *B. r. delattrii* and *B. r. salvini* on the basis of reported hybridization between the 2 subspecies in eastern Guatemala, El Salvador, and Honduras. Despite stating that "there are no apparent differences in song pattern, ethology, or morphology" between *B. r. delattrii* and *B. r. salvini*, Monroe (1968) supplied no supporting information on the vocalizations or behavior of either subspecies. In their field guide to Mexican birds, Howell and Webb (1995) favored a species split. They argued that: (1) *B. r. salvini* are not found in El Salvador and Honduras, so they could not interbreed with *B. r. delattrii* there; (2) there are no confirmed hybrids between *B. r. delattrii* and either *B. r. rufifrons* or *B. r. salvini*; and (3) plumage features (e.g., belly, crown, and auricular color) and song are similar between *B. r. rufifrons* and *B. r. salvini* whereas both differ markedly from *B. r. delattrii.* They also reported that

FIGURE 2. Photographs of adult Rufous-capped Warblers (*Basileuterus rufifrons*) of 3 subspecies found in southern Mexico: *B. r. rufifrons*, Motozintla, Chiapas (**A**); *B. r. rufifrons*, Finca La Victoria, Chiapas (**B**); *B. r. salvini*, Estación de Biología Los Tuxtlas, Veracruz (**C**); *B. r. delattrii*, Finca La Victoria, Chiapas (**D**); and *B. r. delattrii*, Mapastepec, Chiapas (**E**). *B. r. rufifrons* (**A, B**) have a rufous crown and auricular, a large white auricular patch, and a white belly contrasting with the yellow throat. *B. r. delattrii* (**D, E**) have a chestnut crown and auricular, a small white spot below the eye, and a yellow throat and belly. *B. r. salvini* (**C**) have similar head coloration to *B. r. rufifrons*, but have extensive yellow streaking on the white belly.

B. r. delattrii and *B. r. rufifrons* are sympatric in southeastern Mexico and western Guatemala (Howell and Webb 1995), although the presence of hybridization in this contact zone needs confirmation based on genetic data. Recent fieldwork in this region suggested that *B. r. delattrii* and *B. r. rufifrons* are behaviorally isolated in sympatry, based on a lack of observed inter-subspecies pairing and reduced responses to playback of the songs of the other subspecies (Demko et al. 2019). Therefore, the critical final piece of the taxonomic puzzle will be to determine whether *B. r. salvini* is intermediate between *B. r. delattrii* and *B. r. rufifrons*, or is instead similar to one of these 2 divergent subspecies.

Our objective was to conduct a comprehensive study of Rufous-capped Warbler morphological, plumage, and vocal variation, with a particular focus on assessing whether *B. r. salvini* is intermediate between, or more similar to either, the *delattrii* and *rufifrons* groups. Using morphological measurements, audio recordings of vocalizations, and both photographs and spectrometry of plumage color collected throughout the species' range, we sought to more accurately describe phenotypic variation in the clade, as a first step towards reassessing taxonomic relationships within the Rufous-capped Warbler clade.

METHODS

Morphology

We measured Rufous-capped Warbler specimens from 11 natural history museums. We aimed to sample both sexes evenly within geographical regions, and included only adult birds of known sex in our analyses (n = 261 males and 180 females). We also included morphological data collected from 250 live birds in the field (n = 195 males and 55 females) in Costa Rica and southern Mexico from 2013 to 2017. The primary author (A.D.D.) collected all field and museum measurements. A comparison between field and museum-collected data showed that some measurements differed significantly within a subspecies based on sampling method (Supplementary Material Appendix A, Table S1). We therefore included the data collection method (field or museum) as a covariate in our morphological analyses. Although our combined field and museum dataset spanned the entire range distribution of the species and all documented subspecies, our primary focus was on southern Mexico and northern Central America (Guatemala, Honduras, and El Salvador), the region where *B. r. rufifrons* is reported to be sympatric with *B. r. salvini* in the northern part of its range, and with *B. r. delattrii* in the southern part of its range (Monroe 1968, Howell and Webb 1995).

For each individual, we measured 6 standard morphological traits (e.g., Cadena and Cuervo 2010, Halley et al. 2017): wing chord (unflattened wing length), tail length, tarsus length, bill length (nares to tip), and bill depth and bill width (both measured at the anterior end of nares). We measured wing and tail to the nearest 0.5 mm with a wing ruler, and tarsus and bill to the nearest 0.05 mm with dial calipers. For each sex separately, we ran multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) to assess whether individuals could be reliably grouped into subspecies and plumage groups, and used the leave-one-out cross-validation method to determine the most diagnostic morphometric variables (e.g., Sandoval et al. 2017). We analyzed data using 3 classifications: (1) all subspecies divided into 3 plumage-based groups (yellow-bellied *delattrii* group, white-bellied *rufifrons* group, and *B. r. salvini*); (2) the 3 most extensively sampled subspecies with sympatric or parapatric distributions in southern Mexico (*B. r. delattrii*, *B. r. rufifrons*, and *B. r. salvini*); and (3) all 8 subspecies separately. As all 3 analyses yielded similar results, we present the results of the plumage groups analyses in the main text, and we present the results of the 3-subspecies and 8-subspecies analyses in the Supplementary Material.

To compare pairs of plumage groups, we ran an analysis of variance (ANOVA) and diagnosability index tests for the most diagnostic traits in each DFA (Patten and Unitt 2002). The diagnosability test was performed at the 75% level; positive values of the index indicate that the trait is diagnosable between groups, whereas negative values indicate that the trait is not diagnosable (Patten and Unitt 2002). We also ran ANOVA comparing the wing-tail difference (wing length minus tail length) between groups, because of previous reports of between-subspecies variation in this trait; Todd (1929) reported that the *rufifrons* group have shorter wings than tails, whereas the *delattrii* group have longer wings than tails. We conducted all statistical analyses using R 3.5.3 (R Core Team 2019). We confirmed that the assumptions of each statistical test were met by examining histograms and scatterplots of original variables, and quantile-quantile (Q-Q) normal and residual plots of models (Quinn and Keough 2002).

Plumage

To compare variation in plumage patterns, we took digital photographs of the dorsal, ventral, left, and right sides of each museum specimen (n = 261 males and 180 females). Using these photographs, we described 2 plumage traits that have been reported to vary between subspecies. The first trait was the extent of white in the auricular; birds had either a white patch below the eye extending to the cheek, or a small white spot below the eye (there were no birds with intermediate characteristics). The second trait was the extent of yellow plumage coverage on the breast and belly, calculated by dividing the total length from chin to lower edge of the yellow breast patch by the total body length from chin to cloaca, measured using the GIMP2 photo editor. We scored specimens with an entirely yellow breast and belly as 1 (100%) for this trait. A naïve observer, unfamiliar with subspecies variation in these traits, collected all measurements from photographs labeled without subspecies or location information, to avoid potential bias. Some specimens did not have a clear separation between yellow breast and white belly (e.g., see Figure 2C). In those cases, the lower edge of the yellow belly was defined as the border between the end of the solid yellow color and start of streaking, and those individuals were given an additional label: "yellow-streaked".

We used reflectance spectrometry to measure 10 plumage patches per specimen: belly, breast, crown, mantle (upperparts), nape, rump, shoulder, tail, throat, and wing. The primary author (A.D.D.) collected 5 measurements per plumage patch for all specimens, and then averaged these 5 measurements to obtain 1 measurement per patch per individual. In cases where a particular plumage patch was damaged or missing on a specimen (e.g., missing tail feathers), we excluded that measurement from the analysis. We collected plumage reflectance measurements using an Ocean Optics USB 2000 reflectance spectrometer and PX-2 pulsed xenon lamp (Ocean Optics, Dunedin, Florida, USA). The fiber-optic probe was fitted with a rubber tip to maintain the probe at a fixed distance of 5 mm from the surface being measured while excluding external light. We calibrated the readings using a Spectralon white standard (Ocean Optics) after every 10 specimens measured.

Since the age of museum specimens ranged over more than 100 yr (1893–2009), and since reduced reflectance, especially in the ultraviolet (UV) part of the spectrum, has been reported for older museum specimens of other warbler species (McNett and Marchetti 2005, but see Doucet and Hill 2009), we also included specimen collection year as a covariate in the models.

To compare the coloration of each plumage patch by plumage group and sex, we used avian visual modeling, which calculates colors as birds see them using avian tetrachromatic color space models (Goldsmith 1990) in the R *pavo* package (Maia et al. 2019). We used the average UV-sensitive avian visual phenotype in our models, which is representative of the Rufous-capped Warbler's visual system (Endler and Mielke 2005, Stoddard and Prum 2008). We then calculated 4 standard color variables from avian tetrachromatic color space (Stoddard and Prum 2008) in *pavo* (Maia et al. 2019) and compared these variables between plumage groups relative to one another. The first variable was hue angle theta (θ), which is the angle in radians that quantifies colors detected by the long-, medium-, and short-wavelength-sensitive cones (Stoddard and Prum 2008). Hue theta values can range from –π to +π; in our dataset, they ranged from approximately –0.5 to +0.5, with values near –0.5 indicating red-shifted color, values near zero indicating yellow-shifted color, and values near +0.5 indicating green-shifted color. The other values calculated were: hue angle phi (ϕ), the angle in radians that quantifies UV coloration, with a higher value indicating greater UV reflectance in the patch; *r* achieved, the relative distance between a given color patch from the achromatic origin (i.e. the point where all cones are equally stimulated, resulting in black, white, or gray colors), with a larger *r* value indicating a more saturated color; and luminance (brightness; Stoddard and Prum 2008), which is calculated based on the avian double cone in *pavo* (Maia et al. 2019). We then ran separate ANOVA for each plumage patch, with plumage group, sex, and plumage group * sex interaction as factors and collection year as a covariate, followed by Tukey's post-hoc tests calculated with the *emmeans* package (Lenth et al. 2019).

We also used a receptor noise avian visual model (Vorobyev and Osorio 1998) using the average UV-visible visual system, as above, to calculate and compare perceptual differences between plumage patches. Specifically, we calculated the Euclidean distances between the geometric means of each plumage patch, using Cartesian coordinates based on perceptually scaled distances (Pike 2012), such that all distances are in just noticeable differences (JNDs; Vorobyev et al. 2001) and are noise-corrected using the *jnd2xyz* function in *pavo* (Maia and White 2018). If the distances are >1 JND, it suggests that the plumage patches are perceptually different between the categories measured (plumage group or sex). We then used a Cartesian-based MANOVA to test whether the xyz coordinates from the above analysis differed statistically between the categories (Maia and White 2018). Finally, we used bootstrap resampling with the *bootcoldist* function in *pavo* to compare pairwise color space distances for overall chromatic contrast (ΔS). If the mean of ΔS and its lower 95% confidence interval are greater than >1 JND, it suggests that the patches of the groups being compared are perceptually distinct to the birds (Maia and White 2018).

Songs

We measured songs obtained from digital recordings of singing males and females from our own field recordings collected in Mexico and Costa Rica, supplemented with recordings from the University of Florida and the Cornell Lab of Ornithology's Macaulay Library. We selected only high-quality songs for analysis (i.e. those with a high signal-to-noise ratio and minimal overlapping background noise). Our sample size was 405 songs from 126 males (37 *delattrii* group, 75 *rufifrons* group, and 14 *B. r. salvini*) and 18 females (3 *delattrii* group, 14 *rufifrons* group, and 1 *B. r. salvini*). We measured 1–12 songs per individual; within individuals, each song measured was a different variant (i.e. unique sequence of syllable types) to sample within-individual song variation. We included 1–16 individuals from each sampling location.

Using Adobe Audition 3.0 (Adobe, San Jose, California, USA), we high-pass filtered all songs at 1 kHz to remove background noise, and used the lasso selection tool to spot-filter background noise (e.g., vocalizations of other animals) if they overlapped with the frequency range of Rufous-capped Warbler vocalizations. Using Avisoft-SASLab Pro 5.2.09 (R. Specht, Berlin, Germany), we measured 14 acoustic variables commonly used to compare vocalizations of closely related avian taxa (e.g., Toews and Irwin 2008, Cadena and Cuervo 2010, Mason et al. 2014). For whole songs, we measured minimum frequency, maximum frequency, frequency bandwidth, peak frequency, total number of syllables, number of different syllable types, song duration, syllable production rate (total number of syllables/song duration), and syllable versatility. Syllable versatility is the ratio of the number of different syllable types to the total number of syllables, and is useful for quantifying the repetition rate of syllables within a song (Gil and Slater 2000). Since Rufous-capped Warblers have highly variable songs with many syllable types (Demko and Mennill 2019), we chose to include both song- and syllable-based variables in our analysis to provide further resolution. For individual syllables, we measured minimum frequency, maximum frequency, peak frequency, and duration, and then calculated mean values across all syllables within a song.

We used Avisoft's automatic parameter measurement tool to measure all song- and syllable-specific variables, except for song peak frequency, directly from spectrograms. The spectrogram window settings used were fast Fourier transform (FFT) size of 512, time resolution of 1.5 ms, and frequency resolution of 43 Hz; these settings optimized both frequency and temporal resolution across the spectral range of the songs. To standardize measurements across songs, we measured all variables at a threshold amplitude of −20 dB from the peak amplitude. In rare cases where specific syllables could not be measured accurately at this threshold (e.g., faint introductory syllables), we either adjusted the threshold amplitude to measure those syllables, or collected manual measurements from the spectrograms using on-screen cursors. We measured song peak frequency from power spectra with a Hann window, FFT size of 512, and frequency resolution of 62.5 Hz.

To compare acoustic variation in male songs between plumage groups, we first calculated mean values of each variable within individuals to produce a single data point for each individual. We ran separate ANOVA for each variable to assess plumage group differences, and then conducted principal component analysis (PCA) with a correlation matrix and unrotated components to produce composite response variables based on all 14 spectro-temporal variables (e.g., Toews and Irwin 2008, Mason et al. 2014). The first 3 principal components had eigenvalues >1 and accounted for 54.1%, 16.1%, and 8.8% of the total variation (Supplementary Material Table S2). We ran ANOVA to compare principal component scores between the *delattrii* group, the *rufifrons* group, and *B. r. salvini*. To assess whether individual songs could be accurately classified to our predefined plumage groups, we used DFA with leave-one-out cross-validation (Cadena and Cuervo 2010, Halley et al. 2017, Kenyon et al. 2017). We ran DFA using a subset of 8 non-collinear variables (song duration, song minimum frequency, song maximum frequency, peak frequency, number of syllables, number of syllable types, syllable production rate, and syllable versatility). We excluded females from these analyses owing to small sample sizes of female songs; females sing far less often than males in this species (Demko and Mennill 2019). To assess sex-specific differences in the *rufifrons* group and *B. r. salvini* songs, we ran *t*-tests to compare male and female songs for each variable. For multiple comparisons, we applied the Benjamini-Hochberg false discovery rate α-value correction (Benjamini and Hochberg 1995).

RESULTS

Morphology

Rufous-capped Warblers showed range-wide variation in morphology between the *delattrii* and *rufifrons* groups for several characters. Overall, *B. r. salvini* was similar to the *rufifrons* group, rather than being intermediate between the *delattrii* and *rufifrons* groups. For males, the most diagnostic traits in the discriminant analysis were wing and tail length, which together classified 82.9% of individuals to the correct group. Classification accuracy was high for both the *delattrii* (119 of 127 correct, or 93.7%) and *rufifrons* groups (175 of 190 correct, or 92.1%). For *B. r. salvini*, only 28.1% (16 of 57) of individuals were correctly classified as *B. r. salvini*, whereas 68.4% were assigned to the *rufifrons* group. Wing length was significantly different across all 3 groups ($F = 230.6$, df = 2 and 452, $P < 0.001$; Figure 3A), whereas tail length ($F = 67.1$, df = 2 and 443, $P < 0.001$; Figure 3C) was longer for the *rufifrons* group (Tukey's $P < 0.001$) than the other 2 groups (Tukey's $P = 0.92$).

For females, the most diagnostic trait based on discriminant analysis was wing length, which classified 68.4% of individuals to the correct group. As with males, classification accuracy was high for both the *delattrii* (62 of 75 correct, or 82.7%) and *rufifrons* groups (54 of 73 correct, or 74.0%), but low for *B. r. salvini* (12 of 39 correct, or 30.8%); 27 of 39 (69.2%) of *B. r. salvini* individuals were instead classified as *rufifrons* group. Wing length ($F < 0.001$, df = 2 and 230, $P < 0.001$; Figure 3B) and tail length ($F = 16.7$, df = 2 and 218, $P < 0.001$; Figure 3D) were longer for the *rufifrons* group (Tukey's $P < 0.001$) than the other 2 groups (Tukey's $P = 0.17$). For both sexes, the only diagnosable trait was wing length between the *delattrii* group and *B. r. salvini* (males: $D_{ds} = 0.63$; females: $D_{ds} = 0.19$); *delattrii* group birds had longer wings than *B. r. salvini* (Table 1).

The wing-tail difference was significantly different between all 3 groups (ANOVA, males: $F = 431.0$, df = 2 and 443, $P < 0.001$; females: $F = 105.9$, df = 2 and 218, $P < 0.001$), with *B. r. salvini* being intermediate between the *delattrii* and *rufifrons* groups. The mean value was negative for both the *rufifrons* group and *B. r. salvini* (wing shorter than tail) and positive for the *delattrii* group (wing longer than tail; Table 1, Figure 3E,F). Results of the 3-subspecies and 8-subspecies morphological analyses showed similar patterns and are presented in Supplementary Material Appendices B and C.

Plumage

Rufous-capped Warbler subspecies in the same plumage group shared similar facial and underpart color patterns, corroborating previous descriptions (Ridgway 1902, Todd 1929). All birds in the *rufifrons* group and *B. r. salvini* had a white auricular patch below the eye extending to the cheek, whereas all birds in the *delattrii* group had only a small white spot below the eye (Figure 2). All birds in the *rufifrons* group had yellow breast patches extending less than 50% of the body length, and no individuals had entirely yellow bellies. Some individuals of 2 *rufifrons* group subspecies (66.4% of *B. r. rufifrons* and 13.8% of *B. r. jouyi*)

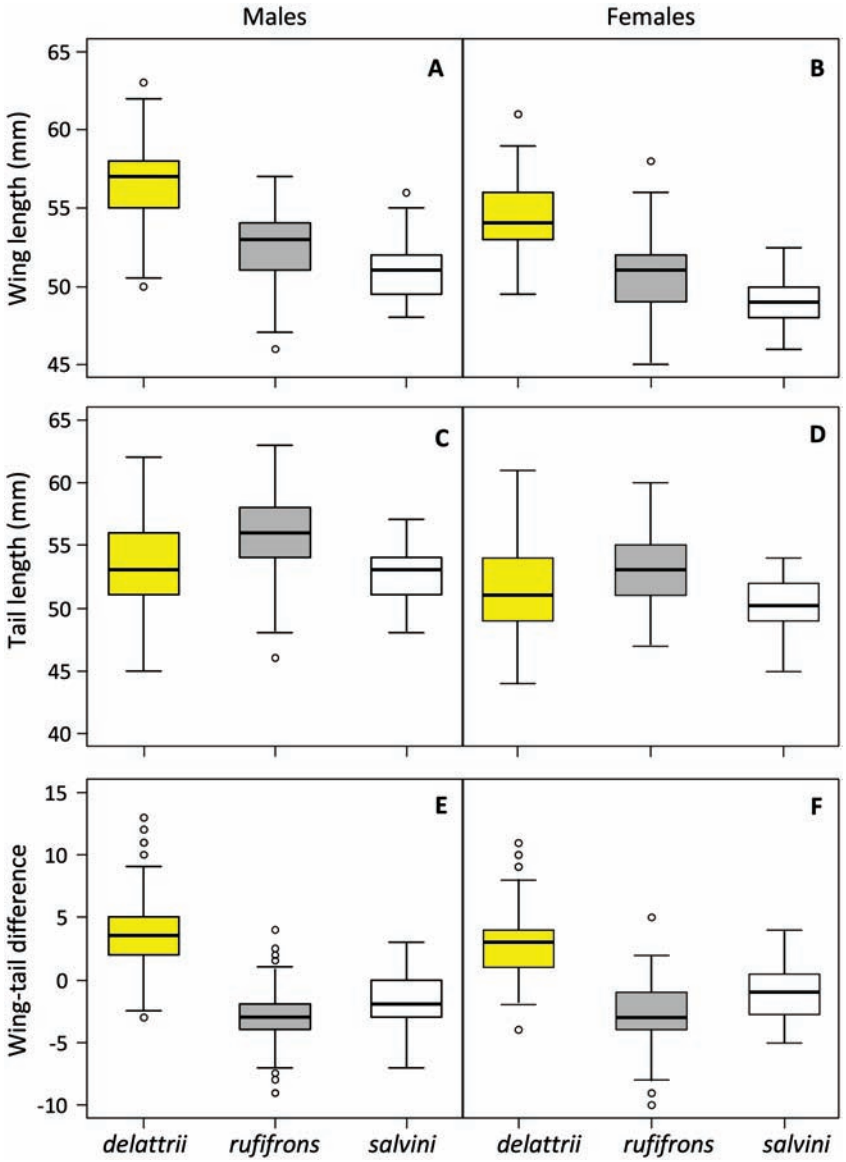

FIGURE 3. Rufous-capped Warblers show morphological differences between the *delattrii* group (yellow), *rufifrons* group (gray), and *B. r. salvini* (white) for males (left) and females (right). Wing length (**A**, **B**) differed significantly, with the *delattrii* group having the longest wings and *B. r. salvini* the shortest wings. Tail length (**C**, **D**) was longer for the *rufifrons* group than the other 2 groups. In both males (**E**) and females (**F**), the *delattrii* group had a positive wing-tail difference (wing longer than tail) and both the *rufifrons* group and *B. r. salvini* had a negative wing-tail difference (wing shorter than tail).

also had yellow streaks on the white belly (Figure 2C). By contrast, all birds in the *delattrii* group had all-yellow breasts and bellies. *B. r. salvini* were intermediate in the extent of yellow coverage on the breast and belly; although the mean percentage of yellow was 65.4% for males and 64.3% for females, individuals of this subspecies had either entirely yellow bellies (26.8%) or yellow streaking mixed into the white portion of the belly (73.2%; Supplementary Material Table S3).

Rufous-capped Warblers differed in coloration between plumage groups in all 10 spectrally measured plumage patches (Supplementary Material Table S4). The crowns of the *rufifrons* group and *B. r. salvini* were rufous (red-orange), and those of the *delattrii* group were chestnut (red-brown; Table 2); these differences were also visible to the naked eye. Using values collected with reflectance spectrometry, the crowns of the *delattrii* group had significantly more red-shifted color (i.e. more negative hue theta), higher UV reflectance (i.e. higher hue phi), and were less bright (i.e. lower luminance) than those of both the *rufifrons* group and *B. r. salvini*. The *rufifrons* group had more saturated crowns (i.e. higher *r* achieved values) than

TABLE 1. Morphological measurements of male and female Rufous-capped Warblers according to plumage group (yellow-bellied *delattrii* group, white-bellied *rufifrons* group, and *B. r. salvini*).

Males	*delattrii* group (n = 176)	*rufifrons* group (n = 211)	*salvini* (n = 69)
Wing length (mm)	57.0 ± 2.2	52.8 ± 2.3	50.8 ± 1.7
Tail length (mm)	53.2 ± 3.3	55.9 ± 3.0	52.6 ± 2.0
Tarsus (mm)	20.7 ± 0.8	20.8 ± 0.7	20.5 ± 0.8
Bill length (mm)	7.3 ± 0.4	6.9 ± 0.4	7.2 ± 0.3
Bill depth (mm)	3.9 ± 0.3	3.8 ± 0.2	3.9 ± 0.2
Bill width (mm)	3.8 ± 0.4	3.6 ± 0.3	3.6 ± 0.2
Wing-tail difference (mm)	3.8 ± 2.7	–3.0 ± 2.1	–1.8 ± 2.1
% yellow in underparts	100 ± 0.0	47.7 ± 4.6	65.4 ± 21.5

Females	*delattrii* group (n = 102)	*rufifrons* group (n = 87)	*salvini* (n = 46)
Wing length (mm)	54.5 ± 2.4	50.8 ± 2.3	49.2 ± 1.5
Tail length (mm)	51.7 ± 3.4	53.4 ± 3.2	50.3 ± 2.0
Tarsus (mm)	20.3 ± 0.9	20.5 ± 0.7	20.3 ± 0.7
Bill length (mm)	7.3 ± 0.4	6.8 ± 0.3	7.1 ± 0.3
Bill depth (mm)	3.9 ± 0.3	3.7 ± 0.2	3.8 ± 0.1
Bill width (mm)	3.8 ± 0.4	3.5 ± 0.3	3.6 ± 0.2
Wing-tail difference (mm)	2.8 ± 2.8	–2.6 ± 2.6	–1.1 ± 2.1
% yellow in underparts	100 ± 0.0	47.7 ± 5.1	64.3 ± 21.0

TABLE 2. Plumage color descriptions by body region in *B. r. delattrii*, *B. r. rufifrons*, and *B. r. salvini* subspecies according to Ridgway (1902), Todd (1929), Howell and Webb (1995), and this study.

Body region	*B. r. delattrii*	*B. r. rufifrons*	*B. r. salvini*
Crown	chestnut (red-brown)	rufous (red-orange)	rufous (red-orange)
Lower auricular	chestnut	white	white
White spot below eye	present	absent	absent
Nape	olive-gray	gray	gray
Mantle (upperparts)	olive	olive-gray	olive-gray to olive
Rump, shoulder	olive	olive-gray	olive
Throat, upper breast	golden yellow	lemon yellow	lemon yellow
Lower breast, belly	golden yellow	brownish white	mixed white-yellow to pale yellow
Wing, tail	dusky, olive border	dusky, yellow-green border	dusky, yellow-green border

the *delattrii* group, whereas *B. r. salvini* did not differ from either the *delattrii* or *rufifrons* groups (Supplementary Material Tables S4, S5; Figure S1). Overall crown color, as measured by Euclidean distances (units in JNDs) between patches, differed between both sexes of the *delattrii* and *rufifrons* groups, and between males of the *delattrii* group and *B. r. salvini*, but was similar between both sexes of the *rufifrons* group and *B. r. salvini*, and between females of the *delattrii* group and *B. r. salvini* (Table 3).

The throats and upper breasts of the *rufifrons* group and *B. r. salvini* were lemon yellow, whereas their lower breast and belly colors differed, with the *rufifrons* group being brownish white and *B. r. salvini* mixed white-yellow to pale yellow. By contrast, the *delattrii* group had golden yellow throats, breasts, and bellies (Table 2). For the belly, all 3 groups differed significantly in hue theta, hue phi, and r achieved, with the *delattrii* group having the highest values (i.e. green-shifted, high-saturation color with higher UV reflectance) and the *rufifrons* group having the lowest values (i.e. yellow-shifted, low-saturation color with lower UV reflectance). The 3 groups did not differ in luminance (Figure 4; Supplementary Material Tables S4, S5). Overall belly color was perceptually different between both sexes of all 3 groups (Table 3). For the breast, the *delattrii* group and *B. r. salvini* had more green-shifted, highly saturated color (i.e. higher hue theta and r achieved values) than the *rufifrons* group. UV reflectance (hue phi) differed significantly across all 3 groups, with the *delattrii* group having the highest values and the *rufifrons* group having the lowest values. Finally, the *delattrii* group had significantly higher luminance values than both the *rufifrons* group and *B. r. salvini* (Supplementary Material Tables S4, S5; Figure S2). The *rufifrons* group differed perceptually in overall breast color from both the *delattrii* group and *B. r. salvini*, whereas the *delattrii* group and *B. r. salvini* were perceptually similar to each other (Table 3). For the throat, there

TABLE 3. Euclidean distances in just noticeable differences (JNDs) between plumage groups for male and female Rufous-capped Warblers. Values of >1 JND (highlighted in bold) indicate perceptual differences between groups.

Patch	Plumage group	Males	Females
Belly	*delattrii-rufifrons*	**6.31**	**6.01**
	delattrii-salvini	**3.55**	**3.54**
	rufifrons-salvini	**2.77**	**2.51**
Breast	*delattrii-rufifrons*	**2.76**	**3.07**
	delattrii-salvini	0.51	0.61
	rufifrons-salvini	**2.87**	**2.99**
Crown	*delattrii-rufifrons*	**1.34**	**1.13**
	delattrii-salvini	**1.22**	0.98
	rufifrons-salvini	0.28	0.20
Mantle	*delattrii-rufifrons*	**2.13**	**2.30**
	delattrii-salvini	0.90	0.83
	rufifrons-salvini	**1.26**	**1.75**
Nape	*delattrii-rufifrons*	**1.21**	**1.33**
	delattrii-salvini	0.93	0.96
	rufifrons-salvini	0.31	0.38
Rump	*delattrii-rufifrons*	**2.11**	**2.49**
	delattrii-salvini	0.97	**1.37**
	rufifrons-salvini	**1.27**	**1.30**
Shoulder	*delattrii-rufifrons*	**1.06**	**1.20**
	delattrii-salvini	0.56	0.78
	rufifrons-salvini	0.98	**1.05**
Tail	*delattrii-rufifrons*	0.53	0.58
	delattrii-salvini	0.75	0.85
	rufifrons-salvini	0.40	0.34
Throat	*delattrii-rufifrons*	0.85	0.61
	delattrii-salvini	**1.50**	**1.39**
	rufifrons-salvini	0.71	**1.19**
Wing	*delattrii-rufifrons*	0.81	0.95
	delattrii-salvini	**1.18**	**1.38**
	rufifrons-salvini	0.65	0.60

were no significant differences in hue theta or luminance, although *r* achieved differed significantly across all 3 groups, with *B. r. salvini* having the highest values (most saturated) and the *delattrii* group having the lowest (least saturated). The *delattrii* group had higher UV reflectance (hue phi values) than the *rufifrons* group (Supplementary Material Tables S4, S5; Figure S3). Overall throat color differed perceptually between both sexes of the *delattrii* group and *B. r. salvini*, and between females of the *rufifrons* group and *B. r. salvini*, whereas it was perceptually similar between both sexes of the *delattrii* and *rufifrons* groups and between males of the *rufifrons* group and *B. r. salvini* (Table 3).

The mantle color varied from olive in the *delattrii* group to olive-gray in the *rufifrons* group, whereas *B. r. salvini* were an intermediate olive to olive-gray (Table 2). The *delattrii* group had significantly more saturated, less bright mantles (i.e. higher *r* achieved and lower luminance values) than the *rufifrons* group and *B. r. salvini*. Hue theta and hue phi differed significantly between all 3 groups, with the highest values, or most green-shifted color, for the *delattrii* group, and the lowest values, or most yellow-shifted color, for the *rufifrons* group (Supplementary Material Tables S4, S5; Figure S4). Overall mantle color differed perceptually between the *rufifrons* group and both the *delattrii* group and *B. r. salvini*, but was perceptually similar between the *delattrii* group and *B. r. salvini* (Table 3).

The napes of the *rufifrons* group and *B. r. salvini* were gray, compared with olive-gray in the *delattrii* group (Table 2). All 3 groups differed significantly in hue theta and hue phi, with the highest values, or green-shifted color with higher UV reflectance, for the *delattrii* group, and the lowest values, or yellow-shifted color with lower UV reflectance, for the *rufifrons* group. Luminance was higher for both the *rufifrons* group and *B. r. salvini* than for the *delattrii* group. The values of *r* achieved did not differ significantly across groups (Supplementary Material Tables S4, S5; Figure S5). Overall nape color differed perceptually between the *delattrii* and *rufifrons* groups, whereas *B. r. salvini* was perceptually similar to both the *delattrii* and *rufifrons* groups (Table 3).

The rumps and shoulders of the *delattrii* group and *B. r. salvini* were olive, compared with olive-gray in the

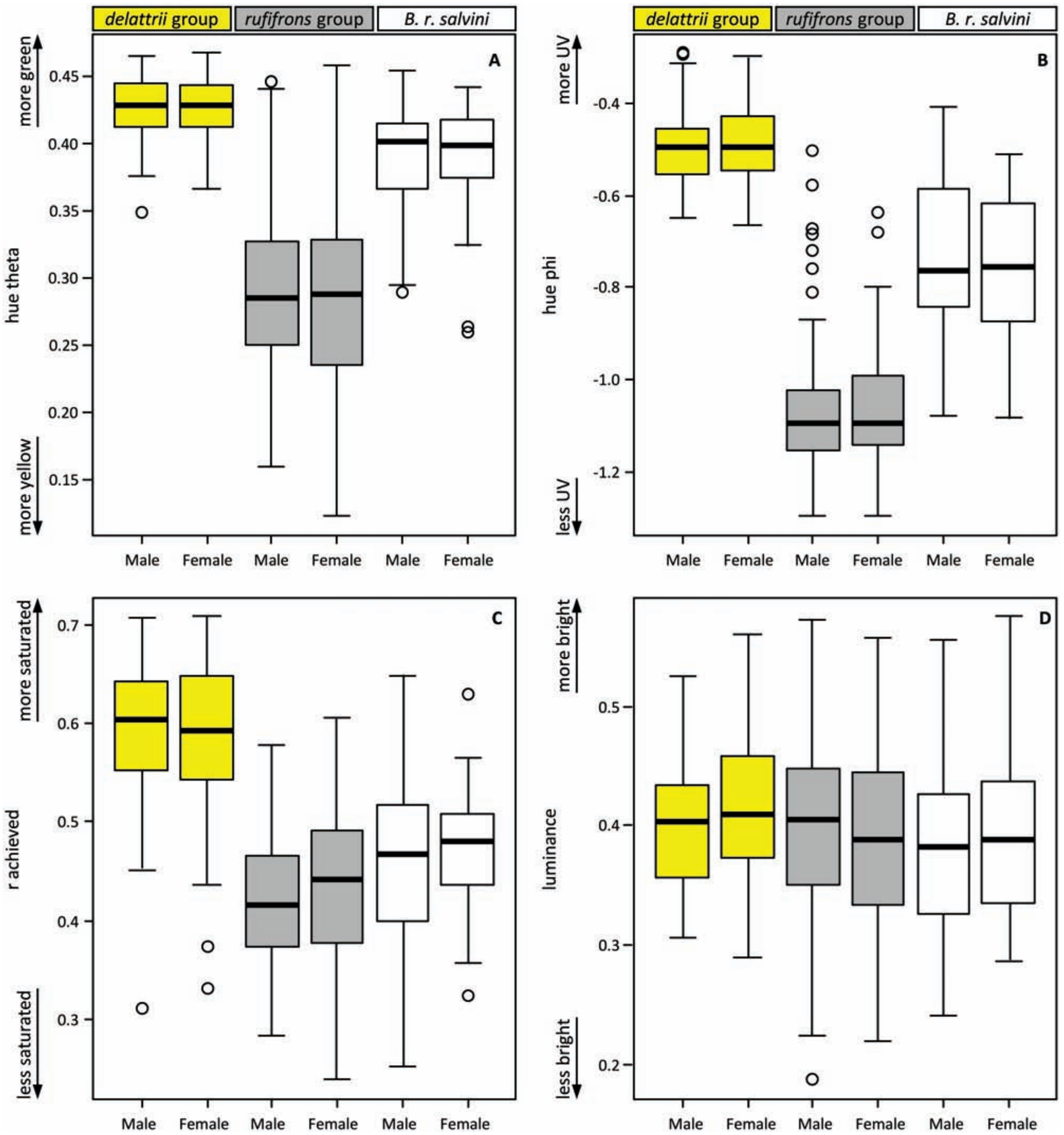

FIGURE 4. Rufous-capped Warblers show plumage color differences between the *delattrii* group (yellow), *rufifrons* group (gray), and *B. r. salvini* (white). Four color features are shown for both males and females: hue theta (**A**), hue phi (**B**), *r* achieved (**C**), and luminance (**D**), between the bellies of Rufous-capped Warblers of the *delattrii* group, *rufifrons* group, and *B. r. salvini*. Remaining plumage patches are shown in the Supplementary Material.

rufifrons group (Table 2). For both patches, all 3 groups differed in hue theta and hue phi, with the highest values, or green-shifted color with higher UV reflectance, for the *delattrii* group, and the lowest values, or yellow-shifted color with lower UV reflectance, for the *rufifrons* group. For the rump, the *delattrii* group had more saturated color (higher *r* achieved) than the *rufifrons* group and *B. r. salvini*. The groups did not differ in luminance for either rump or shoulder, or in *r* achieved for shoulder (Supplementary Material Tables S4, S5; Figures S6, S7). All 3 groups were perceptually different in overall rump color except for males of the *delattrii* group and *B. r. salvini*. Overall shoulder color differed perceptually between both sexes of the *delattrii* and *rufifrons* groups, and between females of the *rufifrons* group and *B. r. salvini*, whereas it was perceptually similar between both sexes of the *delattrii* group and *B. r. salvini*, and between males of the *rufifrons* group and *B. r. salvini* (Table 3).

The tail and wing patches were dusky gray in all individuals, with yellow-green feather borders in the *rufifrons* group and *B. r. salvini*, and olive borders in the *delattrii* group (Table 2). For the tail, the *delattrii* group had higher UV reflectance (hue phi) and lower *r* achieved than both the *rufifrons* group and *B. r. salvini*. The luminance was higher for *B. r. salvini* than for the *delattrii* group, and *B. r. salvini* had higher hue theta, or more green-shifted color, than both the *delattrii* and *rufifrons* groups (Supplementary Material Tables S4, S5; Figure S8). However, overall tail color was perceptually similar between all 3 groups based on Euclidean distances in JNDs (Table 3). For the wing, all 3 groups differed in UV reflectance (hue phi), with the *delattrii* group having the highest and the *rufifrons* group having the lowest values, and for *r* achieved and luminance, with *B. r. salvini* having the highest and the *delattrii* group having the lowest values. The *delattrii* group had higher hue theta values, or more green-shifted color, than the *rufifrons* group (Supplementary Material Tables S4, S5; Figure S9). Overall wing color was perceptually different between the *delattrii* group and *B. r. salvini*, whereas it was perceptually similar between the *rufifrons* group and both the *delattrii* group and *B. r. salvini* (Table 3).

The Cartesian-based MANOVA revealed statistically significant plumage group differences in all 10 patches and sex differences for breast, crown, and rump ($P < 0.05$). Using the bootstrap resampling analysis to further test whether plumage patches were perceptually distinct to the warblers (in addition to our Euclidean distance analyses above), the belly color was perceptually distinct between all 3 groups. For the breast and mantle, the *rufifrons* group was perceptually distinct from both the *delattrii* group and *B. r. salvini*, which were not distinct from one another. For the crown, nape, and rump, only the *delattrii* and *rufifrons* groups were perceptually distinct. For the wing, only the *delattrii* group and *B. r. salvini* were perceptually distinct. For the shoulder, tail, and throat, none of the groups were perceptually distinct from one another.

Rufous-capped Warbler plumage color differed significantly between the sexes for the crown, mantle, nape, tail, and wing (Supplementary Material Table S4). Males of all 3 groups had greater UV reflectance in the crown and tail (i.e. higher hue phi values) and lower saturation in the mantle (i.e. lower *r* achieved values) than females (Supplementary Material Table S4). There was a plumage group * sex interaction where *delattrii* group males had brighter napes (i.e. higher nape luminance) and more green-shifted wing color (i.e. more positive wing hue theta) than females, whereas the *rufifrons* group and *B. r. salvini* did not differ between the sexes in these 2 variables (Supplementary Material Table S5).

There were significant collection year effects for all plumage patches, indicating an influence of specimen age on reflectance. Hue theta values decreased significantly towards zero with age for all plumage patches except for the crown and tail; in other words, hue became more yellow-shifted with increased specimen age. The amount of UV reflectance (hue phi) decreased significantly with increased age for all plumage patches. The saturation (*r* achieved) increased significantly with age for the belly, breast, crown, nape, rump, shoulder, and tail, whereas it decreased significantly for the throat and was similar across ages for the mantle and wing. Brightness (luminance) decreased significantly with age for the belly, breast, and throat; increased with age for the crown, tail, and wing; and was similar across ages for the mantle, nape, rump, and shoulder (Supplementary Material Tables S4, S5). Results of the 3-subspecies plumage analyses showed similar patterns and are presented in Supplementary Material Appendix D.

Songs

Male songs. Rufous-capped Warbler songs differed significantly in both acoustic structure and organization among plumage groups (Table 4), with the *delattrii* group being well-differentiated from the *rufifrons* group and *B. r. salvini* (Figure 5). For 13 of the 14 measured variables, the *delattrii* group differed significantly from the *rufifrons* group and *B. r. salvini*, which were similar to each other; the final variable, syllable peak frequency, differed significantly between all 3 groups (Table 4). PC1 differed significantly in all 3 groups (ANOVA: $F = 395.6$, df = 2 and 123, $P < 0.001$), and corresponded well with acoustic variables distinguishing *delattrii* group songs from *rufifrons* group and *B. r. salvini* songs (Figure 6). Positive loadings corresponded to song duration, number of syllables, and syllable production rate, whereas negative loadings corresponded to all other variables (Supplementary Material Table S2). Therefore, songs with positive PC1 scores (*rufifrons* group and *B. r. salvini*; Figure 5A,C,E) were longer and faster paced, had more syllables but less variety of syllable types, were lower in frequency at both the song and syllable level, and had shorter, narrower bandwidth syllables. Songs with negative PC1 scores (*delattrii* group; Figure 5B,D,F) were shorter and slower paced, had fewer syllables but more variety of syllable types, were higher in frequency at both the song and syllable level, and had longer, wider bandwidth syllables. PC2 and PC3 did not differ significantly between plumage groups (ANOVA PC2: $F = 0.5$, df = 2 and 123, $P = 0.62$; PC3: $F = 0.9$, df = 2 and 123, $P = 0.41$).

TABLE 4. Vocal measurements of male Rufous-capped Warbler songs by plumage group (*delattrii* group, *rufifrons* group, and *B. r. salvini*). All variables were significantly different between the *delattrii* group and both the *rufifrons* group and *B. r. salvini*, aside from syllable peak frequency, which was significantly different across all 3 groups.

Vocal variable	*delattrii* (*n* = 37)	*rufifrons* (*n* = 75)	*salvini* (*n* = 14)
Song duration (s)	2.24 ± 0.37	2.77 ± 0.85	3.04 ± 1.06
Song maximum frequency (Hz)	8,906 ± 436	7,519 ± 639	7,460 ± 641
Song minimum frequency (Hz)	3,292 ± 292	2,647 ± 314	2,760 ± 191
Song bandwidth (Hz)	4,844 ± 711	5,624 ± 723	5,624 ± 723
Song peak frequency (Hz)	5,907 ± 384	5,417 ± 555	5,271 ± 533
Syllable duration (s)	0.08 ± 0.02	0.06 ± 0.01	0.06 ± 0.01
Syllable maximum frequency (Hz)	7,290 ± 383	5,914 ± 326	5,709 ± 297
Syllable minimum frequency (Hz)	4,660 ± 238	3,952 ± 271	3,832 ± 253
Syllable bandwidth (Hz)	2,630 ± 474	1,962 ± 344	1,877 ± 290
Syllable peak frequency (Hz)	5,893 ± 224	4,950 ± 299	4,654 ± 231
Number of syllables	15.6 ± 3.4	26.7 ± 9.3	30.0 ± 11.6
Number of syllable types	10.9 ± 3.6	6.1 ± 1.8	5.8 ± 1.2
Syllable versatility index	0.69 ± 0.11	0.24 ± 0.05	0.21 ± 0.06
Syllable production rate (syllables/s)	6.9 ± 0.8	9.7 ± 1.3	9.8 ± 1.2

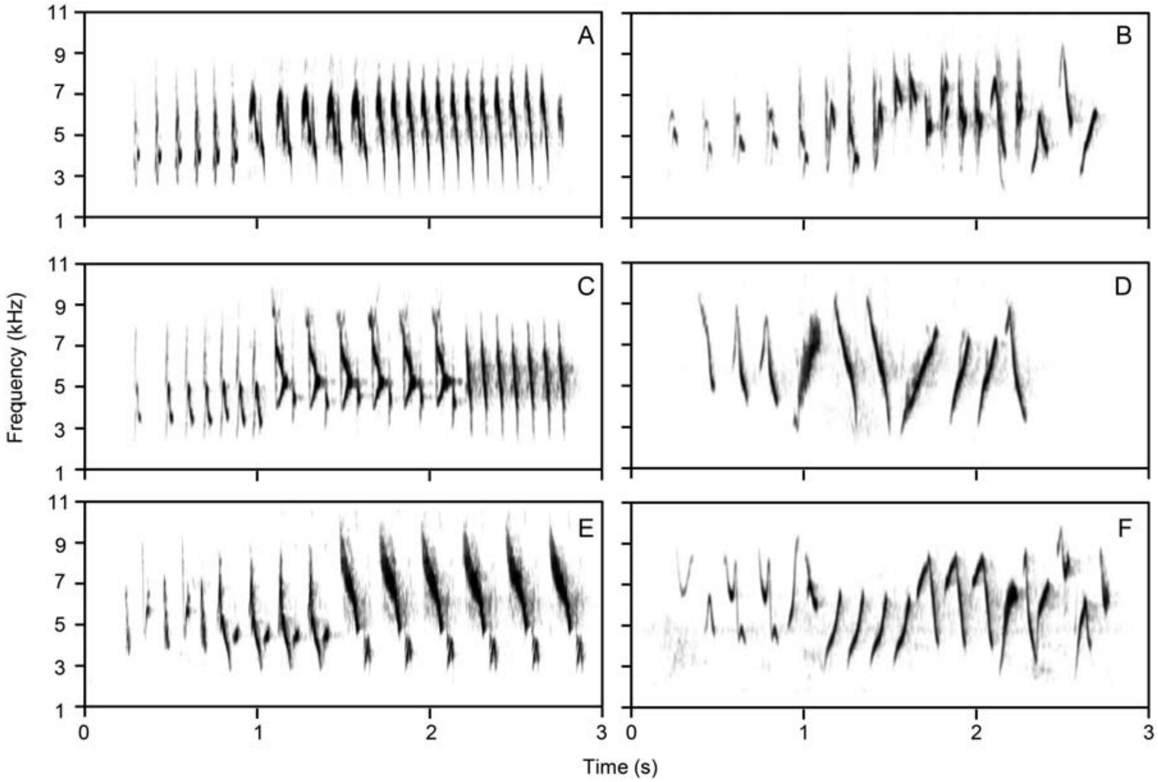

FIGURE 5. Song spectrograms of Rufous-capped Warbler male songs: allopatric *B. r. rufifrons,* Yagul, Oaxaca, Mexico (**A**); allopatric *B. r. delattrii*, Santa Rosa, Guanacaste, Costa Rica (**B**); allopatric *B. r. salvini*, Estación de Biología Los Tuxtlas, Veracruz, Mexico (**C**); allopatric *B. r. delattrii*, Mapastepec, Chiapas, Mexico (**D**); sympatric *B. r. rufifrons*, Finca La Victoria, Chiapas, Mexico (**E**); and sympatric *B. r. delattrii*, Finca La Victoria (**F**). Songs of *rufifrons* group (**A**, **E**) and *B. r. salvini* (**C**) are structurally similar to one another, and differ from *delattrii* group songs (**B**, **D**, **F**). Songs from sympatric *B. r. rufifrons* (**E**) and *B. r. delattrii* (**F**) resemble allopatric songs of their own subspecies rather than being intermediate or mixed.

Discriminant analysis results also showed that *delattrii* group songs differed from *rufifrons* group and *B. r. salvini* songs. Songs differed significantly between plumage groups according to MANOVA (Wilk's $\Lambda = 0.06$, $F = 46.9$, df = 16 and 232, $P < 0.001$). The most diagnostic trait according to discriminant analysis was the syllable versatility index (the ratio of the number of different syllable types to the total number of syllables), which correctly classified 88.1% of individuals.

Most *delattrii* group songs (97.3%, or 36 of 37) were assigned to the correct group. All *rufifrons* group (75 of 75) and *B. r. salvini* (14 of 14) songs were classified as *rufifrons* group.

Male and female song comparison. Although female song output is lower than male song output in Rufous-capped Warblers (Demko and Mennill 2019), we detected female songs in all 3 groups. Male and female *rufifrons* group and *B. r. salvini* songs differed significantly in 9 of the 14 measured acoustic variables (Table 5). In comparison with male songs, female songs were shorter with higher maximum frequency and bandwidth. Syllables of female songs were also shorter, with higher maximum frequency, peak frequency, and bandwidth, than male syllables. Although female songs had fewer syllables than male songs, they had a greater variety of syllable types (i.e. higher syllable diversity index). Male and female songs shared similar song and syllable minimum frequency, song peak frequency, number of syllable types, and syllable production rate (Figure 7). In contrast to female *delattrii* group songs, which have similar syllable types as male songs (Demko and Mennill 2019), female *rufifrons* group songs are structurally distinct from those of males (Figure 7).

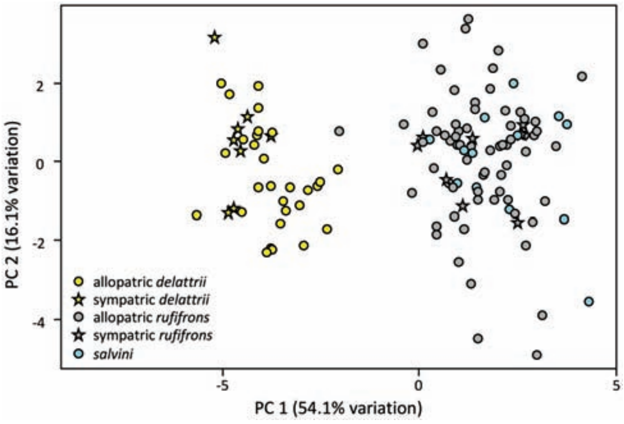

FIGURE 6. Male songs of Rufous-capped Warblers in the *delattrii* group were distinct from those of the *rufifrons* group and *B. r. salvini* based on PC1 scores. Individuals of both sympatric *B. r. delattrii* (yellow stars) and *B. r. rufifrons* (gray stars) fell within the average range of PC1 scores for their subspecies in allopatry, whereas PC2 scores did not differ significantly between subspecies.

DISCUSSION

Based on data collected from live birds, museum specimens, and archived sound recordings sampled across the range of Rufous-capped Warblers, we found considerable differences between the *delattrii* and *rufifrons* groups of subspecies in morphology, plumage pattern, plumage color, and song. Our analyses also show that *B. r. salvini* resemble the *rufifrons* group rather than being intermediate between the *delattrii* and *rufifrons* groups, or similar to the *delattrii* group only. This suggests that Rufous-capped Warblers comprise 2 distinct groups: *delattrii* and *rufifrons-salvini*. Our results align with historical taxonomic groupings based upon morphology and plumage color (Todd 1929) and recent evidence based on field observations (Howell and Webb 1995) rather than the current classification as a single species (Monroe 1968). Additionally, the vocal divergence between the *delattrii* and *rufifrons-salvini* groups, described for the first time in our study, provides further evidence of distinctiveness between the 2 groups.

Morphology

Overall, our morphological analyses suggest that the *delattrii* group is distinct from the *rufifrons* group and *B. r. salvini*. Interestingly, the groups also differ in body shape as well as size. Our wing-tail difference measurements corroborate the analyses of Todd (1929), who also noted that

TABLE 5. Vocal measurements of male and female *rufifrons* group and *B. r. salvini* songs. Male and female songs differed significantly in 9 of the 14 measured variables (highlighted in bold).

Vocal variable	Males (*n* = 89)	Females (*n* = 15)	*t*-value	*P*-value
Song duration (s)	**2.82 ± 0.89**	**1.90 ± 0.80**	**–4.05**	**<0.001**
Song maximum frequency (Hz)	**7,509 ± 636**	**8,316 ± 595**	**4.81**	**<0.001**
Song minimum frequency (Hz)	2,665 ± 300	2,692 ± 287	0.33	0.75
Song bandwidth (Hz)	**4,844 ± 711**	**5,624 ± 723**	**3.87**	**0.001**
Song peak frequency (Hz)	5,394 ± 551	5,597 ± 521	1.39	0.18
Syllable duration (s)	**0.06 ± 0.01**	**0.05 ± 0.01**	**–6.78**	**<0.001**
Syllable maximum frequency (Hz)	**5,881 ± 328**	**6,589 ± 388**	**6.68**	**<0.001**
Syllable minimum frequency (Hz)	3,933 ± 271	3,968 ± 483	0.27	0.79
Syllable bandwidth (Hz)	**1,948 ± 336**	**2,622 ± 645**	**3.95**	**0.001**
Syllable peak frequency (Hz)	**4,903 ± 308**	**5,562 ± 520**	**4.77**	**<0.001**
Number of syllables	**27.2 ± 9.7**	**18.2 ± 8.0**	**–3.91**	**<0.001**
Number of syllable types	6.0 ± 1.7	5.2 ± 2.2	–1.31	0.21
Syllable versatility index	**0.23 ± 0.05**	**0.29 ± 0.08**	**2.75**	**0.01**
Syllable production rate (syllables/s)	9.7 ± 1.3	9.6 ± 0.9	–0.38	0.71

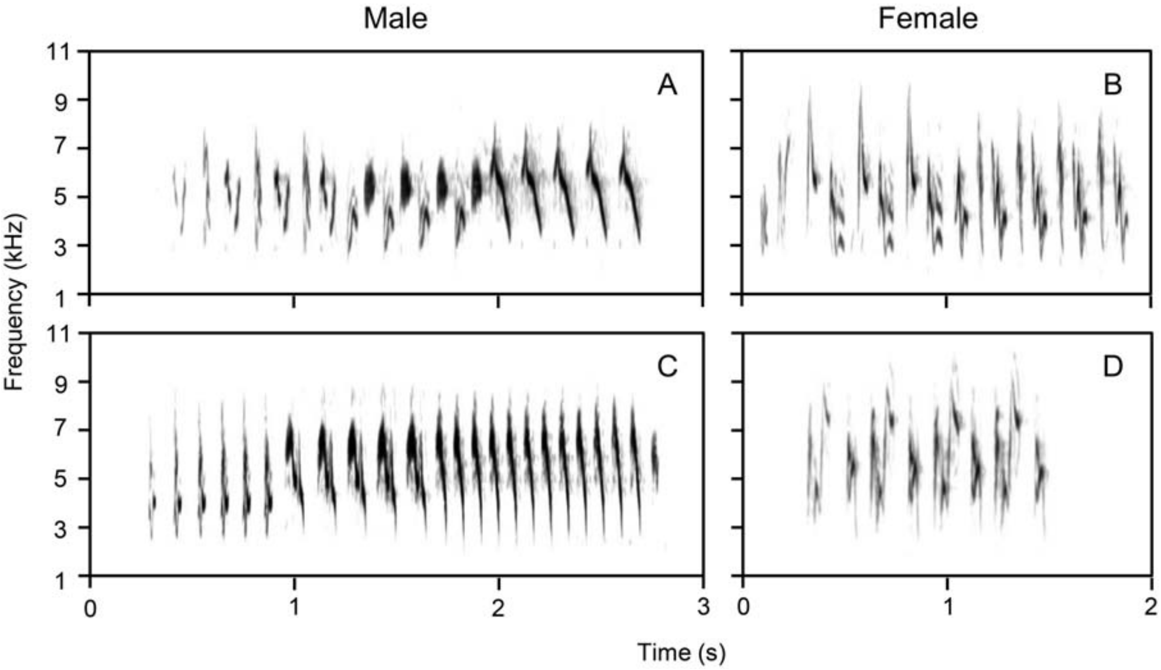

FIGURE 7. Song spectrograms of male and female Rufous-capped Warbler songs of the *B. r. rufifrons* subspecies from Motozintla, Chiapas, Mexico (**A**, **B**) and Yagul, Oaxaca, Mexico (**C**, **D**). Female songs and syllables are shorter, have higher maximum and peak frequency, and larger bandwidth than male songs.

all *rufifrons* group subspecies as well as *B. r. salvini* have shorter wings than tails, and all *delattrii* group subspecies have longer wings than tails. Furthermore, our discriminant analysis results suggest that *B. r. delattrii* is a well-defined taxon, but that *B. r. rufifrons* and *B. r. salvini* are not well-differentiated as separate taxa. The discriminant analysis of all 8 subspecies further supports the separation of the *delattrii* and *rufifrons* groups, as most of the incorrect assignments for a given subspecies were to another subspecies within the same group.

Our morphological analyses did reveal some overlap between plumage groups, since the only diagnosable trait was the difference in wing length between the *delattrii* group and *B. r. salvini.* The overlap between groups may be attributable to the similar overall size of all *Basileuterus* warblers (Curson 2010). Although not explicitly tested in our study, particular subspecies or populations may also be locally adapted to specific diets, which could explain why traits related to foraging (e.g., bill size) varied widely both within and between subspecies (e.g., Benkman 2003, Francis and Guralnick 2010, Aleixandre et al. 2013, Riyahi et al. 2013). Another possibility is that morphological divergence is an adaptation to variation in temperature or other climatic variables. Indeed, a separate study testing ecogeographic rules using the same museum dataset found that Rufous-capped Warblers living in regions with lower average annual temperatures had longer wings and tails than those living in warmer regions (Bastien 2018). Further studies should assess these relationships within each subspecies, and, in particular, investigate whether the unique morphological features of *B. r. salvini*, such as shorter wings compared with other subspecies, are in fact ecological adaptations to their habitat.

Plumage

We found that plumage color varies more than morphology among Rufous-capped Warblers, and that the differences between plumage groups vary depending on the plumage patch examined. According to our most conservative analysis, which assessed perceptual distinctiveness between plumage groups, the belly was the only distinct patch between all 3 groups. For the crown, nape, and rump, the *delattrii* and *rufifrons* groups were both distinct from one another, whereas *B. r. salvini* were intermediate and therefore not distinct from either group. For the breast and mantle, the *delattrii* group and *B. r. salvini* were similar to each other but distinct from the *rufifrons* group. Unlike the morphological comparisons, no plumage patches were perceptually similar between the *rufifrons* group and *B. r. salvini* while also being distinct from the *delattrii* group.

Our use of spectral measurements to analyze plumage color revealed that UV reflectance differed among plumage groups, with the *delattrii* group having higher overall UV reflectance (i.e. higher hue phi values) than the other groups. Previous Rufous-capped Warbler taxonomic comparisons qualitatively described plumage colors and classified each subspecies based on their geographical ranges and subtle color variation relative to the reference subspecies *B. r. delattrii* and *B. r. rufifrons* (Ridgway 1902, Todd 1929, Howell and Webb 1995; Table 2). Our analyses used quantitative spectrometry and avian visual models to confirm the overall differences and similarities in plumage characteristics described by earlier researchers, while also providing new insights into color variation which is invisible to human eyes (e.g., UV reflectance).

The large variation in plumage coloration among subspecies and plumage groups could result from ecological selection, wherein plumage color evolves to maximize either conspicuousness or crypsis relative to the environment (Endler and Théry 1996, Doucet et al. 2007, Simpson and McGraw 2018). All 3 plumage groups have particular habitat preferences; the *rufifrons* group prefers dry, open habitats, the *delattrii* group prefers dry to semi-humid, forested sites, and *B. r. salvini* prefers humid, open habitats (Curson 2010). In the forested habitat of the *delattrii* group, olive-green upperparts would be more cryptic, whereas a deep red crown and yellow breast, which are potentially sexually selected signals, would be more conspicuous (e.g., Doucet et al. 2007, Simpson and McGraw 2018). Furthermore, female mating preferences could result in plumage features such as a yellow *B. r. delattrii* belly introgressing into adjacent *B. r. rufifrons* populations to produce intermediate *B. r. salvini* plumage. A similar scenario occurred when yellow collar color introgressed into white-collared populations across a hybrid zone between Golden-collared Manakins (*Manacus vitellinus*) and White-collared Manakins (*M. candei*; Stein and Uy 2006). However, since no confirmed hybrids exist between *B. r. delattrii* and *B. r. salvini* (Todd 1929, Howell and Webb 1995), genetic analyses will be necessary to assess the presence and extent of historical introgression of plumage traits between these 2 subspecies.

An intriguing finding of our plumage analysis was that although Rufous-capped Warblers appear sexually monochromatic to humans, several plumage patches are in fact sexually dichromatic. Overall, our findings coincide with 2 studies based on spectral reflectance data, one from 166 North American monochromatic passerine species, and the other across 376 species in the cardinal and tanager clades, in which over 90% of the putatively monochromatic species were actually dichromatic based on avian visual systems (Eaton 2007, Burns and Shultz 2012). We found that females of the *delattrii* group, *rufifrons* group, and *B. r. salvini* all differed in crown color from males within the same group. The presence of sexual dichromatism suggests that the crown may be a signal used in mate choice or sex recognition. Mate choice experiments using visual models of warblers with varying crown colors (Baldassarre and Webster 2013) may be useful to further explore the role of these plumage patches as mating signals. Other sex-specific differences were found only in the *delattrii* group, providing further evidence that the *delattrii* group is distinct from the *rufifrons* group and *B. r. salvini.* Further research on little-studied monochromatic tropical species, particularly bright monochromatic species like the Rufous-capped Warbler, will likely reveal other cases of cryptic sexual dichromatism (e.g., Mennill et al. 2003, Mays et al. 2006).

Songs

Male Rufous-capped Warbler songs separated distinctly into 2 groups: *delattrii* and *rufifrons-salvini.* These vocal differences further suggest that *B. r. salvini* are conspecific with *B. r. rufifrons* (Todd 1929, Howell and Webb 1995) rather than being similar to *B. r. delattrii* or intermediate between *B. r. delattrii* and *B. r. rufifrons* (Ridgway 1902, Monroe 1968). Male song is used to attract mates and defend territories (Catchpole and Slater 2008), and may therefore act as a strong isolating barrier even between closely related taxa without large morphological or plumage variation (Toews and Irwin 2008, Dingle et al. 2010). Indeed, a playback study in southern Mexico showed that both *B. r. delattrii* and *B. r. rufifrons* responded more strongly to own-subspecies than other-subspecies male songs in sympatry than in allopatry (Demko et al. 2019), suggesting that song could serve as an isolating barrier between subspecies (e.g., Irwin et al. 2001, Dingle et al. 2010, Benites et al. 2015). Observations in the sympatric zone also suggest that *B. r. delattrii* and *B. r. rufifrons* territories overlap between subspecies, but that the warblers still mate assortatively (Demko et al. 2019). Further evidence for vocal divergence in sympatry is that among the subset of sympatric male songs measured in our study (*B. r. delattrii*: $n = 9$; *B. r. rufifrons*: $n = 9$), all fit within the average range of PC1 values for their subspecies (Figure 6). Future genetic analyses will assess the presence of gene flow between these 2 subspecies in sympatry.

As with plumage divergence, the marked vocal divergence observed between the *delattrii* and *rufifrons-salvini* groups could result from ecological selection (Wilkins et al. 2013). The Acoustic Adaptation Hypothesis states that acoustic signals have evolved to transmit optimally in an animal's habitat, since both vegetation features (Morton 1975) and ambient noise levels (Slabbekoorn and Smith 2002) may affect signal transmission. In Rufous-capped Warblers, the *rufifrons* group and *B. r. salvini*, which live primarily in open habitats, have many rapid trilled syllables in their songs, whereas the *delattrii* group, which prefers forested habitats, has slower paced songs with larger internote intervals. Both types of songs would be expected to transmit well in their respective environments according to the Acoustic Adaptation Hypothesis (Morton 1975). In Rufous-collared Sparrows (*Zonotrichia capensis*), a similar pattern of vocal variation occurs wherein songs from open-habitat populations are lower frequency, narrower bandwidth, and contain longer, faster trills than songs from forest-dwelling populations (Handford and Lougheed 1991). However, the Acoustic Adaptation Hypothesis is not universally supported across all Rufous-collared Sparrow populations (Kopuchian et al. 2004, Lijtmaer and Tubaro 2007), and there is little evidence of local song adaptation in other species where song varies little structurally across populations (e.g., Rufous-and-white Wren [*Thryophilus rufalbus*]; Graham et al. 2017). In Rufous-capped Warblers, it is also likely that ecological selection is not the sole explanation for population-level vocal differences since many song features, such as frequency, are inconsistent with the Acoustic Adaptation Hypothesis (Morton 1975). A small study comparing habitat features of *B. r. delattrii* and *B. r. rufifrons* territories within and outside the Mexican sympatric zone showed that vegetation (e.g., number of trees, canopy cover) did not differ significantly between the 2 subspecies' territories within the contact zone, but did differ between subspecies in allopatric sites (Vargas-Herrera et al. 2017). Since songs are similar within Rufous-capped Warbler subspecies in both sympatric and allopatric areas, further work should measure whether site-specific factors (e.g., ambient noise) may influence song structure (e.g., Slabbekoorn and Smith 2002). Additionally, our sample of songs was concentrated in southern Mexico and Costa Rica, so further recordings from sites throughout the Rufous-capped Warbler range, coupled with vegetation sampling, sound transmission experiments, and ambient noise measurements at the same sites, could clarify the role of ecological selection in shaping song structure in this species.

Vocal divergence between Rufous-capped Warbler plumage groups was also apparent in female songs of both the *delattrii* and *rufifrons* groups, which differed from one another while being structurally similar to their male counterparts. Female *delattrii* songs are shorter, with fewer syllables and syllable types and higher maximum frequency than male songs (Demko and Mennill 2018). These songs appear to serve a territory defense function in intense interactions such as playback-simulated conspecific territorial intrusions by pairs (Demko and Mennill 2018), yet are rarely used spontaneously (Demko and Mennill 2019). Female *rufifrons* group songs were also shorter, with fewer syllables and higher maximum frequency, than male songs. The syllables themselves were also shorter, and of higher maximum frequency and larger bandwidth. Interestingly, female singing behavior of the 2 subspecies may also differ: *B. r. rufifrons* and *B. r. salvini* females appeared to produce more spontaneous songs in response to their male partner's songs during focal recordings (A. D. Demko personal observation) and sang more frequently in response to playback during an experimental study than did *B. r. delattrii* females (Demko et al. 2019). Given that female song is common yet poorly studied in tropical songbird species (Stutchbury and Morton 2001, Odom and Benedict 2018), and that the *delattrii* and *rufifrons* groups appear to be vocally distinct based on our analyses, further investigations of female song in both groups would be informative to explore vocal evolution in the family Parulidae.

CONCLUSION

Our research revealed that the *rufifrons* group and *B. r. salvini* are well-differentiated from the *delattrii* group in morphology, song, and some plumage traits. The low responses to other-subspecies song and apparent lack of inter-subspecies territoriality and hybridization in a sympatric zone between *B. r. delattrii* and *B. r. rufifrons* in southern Mexico further suggests reproductive isolation between the 2 groups (Demko et al. 2019). Our results therefore suggest the presence of 2 distinct groups within this species complex: the Rufous-capped Warbler (*Basileuterus rufifrons*), comprised of the 5 northern subspecies (*B. r. caudatus*, *dugesi*, *jouyi*, *rufifrons*, and *salvini*), and the Chestnut-capped Warbler (*Basileuterus delattrii*), comprised of the 3 southern subspecies (*B. d. actuosus*, *delattrii*, and *mesochrysus*). Ongoing genomic analyses of samples from the *B. r. delattrii* and *B. r. rufifrons* contact zone and other sites throughout the Rufous-capped Warbler's range in Mexico and Central America will compare patterns of range-wide phenotypic and genetic divergence, and will be critical for further refinement of the taxonomic classification proposed here.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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Data depository: Analyses reported in this article can be reproduced using the data provided by Demko et al. (2020).

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