



Rufous-capped Warblers *Basileuterus rufifrons* show seasonal, temporal and annual variation in song use

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In the majority of songbird species, males have repertoires of multiple song types used for mate attraction and territory defence. The wood-warblers (family Parulidae) are a diverse family of songbirds in which males of many migratory species use different song types or patterns of song delivery (known as ‘singing modes’) depending on context. The vocal behaviour of most tropical resident warblers remains undescribed, although these species differ ecologically and behaviourally from migratory species, and may therefore differ in their vocal behaviour. We test whether male Rufous-capped Warblers *Basileuterus rufifrons* use distinct singing modes by examining song structure and context-dependent variation in their songs. We recorded multiple song bouts from 50 male Warblers in a Costa Rican population over 3 years to describe seasonal, diel and annual variation in song structure and vocal behaviour. We found that Rufous-capped Warbler songs are complex, with many syllable types shared both within and between males’ repertoires. Males varied their song output depending on context: they sang long songs at a high rate at dawn and during the breeding season, and shortened songs in the presence of a vocalizing female mate. Unlike many migratory species, Rufous-capped Warblers do not appear to have different singing modes; they did not change the song variants used or the pattern of song delivery according to time of day, season or female vocal activity. Our research provides the first detailed vocal analysis of any *Basileuterus* warbler species, and enhances our understanding of the evolution of repertoire specialization in tropical resident songbirds.

Keywords: dawn chorus, singing modes, song repertoires, tropical songbird, vocalizations, wood-warbler.

The songs of birds are multipurpose signals that serve diverse functions including mate attraction and territory defence (Catchpole & Slater 2008). In over 70% of songbird species, males have repertoires of multiple song types that may serve specialized functions (MacDougall-Shackleton 1997, Catchpole & Slater 2008). Many species vary their use of particular song types or syllable types depending on breeding status, time of day and level of aggressive motivation (e.g. Järvi *et al.* 1980, Nelson & Croner 1991, Kunc *et al.* 2005). Birds can also adjust their vocal behaviour depending on context by using different patterns of song delivery (e.g. Wiley *et al.* 1994, Trillo &

Vehrencamp 2005) or by varying their vocal output through changes in song rate (e.g. Benedict *et al.* 2012, Szymkowiak & Kuczyński 2016) or song length (e.g. Nelson & Poessel 2011). The evolution of specialized song types or vocal behaviour may be constrained by phylogeny (Mann *et al.* 2009), although female choice, male–male competition and cultural drift probably drive repertoire diversity (Byers & Kroodsma 2009, Price 2013). Detailed vocal descriptions provide valuable insight into the evolution of acoustic communication and lay critical groundwork for comparative studies between closely related species (e.g. Price & Lanyon 2004, Mann *et al.* 2009, Mason *et al.* 2017).

In many territorial bird species with repertoires of multiple song types, males share song types

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with neighbouring males and use them during territorial interactions (e.g. Beecher *et al.* 2000a, Vehrencamp *et al.* 2007, Camacho-Schlenker *et al.* 2011). Collectively, studies of such species suggest that song sharing is important for territory establishment and ongoing territory defence. For example, male Song Sparrows *Melospiza melodia* match song types with neighbours during male–male territorial interactions (Beecher *et al.* 2000b) and males with more shared songs have longer territory tenure (Beecher *et al.* 2000a). Males of many species use their repertoires differently across years through differential repertoire use or even learning new songs, in order to better match the song types or syllables used by their neighbours (e.g. McGregor & Krebs 1989, Payne & Payne 1993, Lemon *et al.* 1994, Vargas-Castro *et al.* 2012, 2015). Within and across species, song sharing is more prevalent in resident populations or short-distance migrants with high return rates than in long-distance migrants (Handley & Nelson 2005, Yoon *et al.* 2013), although some migratory populations show a high degree of sharing (Foote & Barber 2007). While much research has explored repertoire use during the breeding season in temperate songbird populations, little is known about seasonal and annual variation in the vocal behaviour of tropical resident species.

Tropical birds exhibit life-history traits which differ from those in temperate birds, including widespread year-round territoriality and long-term pair bonds, and these differences may influence the structure and function of their vocalizations (Stutchbury & Morton 2001). In tropical resident birds, singing for mate attraction and territory defence is not confined to the breeding season (Fedy & Stutchbury 2005; Topp & Mennill 2008; Tobias *et al.* 2011; Odom *et al.* 2017) as it is in most temperate species (Catchpole & Slater 2008). Although there are few detailed vocal analyses, studies of tropical resident songbirds have revealed complex behaviours such as song-matching with neighbouring males during territorial interactions (e.g. Vehrencamp *et al.* 2007, Price & Yuan 2011), song sharing combined with annual variation in song type use (Vargas-Castro *et al.* 2012, 2015) and use of different patterns of song delivery depending on context (e.g. Staicer 1996a, Molles & Vehrencamp 1999).

The wood-warblers (family Parulidae) are a diverse family that includes both resident and migratory species, and studies of the vocalizations of some migratory wood-warblers have revealed an

interesting system of vocal behaviour. Males in the genera *Setophaga*, *Mniotilta* and *Vermivora* use two distinct subsets of songs or patterns of song delivery, known as ‘singing modes’, which vary in structure and context of use (Spector 1992). Type I songs are primarily used during day singing or male–female interactions and are often delivered in repeat mode (i.e. eventual variety, or repetition of one song type), whereas Type II songs are used during dawn singing or male–male interactions and are typically delivered in serial mode (i.e. immediate variety, or switching between multiple song types; Wiley *et al.* 1994, Staicer *et al.* 2006). Males of some migratory warbler species share more song types with neighbours than with non-neighbours (Lemon *et al.* 1994, Beebe 2002, Janes & Ryker 2006, Demko *et al.* 2016) and add or drop songs from their repertoires between years depending on their use by neighbours (Lemon *et al.* 1994, Demko *et al.* 2016). According to the latest phylogenetic classification of the Parulidae, related species tend to share similar vocal behaviour (Spector 1992, Lovette *et al.* 2010), including both temperate and tropical *Setophaga* warblers (Spector 1992, Staicer 1996a). However, recent work on the genera *Cardellina* (Ammon & Gilbert 1999, Demko *et al.* 2013) and *Geothlypis* (Byers 2015) shows that congeners can exhibit different vocal behaviour.

Rufous-capped Warblers *Basileuterus rufifrons* are common tropical resident warblers that defend year-round territories (Contreras-González *et al.* 2010, Curson 2010). As with other *Basileuterus* warblers, their vocal repertoire is undescribed; temporal, seasonal and annual variation in song type use or patterns of song delivery remain undocumented. The objective of our study is to test hypotheses related to repertoire structure and singing behaviour by describing song structure and vocal activity of a Costa Rican population of the subspecies *B. r. delatarii*. To test whether males have two singing modes, as for many temperate warblers, we investigated repertoire size and organization, and seasonal and temporal variation in use of different song types or patterns of song delivery. Based on the hypothesis that male Rufous-capped Warblers use two singing modes, we predicted that they would use specific song types or patterns of song delivery during particular seasons (non-breeding and breeding) or times of day (dawn and daytime; Spector 1992). We also investigated the potential role of repertoire sharing in mediating conspecific interactions by analysing repertoire sharing between individuals, and annual

variation in use of specific song types and syllables in the repertoire. Based on the hypothesis that songs are important in mediating conspecific interactions for Rufous-capped Warblers, we predicted that males should share more songs with neighbours than with non-neighbours, and that use of specific song types and syllables should change across years (e.g. Lemon *et al.* 1994, Demko *et al.* 2016). We also briefly describe non-song vocalizations (calls). Our research is the first quantitative vocal analysis of any species in the tropical resident genera *Basileuterus*, *Myioborus*, and *Myiothlypis*, and provides a foundation for understanding the evolution of repertoire specialization in this group of tropical resident songbirds.

METHODS

Study site and data collection

From April to July 2013–2015, we studied a colour-ringed population of Rufous-capped Warblers in Sector Santa Rosa, Área de Conservación Guanacaste, northwestern Costa Rica (10°51'N, 85°36'30"W). These Warblers are common residents in second-growth and mature forest areas of this tropical dry forest. The time period of data collection coincided with the end of the dry (non-breeding) season (December to mid-May) and the beginning of the rainy (breeding) season (mid-May to November; Campos & Fedigan 2013). Over three field seasons, we sampled 50 focal males (2013: $n = 14$; 2014: $n = 26$; 2015: $n = 31$); 13 males were sampled in two consecutive years, and four males were sampled in all 3 years. We collected dawn and daytime recordings of territorial males by using a Marantz PMD660 digital recorder, Sennheiser ME62 omnidirectional microphone and Telinga parabola. At least once per season, we collected continuous dawn chorus recordings for each male, beginning at the male's first song of the morning (approximately 04:45 h CST) until the end of the period of continuous song that we considered to be the dawn chorus (approximately 06:00 h). We collected 30–60 min daytime recordings between 06:30 and 12:00 h approximately weekly from each male.

We captured focal birds in mist-nets using conspecific playback, and gave each bird a unique combination of colour-rings to identify individuals and differentiate between the sexes (Rufous-capped Warblers are sexually monomorphic). During the pre-breeding and breeding season (late

April to July), we sexed birds in the hand by observing a cloacal protuberance for males or a brood patch for females. When we could not determine the bird's sex based on these characteristics, we instead determined sex based on their behaviour during territorial observations. Only males sing a continuous dawn chorus bout, and females are the primary nest-builders and sole incubators (Stiles & Skutch 1989, Demko & Mennill 2018a). Forty-six of the 50 focal males were colour-ringed. As the Warblers have individually distinctive song repertoires, we were able to confirm the identity of the four un-ringed males by obtaining at least two recordings of a male with a similar song repertoire on the same territory within the same year.

Repertoire size and song organization

Using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, USA), we annotated all male focal recordings and classified vocalizations at several levels of organization. We defined a syllable as the smallest continuous trace on a spectrogram (Catchpole & Slater 2008). We categorized each syllable based on its shape, duration and frequency bandwidth, and thus produced a syllable catalogue for each focal male and a syllable pool of all syllable types observed in all males in the population (Byers 1995). A.D.D. classified all syllables. To ensure objectivity, a second observer classified syllables for 50 songs and obtained > 95% agreement in classification using two interobserver reliability scores (Demko & Mennill 2018b). We defined a song variant as a unique sequence of syllables in the same order, excluding consecutive repetitions of the same syllable type within a song. More generally, a song was a syllable sequence separated by at least 0.5 s from another syllable sequence.

We measured several variables in order to describe song and repertoire organization for all 50 males. First, we calculated the total number of syllables per song variant, and the number of different syllable types per song variant (Rendall & Kaluthota 2013). We then used these values to calculate a syllable diversity index, which is the ratio of the number of different syllable types to the total number of syllables (Gil & Slater 2000, dos Santos *et al.* 2016). We calculated this index for each song variant, and then calculated an average of these values across all of a male's recorded song variants to obtain an average syllable diversity

score for each male. A value of 1 indicates that every syllable within a song is used only once, whereas a value close to 0 indicates that syllable types are frequently repeated within a song. We measured syllable repertoire size and song variant repertoire size, and then used Kendall's T correlations to test whether these measures were correlated with the number of songs recorded (Podos *et al.* 1992, Gil & Slater 2000).

Our recordings revealed that Rufous-capped Warbler songs are complex and not visually classifiable into song types (i.e. song variants that share similar sequences of syllables), in contrast to many other warbler species (e.g. Byers 1995, Staicer 1996a). Therefore, we used similarity indices and cluster analyses to quantify the degree of within-male repertoire organization in order to determine whether a male's song variants can be objectively grouped into song types (Podos *et al.* 1992, Gil & Slater 2000). We used Jaccard's distance adjusted for differences in song length to compare the number of syllable types shared between each of a male's song variants. We used the 'designdist' function in the 'vegan' R package (Oksanen *et al.* 2017) to calculate pairwise Jaccard's distances between all of a male's song variants to produce a distance matrix (e.g. MacDougall-Shackleton *et al.* 2009, Sosa-López & Mennill 2013). The adjusted Jaccard coefficient, $S_j(\text{adj})$, was calculated as:

$$S_j(\text{adj}) = c / ((a + b + c) - d) \quad (1)$$

For two songs, X and Y, a was the number of unique syllables found in song X, but not in song Y; b was the number of unique syllables found in song Y, but not in song X; c was the number of shared syllables in songs X and Y; and d was the difference between the number of syllables in songs X and Y. We then used the 'pvclust' package (Suzuki & Shimodaira 2015) to test for the presence of clusters (song types) using hierarchical cluster analysis with average linkage. Cut-off values were selected for each cluster based on a bootstrapping analysis which assesses the probability ($\alpha = 0.05$) of obtaining a specific cluster compared with randomized groupings based on 1000 replications.

Seasonal and temporal variation in song use

To test whether male Rufous-capped Warblers use distinct singing modes, we calculated song rate

(number of songs/min), number of song variants used, syllable diversity index and song duration for multiple 20-song bouts per male (total number of bouts: $n = 141$, number of males: $n = 44$, number of bouts per male: 1–12). A song bout was a sequence of consecutive recorded songs separated by < 30 s (dos Santos *et al.* 2016). Song rate and song duration are standard measures of song output, and are known to differ between singing modes and times of day in other warbler species (e.g. Spector 1991, Staicer *et al.* 2006, Price & Crawford 2013). To calculate the relative occurrence of unique song variants within a bout, we calculated a Shannon–Wiener index using the 'vegan' R package (Oksanen *et al.* 2017). This index is often used to measure species richness in ecological communities and is also useful for calculating the relative occurrence of commonly and rarely used song variants within a bout (Molles & Vehrencamp 1999). To assess whether Rufous-capped Warblers used different patterns of song delivery (eventual or immediate variety), we calculated the switching rate within song bouts, which is the number of transitions between different song variants divided by the total possible number of transitions (the number of songs in the bout minus 1). A switching rate of 1 indicates that each successive song variant in a bout is different (high-switching serial mode), whereas a switching rate of 0 indicates that each successive song variant is the same (low-switching repeat mode; Molles & Vehrencamp 1999). We were interested in whether female vocal activity influenced male singing behaviour, so when we recorded female calls in the background of the male focal recording during a song bout, we counted the female as 'vocal', and otherwise counted her as 'silent'. It is likely that females also attend to male vocalizations even when not vocalizing themselves. However, as the behaviour of females was more difficult to monitor when they were silent, we confined our analysis to vocalizing females. Because males of warbler species with two song categories use primarily Type II singing during the dawn chorus (Spector 1992), we also calculated the percentage of song variants that focal males used during both periods, compared with those used exclusively at dawn, for a subset of males ($n = 15$) with at least 50 songs recorded in each period in any given year.

We used linear mixed models to test the influence of season (non-breeding season vs. breeding

season), time of day (dawn vs. day), whether the female vocalized near the male or did not (vocal vs. silent), and the interaction effect between season and time of day on each of the response variables. In this analysis, we used season, time of day, season \times time interaction, and female vocal activity as fixed effects, and bird identity as a random effect. We used likelihood ratio tests to estimate P -values of fixed effects, and ran *post hoc* tests to quantify all significant effects using the R ‘multcomp’ package (Hothorn *et al.* 2017). For song switching rate, we applied the arcsine transformation to the response variable to meet the assumptions of linear mixed model analysis.

Syllable sharing

As male Rufous-capped Warbler repertoires consist of song variants comprising combinations of syllables rather than discrete song types (Fig. 1), we quantified repertoire sharing at the level of the syllable. We calculated the adjusted Jaccard similarity index to compare the presence or absence of specific syllable types in the syllable repertoires of all males to one another (MacDougall-Shackleton *et al.* 2009, Sosa-López & Mennill 2013). Using the pairwise sharing coefficients, we calculated the proportion of between-male syllable sharing within the study population. We then tested for the presence of clusters (groups of males with similar syllable repertoires) using hierarchical cluster analysis with average linkage, followed by bootstrapping analysis at $\alpha = 0.05$ with 10 000 replications. We

ran separate analyses for 2013 ($n = 14$), 2014 ($n = 26$) and 2015 ($n = 31$).

Annual variation in song use

To document annual variation in repertoire use by focal males, we analysed syllable repertoires and song bouts from all males with 2–3 years of available song recordings ($n = 17$). For each male, we measured whether specific song variants or syllables were added or dropped across years within the male’s observed repertoire. This could indicate differential use of the existing song repertoire based on the presence or absence of specific neighbouring males that share those song types (e.g. Payne & Payne 1993, Nordby *et al.* 2007) or learning of new songs by males across years (e.g. Vargas-Castro *et al.* 2015). To quantify the proportion of song variants and syllables changed in a given male’s repertoire between years, we calculated the Sørensen–Dice index (SD) (Eriksen *et al.* 2011, Vargas-Castro *et al.* 2015):

$$SD = 1 - (2N_s / (R_1 + R_2)) \quad (2)$$

where, N_s is the number of song variants or syllables used in both years, R_1 is the repertoire size in year 1 and R_2 is the repertoire size in year 2. A value of 0 indicates that the repertoires were the same between years, and a value of 1 indicates that the entire repertoire composition changed between years. We converted the values to percentages in the Results. We conducted all

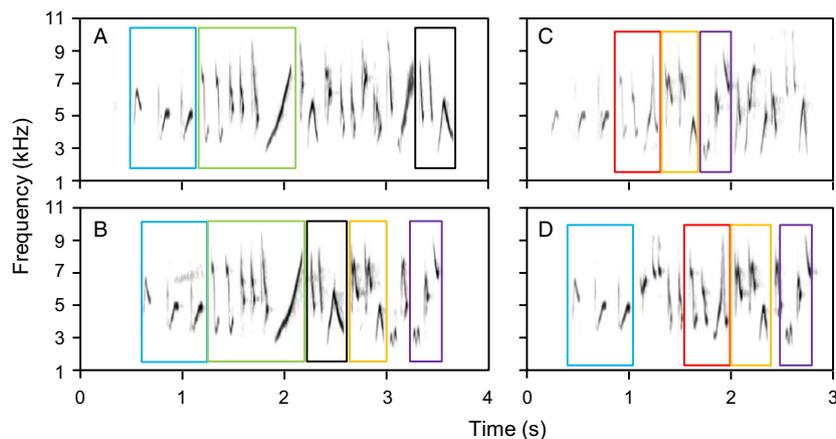


Figure 1. Sound spectrograms depicting examples of four song variants from one male Rufous-capped Warbler. This male used each syllable type in multiple song variants. For example, he used the same three-syllable group (in black box) at the end of song (a) and middle of song (b), and he used the syllable groups in the yellow and purple boxes in songs (b), (c) and (d).

statistical analyses using R v.3.4.3 (R Development Core Team 2017).

Non-song vocalizations and female song

In addition to male songs, we sampled calls produced by Rufous-capped Warblers on our focal recordings, as describing calls is a critical first step towards quantifying sex-specific differences in call structure and function (Benedict & Krakauer 2013, Digby *et al.* 2013). Owing to a small number of available high-quality call recordings from known-sex individuals, we provide a qualitative description of 'chip' call types recorded from male and female Rufous-capped Warblers during territorial interactions. We also recorded rare instances of female song during our focal recording collection and qualitatively describe these vocalizations.

RESULTS

Male repertoire size and song organization

Our analyses revealed that male Rufous-capped Warblers have complex vocal repertoires composed of many song variants produced from a small pool of syllables. On average, males had repertoires of 181 ± 166 song variants (range: 22–820) and 42 ± 9 syllable types (range: 26–64; $n = 50$). There was little syllable repetition within songs; the average within-male syllable diversity was 0.78 ± 0.06 (range: 0.63–0.90). As the song variant repertoire size was strongly correlated with the number of songs recorded (Kendall's $T = 0.63$, $P < 0.001$, $n = 50$), which varied considerably between males (range: 62–2491), we chose a subset of males that had been recorded extensively (> 500 songs; $n = 24$) to describe accurately the relationship between aspects of repertoire complexity. There was a significant positive correlation between song variant repertoire size and the number of songs recorded ($T = 0.32$, $P = 0.03$, $n = 24$), although syllable repertoire size was not significantly correlated with the number of songs ($T = 0.11$, $P = 0.47$, $n = 24$). Males with larger syllable repertoires did not have larger song variant repertoires, as syllable and song variant repertoire sizes were not significantly correlated ($T = 0.18$, $P = 0.22$, $n = 24$). Rufous-capped Warbler repertoires were not objectively classifiable into song types (i.e. groups of song variants that share

similar sequences of syllables). Repertoire size estimates based on shared syllable types ranged from one to 60 song types (mean \pm sd = 14.7 ± 14.3), and these categories were not consistent with visual classification of song variants based on syllable similarity.

Seasonal and temporal variation in song use

Male Rufous-capped Warblers showed seasonal and temporal variation in song rate during active singing bouts. For song rate, there was a significant season \times time of day interaction (Table 1). During the non-breeding season, males ($n = 44$) sang at a similar rate during dawn and daytime singing (estimate = -0.11 ± 0.97 , $t = -0.1$, $P = 0.91$; Fig. 2a), but during the breeding season, males sang at a significantly higher rate at dawn than during the day (estimate = 2.72 ± 0.37 , $t = 7.4$, $P < 0.001$; Fig. 2b). Female vocal activity did not have a significant effect on male song rate (Table 1).

Song duration varied according to season, time of day and female vocal activity. For song duration, there was a significant season \times time of day interaction (Table 2). During the non-breeding season, songs were of similar length during both dawn and daytime singing (estimate = -0.03 ± 0.11 , $t = -0.3$, $P = 0.75$; Fig. 3a), but during the breeding season, males sang significantly longer songs at dawn than during the day (estimate = 0.20 ± 0.04 , $t = 4.8$, $P < 0.001$; Fig. 3b). Males also sang longer songs overall during the

Table 1. Linear mixed model (LMM) and *post hoc* comparison results of variation in song rate of male Rufous-capped Warblers ($n = 44$) according to season, time of day and female vocal activity; significant effects are highlighted in bold.

Song rate			
Full LMM	χ^2	df	P-value
Time of day	37.67	1	< 0.001
Season	8.92	1	0.003
Female vocal activity	0.57	1	0.45
Time of day \times Season	7.28	1	0.007
<i>Post hoc</i> comparisons			
	Estimate \pm se	t-value	P-value
Breeding season			
Dawn-Day	2.72 \pm 0.37	7.4	< 0.001
Non-breeding season			
Dawn-Day	-0.11 ± 0.97	-0.1	0.91

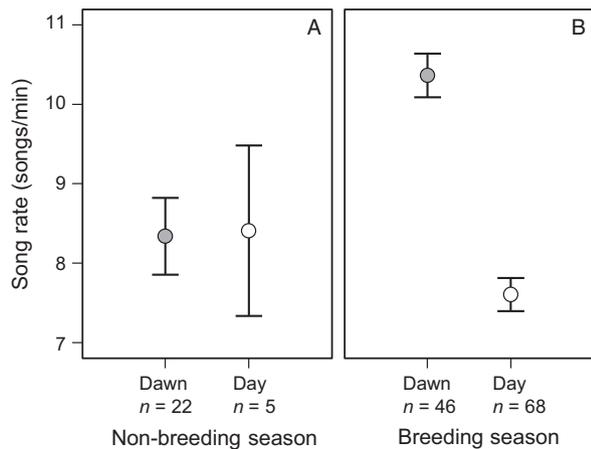


Figure 2. Male Rufous-capped Warblers ($n = 44$) sang at similar song rates during dawn and daytime singing in the non-breeding season (a) but sang at significantly higher rates during dawn singing than during the day during the breeding season (b). Error bars represent standard error around the mean. Sample sizes below bars indicate the number of song bouts analysed.

breeding season than during the non-breeding season (estimate = -0.31 ± 0.05 , $z = -5.7$, $P < 0.0001$). Female vocal activity had a significant effect on male song duration (Table 2); males sang shorter songs when the female was vocalizing than when she was silent (estimate = -0.11 ± 0.05 , $z = -2.13$, $P = 0.03$; Table 3).

The switching rate between song variants changed significantly with time of day (likelihood ratio test: $\chi^2_1 = 3.85$, $P = 0.05$; Table S1). Switching rates were higher during dawn singing than daytime singing (estimate = -0.05 ± 0.02 , $z = -2.2$, $P = 0.03$), although switching rates were high (mean > 0.90 ; Table 3) during both time periods. There was no significant variation in song variant diversity (Shannon–Wiener index), syllable diversity or the number of song variants per bout by season, time of day or female vocal activity (Table 3, Tables S2–S4). Males used many song variants exclusively during dawn or daytime singing; males ($n = 15$ with the most songs recorded) used $77.3 \pm 11.2\%$ (range: 50–90%) of their song variants exclusively in dawn or daytime singing within a given year.

Syllable sharing

Males shared many syllable types with neighbours. In a cluster analysis of syllable similarity across all 3 years, 49 of the 50 focal males grouped into

Table 2. Linear mixed model (LMM) and *post-hoc* comparison results of variation in song duration of male Rufous-capped Warblers ($n = 44$) according to season, time of day, and female vocal activity; significant effects are highlighted in bold.

Song duration			
Full LMM	χ^2	df	<i>P</i> value
Time of day	16.68	1	< 0.001
Season	24.77	1	< 0.001
Female vocal activity	4.62	1	0.03
Time of day \times Season	3.90	1	0.05
<i>Post-hoc</i> comparisons			
Breeding season	Estimate \pm se	<i>t</i> -value	<i>P</i> -value
Dawn-Day	0.20 \pm 0.04	4.8	< 0.001
Non-breeding season			
Dawn-Day	-0.03 ± 0.11	-0.32	0.75

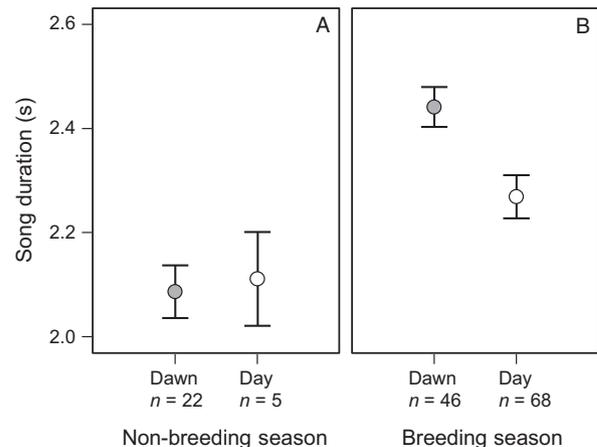


Figure 3. Male Rufous-capped Warblers ($n = 44$) sang songs of similar duration during dawn and daytime singing in the non-breeding season (a) but sang significantly longer songs at dawn than during the day during the breeding season (b). Error bars represent standard error around the mean. Sample sizes below bars indicate the number of song bouts analysed.

three to five clusters of males with similar syllable repertoires (Fig. 4). Average syllable sharing between all males in the population was low (mean \pm sd: $S_j(\text{adj}) = 0.11 \pm 0.09$) but was highly variable across pairs of males (pairwise range: 0.01–0.90). Males shared twice as many syllables with other males within the same cluster ($S_j(\text{adj}) = 0.16 \pm 0.13$; within-group range: 0.15–0.44; pairwise range: 0.02–0.90) than with males in different clusters ($S_j(\text{adj}) = 0.08 \pm 0.04$; pairwise range: 0.01–0.26). Within years, males in

Table 3. Comparison of acoustic variables measured from 20-song bouts ($n = 141$) of male Rufous-capped Warblers ($n = 44$ males). Data are summarized relative to time of day, season and female vocal activity; all values are mean \pm sd. The sample sizes next to each category indicate the number of bouts analysed.

Acoustic variable	Pre-breeding season		Breeding season		Female vocal activity	
	Dawn ($n = 22$)	Day ($n = 5$)	Dawn ($n = 68$)	Day ($n = 46$)	Vocal ($n = 26$)	Silent ($n = 115$)
Song rate (songs/min)	8.33 \pm 2.30	8.40 \pm 2.41	10.36 \pm 2.27	7.59 \pm 1.46	8.38 \pm 2.00	9.23 \pm 2.46
Song duration (s)	2.09 \pm 0.24	2.11 \pm 0.20	2.44 \pm 0.31	2.27 \pm 0.28	2.16 \pm 0.25	2.36 \pm 0.32
Number of song variants	14.05 \pm 3.47	15.00 \pm 3.54	13.84 \pm 3.83	14.07 \pm 3.46	14.04 \pm 3.88	13.97 \pm 3.57
Song variant diversity	2.44 \pm 0.41	2.54 \pm 0.40	2.46 \pm 0.38	2.47 \pm 0.37	2.43 \pm 0.45	2.47 \pm 0.36
Switching rate	0.97 \pm 0.07	0.94 \pm 0.07	0.97 \pm 0.05	0.95 \pm 0.07	0.94 \pm 0.09	0.96 \pm 0.05
Syllable diversity	0.80 \pm 0.08	0.82 \pm 0.10	0.79 \pm 0.07	0.80 \pm 0.07	0.81 \pm 0.08	0.79 \pm 0.07

nearby locations at the study site had similar syllable repertoires. In 2015, there were three exceptions: males 92, 93 and 94 grouped vocally with males outside of their geographical area (Fig. 4): male 92 had no immediate neighbours among the other focal birds in the study population; males 93 and 94 in the IQ Trail area both claimed their territories in mid-June and probably moved there from other locations where they would have been exposed to different syllable and song types. Most males present in more than 1 year remained in the same cluster across years (Fig. 4).

Annual variation in song use

Males varied both the syllable types and song variants used in their repertoires between years. Males ($n = 17$) changed $79.8 \pm 17.0\%$ (range: 42.6–100%) of their song variants between seasons. They changed relatively few syllable types, however, showing only an $8.4 \pm 9.3\%$ turnover of syllables between seasons (range: 0–45%). Nearly half (mean \pm sd = $40.6 \pm 22.5\%$) of the syllables that males changed between seasons were ‘rare’ syllables that occurred in only one or two annotated songs in any given year. The percentage of rare syllables present in all of a male’s changed syllables varied considerably between individuals (range: 0–83.3%) and may reflect variation in sampling effort (i.e. rare syllables are more likely to be missed in a smaller sample of songs).

Non-song vocalizations

Male and female Rufous-capped Warblers produced call notes during a variety of conspecific interactions. Both sexes produced at least six different ‘chip’ call variants (Fig. 5a) during territorial

interactions with other warblers and during foraging activities, especially during the non-breeding season. Females ($n = 17$) also gave ‘chip’ calls when vocalizing near a singing male partner (Fig. 5a). Both sexes also produced high-pitched, short-duration alarm calls during perceived threats to their nest-site or fledglings (Fig. 5b).

Female song

Female Rufous-capped Warblers sing rarely. In our 3-year study, we recorded confirmed spontaneous song from a ringed female only once, on a dawn chorus recording on 4 June 2015 at the start of the breeding season. This was the day after the first major rain event of the season, and the first day when we observed female Warblers nest-building that year. The singing female had recently paired with a new mate, her former neighbour, after 26 May. In a concurrent playback study, we found that female Rufous-capped Warblers occasionally sing in response to conspecific playback of male songs and female calls (Demko & Mennill 2018b). The female songs produced spontaneously during the current study were similar in structure to the songs females produce in response to playback in that they were shorter with fewer syllables and syllable types than male songs (Demko & Mennill 2018b).

DISCUSSION

Male Rufous-capped Warblers have large, complex repertoires of song variants produced from a small pool of approximately 45 syllables. In support of the hypothesis that Rufous-capped Warbler songs are important in mediating conspecific interactions, our results suggest that males may use shared

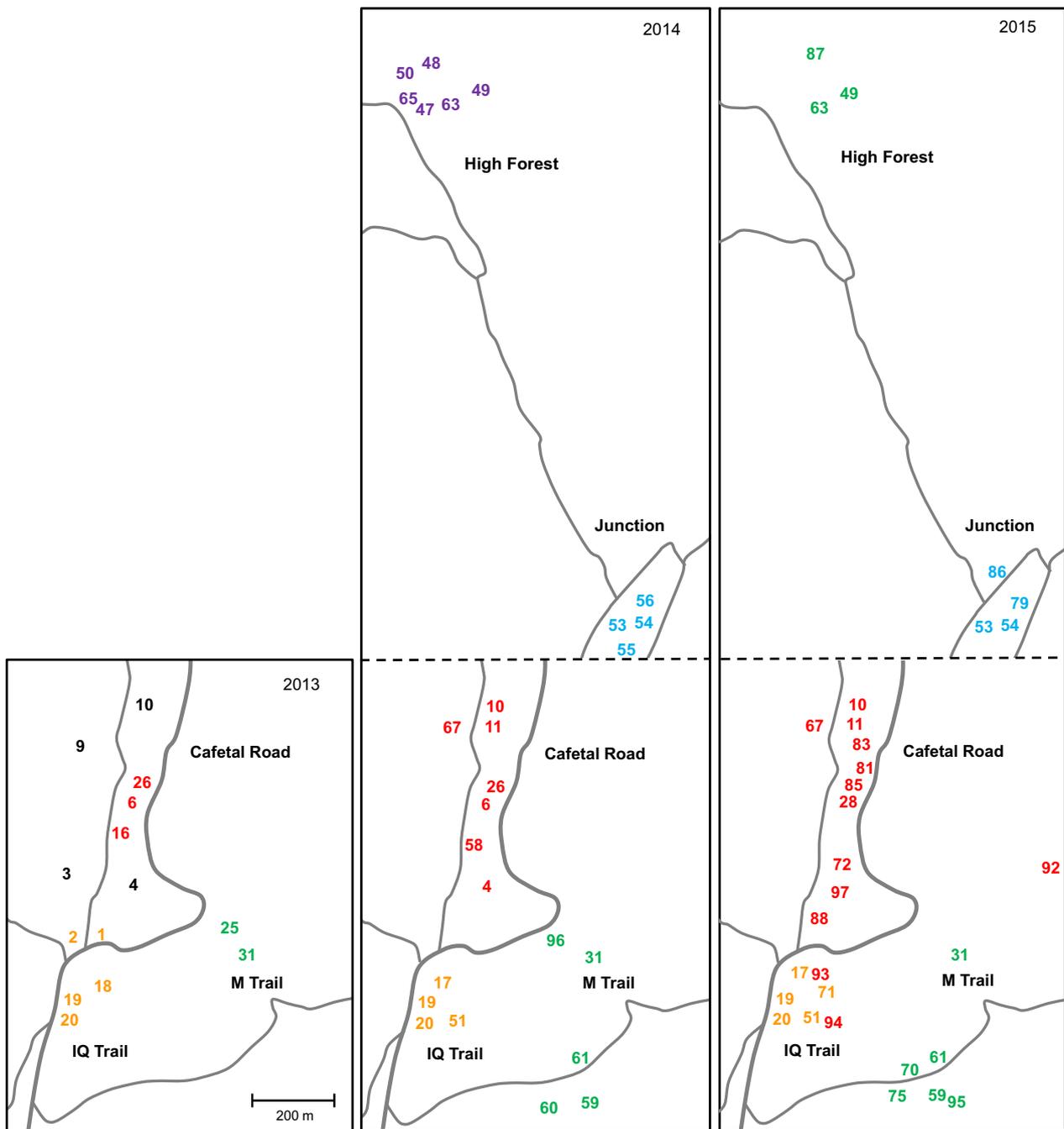


Figure 4. Male Rufous-capped Warblers clustered into three to five groups in 2013–2015 according to syllable repertoire similarity. Each group consisted of neighbouring males from the same location at the study site (High Forest, Cafetal Road, Junction, M Trail, and IQ Trail), except for birds 92 (M Trail) and 93 and 94 (IQ Trail) in 2015. Numbers represent individual males (2013: $n = 14$; 2014: $n = 26$; 2015: $n = 31$) and colours indicate cluster membership. Breaks in the 2014 and 2015 maps indicate gaps without monitored territories; the distance between the north end of the bottom map and south end of the top map is approximately 650 m.

songs and syllables during these interactions, given that they share more syllable types with neighbours than with non-neighbours. They also use the

same syllables across years, but they change the particular song variants used annually. Rufous-capped Warblers also have complex vocal

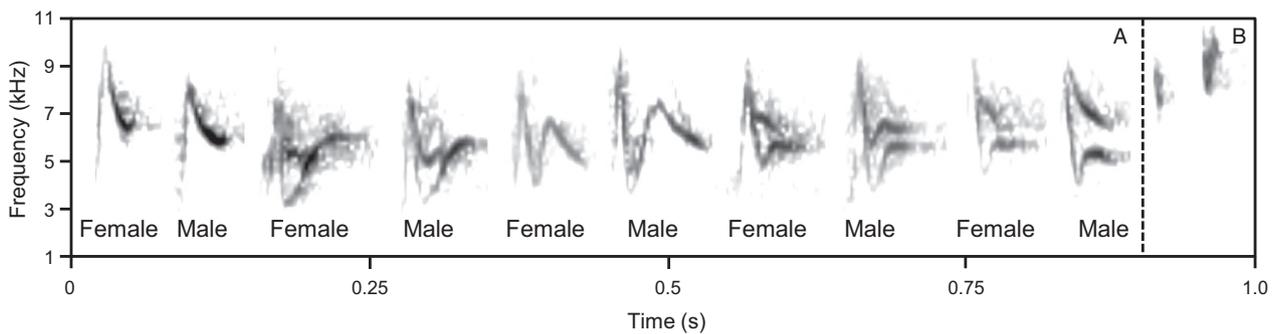


Figure 5. Examples of Rufous-capped Warbler ‘chip’ calls produced by both sexes during territorial interactions and foraging (a), and an alarm call used by both sexes during perceived threats to the nest-site or fledglings (b). Calls in (a) were recorded from different individual males and females and represent our best-quality recordings; calls in (b) are from individuals of unknown sex.

behaviour: they vary song structure and use according to season, time of day and social context. In particular, males sing at the highest rates with the longest songs during the breeding season dawn chorus, but sing shortened songs in the presence of a vocalizing female. Although switching rates between songs were higher at dawn than during the day, males switch frequently between songs at all times of day. We did not find support for the hypothesis that Rufous-capped Warblers use two singing modes; in contrast to many wood-warblers, this species sings with immediate variety and high within-song complexity irrespective of time of day, breeding status or female vocal activity. The vocal behaviour of Rufous-capped Warblers, which display complex and variable repertoires without apparent singing modes, differs from other warbler species studied to date (e.g. Spector 1992, Demko *et al.* 2013) but is similar to other songbird species with complex multi-syllable repertoires (e.g. Willow Warblers *Phylloscopus trochilus*: Gil & Slater 2000, House Wrens *Troglodytes aedon*: Rendall & Kaluthota 2013).

We found that although Rufous-capped Warblers do not have two distinct singing modes, their complex repertoires differ in structure and use from other wood-warbler species (reviewed in Spector 1992). Warblers with two singing modes typically only sing structurally complex songs with immediate variety in Type II singing (e.g. Byers 1995); in warblers with a single singing mode, males generally sing a single, stereotyped primary song type in most contexts (Lein 1981, Ritchison 1995). Apart from Rufous-capped Warblers, the only known single-mode singers with complex songs are three tropical *Geothlypis* species, which, in contrast to their other tropical resident and

migratory congeners, have elaborate songs (Byers 2015). Interestingly, many comparative studies in songbirds to date suggest that breeders in higher-latitude or seasonally variable habitats, rather than tropical breeders, have more elaborate songs, perhaps owing to heightened sexual selection pressures (e.g. Botero *et al.* 2009, Weir & Wheatcroft 2011, Kaluthota *et al.* 2016, Xing *et al.* 2017). Further detailed work on the vocal behaviour of the tropical resident genera *Basileuterus*, *Myioborus* and *Myiothlypis* is necessary to discern large-scale patterns in repertoire use in the family Parulidae.

Males show the highest song output during the breeding season dawn chorus, when they increase both song rate and song duration. This pattern is similar to that observed for many migratory warbler species (Spector 1992, Staicer *et al.* 1996) and the well-studied tropical resident Adelaide’s Warbler *Setophaga adelaidae*, which sings a dawn chorus only during the breeding season, even though it is territorial year-round (Staicer 1996b). In many songbird species, dawn chorus singing serves to defend territories against rival males (e.g. Liu 2004, Amrhein & Erne 2006, Foote *et al.* 2011). This is probably a function of the dawn chorus in Rufous-capped Warblers as well, as they appear to be more exclusively territorial in the breeding season. During the non-breeding season, we occasionally observed non-territorial adult Warblers on a focal pair’s territory, but never during the breeding season (A. Demko pers. obs.). High song output, particularly high song rate, may also be a male signal to social or extra-pair female mates (e.g. Cockburn *et al.* 2009). In several species, males with higher dawn song rates within a population show reproductive benefits: they obtain a mate earlier (Hofstad *et al.* 2002, Murphy *et al.* 2008) or have

female mates that lay eggs earlier (Poesel *et al.* 2001). Furthermore, male Field Sparrows *Spizella pusilla* sing at the highest rates at dawn during the incubation and nestling periods (Zhang *et al.* 2015), suggesting that high song rate in this species is a signal to other males and possibly extra-pair females. Further analyses examining seasonal variation in song output in individual warblers of known breeding status would be valuable to determine the function of the increased song rate and song length we observed during the dawn chorus.

Male Rufous-capped Warblers sing shorter songs when their female partner is vocalizing nearby. This finding corresponds with a recent hypothesis suggesting that short, simple songs are directed to females and better allow them to detect and compare the quality of male vocalizations (Price 2013). Indeed, use of short or stereotyped songs near females is documented for other songbird species with both single-song repertoires (Nelson & Poesel 2011) and specialized singing modes (Ficken & Ficken 1967, Kroodsmma *et al.* 1989). Shortened songs may be directed signals to stimulate the female during her fertile period, and to leave the nest during the incubation period, as shorter songs are thought to draw less attention from predators or rivals (Nelson & Poesel 2011). However, males also use long, complex songs at times when both male and female conspecifics would be listening, such as during the dawn chorus. Therefore, variation in specific song components (e.g. song duration) may convey different messages to male and female conspecifics depending on context of use (e.g. Molles 2006). Future work comparing responses of both sexes to different patterns of song delivery and song durations would be useful to determine the intended receivers and social function of each signal component.

The finding that males in our population share many syllable types with their neighbours suggests that using particular song or syllable types is beneficial for territory defence during male–male interactions (Beecher & Brenowitz 2005). In many songbird species, males use shared song types or series of syllables to interact with conspecific neighbours during territorial boundary disputes (e.g. Beecher *et al.* 2000b, Anderson *et al.* 2005, Vehrencamp *et al.* 2007, Price & Yuan 2011). This is likely in Rufous-capped Warblers as well, as pairs establish and defend territories year-round using their songs (Demko & Mennill 2018b), and share the same neighbours over multiple years

(this study). As female Rufous-capped Warblers also sing during conspecific interactions, use of shared songs may also be important in male–female interactions. In Banded Wrens *Thryophilus pleurostictus*, a species with female singing behaviour similar to that of Rufous-capped Warblers (i.e. females sing shorter, less complex songs than males and do not sing coordinated duets), female song is primarily used in male–female communication between pair members and in territory defence (Hall *et al.* 2015). Further experimental work could clarify whether Rufous-capped Warblers and other year-round resident tropical species with long-term territory tenure across years use particular matching songs or syllables during intra-sexual and intersexual conspecific interactions (e.g. Beecher *et al.* 2000a, Vehrencamp *et al.* 2007).

The large annual turnover in the specific song variants used by male Rufous-capped Warblers suggests benefits to changing songs over time. One explanation is that specific song variants convey messages to other individuals in the population, and that presence or absence of those individuals across seasons or years may drive annual song turnover. In many songbirds, males can add or drop songs or syllables in order to more closely match the repertoires of neighbouring males (McGregor & Krebs 1989, Lemon *et al.* 1994, Nicholson *et al.* 2007, Demko *et al.* 2016). Another explanation for the observed pattern of song sharing is cultural drift, whereby males vary their repertoire use over time, based on copying of specific syllables or variants in the population (e.g. Byers *et al.* 2010). In Rufous-capped Warblers, an analysis of countersinging bouts between neighbouring males would be necessary to evaluate whether males use matching songs during vocal interactions, and whether arrival or departure of specific neighbours affects whether a focal male uses particular song variants in a given year.

Our study revealed that Rufous-capped Warblers have complex repertoires composed of a finite number of syllables that males can recombine to produce a large number of song variants, or unique sequences of syllables. Syllables, rather than whole songs, appear to be the fundamental learned unit of the repertoire. Males share many syllable types with neighbours and change the song variants and syllables used across years, suggesting that both sharing and annual song variation are important signals to conspecifics. Males vary their singing behaviour primarily by increasing song rate and song duration during the breeding season dawn chorus,

perhaps as a strategy to defend territories from other males, and by decreasing song duration near female mates, perhaps as an advertisement signal. Our results suggest that in contrast to other migratory and tropical resident warblers studied to date, Rufous-capped Warblers have complex repertoires and vocal behaviour without apparent singing modes. Our research thus contributes towards comparative studies of repertoire specialization across the family Parulidae. Our study will also inform a comparison of vocalizations and vocal behaviour with a northern subspecies of Rufous-capped Warbler *B. r. rufifrons*, which has vocalizations, plumage patterns and territorial behaviour distinct from those of the southern *B. r. delatirii* (Curson 2010, A. Demko unpubl. data).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Linear mixed model results of variation in switching rate of male Rufous-capped Warblers ($n = 44$) according to season, time of day and female vocal activity; significant effects are highlighted in bold.

Table S2. Linear mixed model results of variation in song variant diversity index of male Rufous-capped Warblers ($n = 44$) according to season, time of day and female vocal activity. No effects were significant.

Table S3. Linear mixed model results of variation in syllable diversity index of male Rufous-capped Warblers ($n = 44$) according to season, time of day and female vocal activity. No effects were significant.

Table S4. Linear mixed model results of variation in number of song variants used by male Rufous-capped Warblers ($n = 44$) according to season, time of day and female vocal activity. No effects were significant.