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Characterising the flight song: repeatable individual variation of Ovenbird song features

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ABSTRACT

The songs of most passerines have been well described; however, songs from some species are more difficult to record and have yet to be characterised. The Ovenbird (*Seiurus aurocapilla*) flight song occurs rarely, is complex in its syllable composition, and its function is still not well understood. We examine the structure of the Ovenbird flight song using the largest sample of warbler flight songs to date ($n = 396$, 23 individuals) from autonomous recordings made in Sault Ste. Marie, Canada. We characterised the syllable repertoire of this song, examined song syntax, compared syllable sharing among males, and estimated repeatability of several song features. Syllable repertoires varied among males and they appeared to transition differently between syllables while singing, but we found no evidence for syllable sharing between neighbours. Male Ovenbirds were significantly repeatable in the syllable compositions of their flight songs, but repeatability estimates were lower for terminal compared to introductory segments. We find weak evidence of a negative relationship between song features at the within-individual level, suggesting that individuals also demonstrate considerable plasticity when singing. Understanding variation in the Ovenbird flight song will lead to a better understanding of the function(s) of this song type.

Introduction

The songs of birds have primarily been shown to function in mate attraction and territory defence, and therefore have important fitness implications. Songs can vary in many ways including, for example, the composition or structure of songs (Catchpole and Slater 2008). Variation in these song features is thought to provide information to receivers about the signaller (e.g. Vehrencamp et al. 2013). Within the song system of a given species, different types of songs or song delivery patterns may be used to communicate this information to either mates or rivals (Byers 1996a; Trillo and Vehrencamp 2005). The composition of song repertoires is highly variable both among and within species (reviewed in Krebs and Kroodsma 1980). A repertoire can consist of discrete song types where variation within a song type is less than variation among song types (Podos et al. 1992) or may consist of notes or syllables that can be

combined in different ways to produce songs (Catchpole 1976). The composition of an individual's repertoire may convey information about the quality or status of the signaller (reviewed in Krebs 1977; Krebs and Kroodsma 1980; Searcy 1992; Potvin et al. 2015).

Many songbirds are also known to share song type or syllable repertoires with their neighbours (e.g. Hill et al. 1999; Koetz et al. 2007). Song or syllable sharing often declines with distance (e.g. Wilson et al. 2000) because sharing is usually the result of song learning (Beecher and Brenowitz 2005) and, therefore, can result in the formation of dialects (Baker and Cunningham 1985). However, this is not always consistent across species as spatial patterns are not always related to song or syllable sharing (Whitney and Miller 1987) and it is possible for different song categories to show different patterns (e.g. Byers 1996b).

In addition to among-species and among-population variation in song features and repertoires, there has been a growing area of research that demonstrates differences in song features (e.g. song composition, length, frequency, etc.) among individuals existing in the same population, but few studies have shown how song features and structure may vary within individuals (but see Saldívar and Massoni 2017). Playback studies have revealed that individuals respond to fine-scale variation in song structure (e.g. Searcy et al. 2000), suggesting that within-individual song variation may be common. Individuals within the same environment may use song features to convey information differently from one another, but may also show plasticity in their expression of these features. Repeatable among-individual differences in song features have been demonstrated (Gil and Slater 2000; Pavlova et al. 2007; Murphy et al. 2008; Guillette and Sturdy 2011; Snijders et al. 2015; Zsebők et al. 2017; Naguib et al. 2019; Zipple et al. 2019). In other words, individuals seem to differ in how they use song features consistently over time and contexts which produces variation that selection may act on. If individuals are consistent in how they communicate information over time, and individuals communicate differently from one another, it is possible that bird songs convey reliable information about the signaller over time and contexts (e.g. male quality; Nowicki et al. 2000; Catchpole and Slater 2008).

Among wood warblers specifically, there is considerable variation in repertoire composition (Spector 1992). One group of warblers (of the *Helmitheros, Protonotaria, Limnothlypis, Seiurus, Oporornis, Geothlypis, Parkesia, Cardellina* genera) often has two categories of songs; a single primary song type used for both mate attraction and territory defence and a single extended song type of unclear function that may vary in composition. Within this group, the primary song is composed of a single repeated syllable while the extended song is more complex and includes call notes, primary song syllables, as well as additional syllables (reviewed in Spector 1992). Extended songs may be given in flight and may be structured to include an introductory portion composed of a number of notes or syllables, an intermediate segment including several primary song syllables, and a terminal segment composed of a number of notes and syllables. Like other members of this group, male Ovenbirds (*Seiurus aurocapilla*) sing a multi-purpose primary song as well as an extended song that is sung infrequently in either intense close interaction with conspecifics, in flight above the canopy, or while perched (Chapman 1907; Hann 1937; Lein 1981). In the literature, this song has been given a number of names including flight song, attenuated song, and extended song; we will use flight song to be consistent with other work on this vocalisation, despite the fact that these vocalisations may most often be produced while perched (Lein 1981; JRF pers obs).

Variation in the structure of the flight song among and within individuals has not been extensively described. A descriptive study by Lein (1981) reported differences among and within a few individual Ovenbird flight songs, but the degree and nature of this variation, however, was not quantified. Thus, the Ovenbird flight song has not yet been fully characterised. It is also still unknown whether male Ovenbirds share syllables of their flight songs with neighbours, transition between syllables similarly during song, or are repeatable in specific features of this song type. Flight songs are generally sung in a single instance and at low light levels (Lein 1981), making their occurrence difficult to predict and study. The recent development of cheap, small, and easy to deploy autonomous recording units has created the possibility of recording individuals over long timescales, making the study of rare vocalisations like the flight songs of warblers possible (Blumstein et al. 2011).

In this study, we characterised the syllable repertoire of individual Ovenbird flight songs from automated recordings to more closely examine syllable sharing and song structure between individuals, consistent individual differences of flight song features, and potential covariation between song features. More specifically, we aimed to (1) characterise the flight song syllable repertoire of Ovenbirds, (2) visually and descriptively compare how individuals transition between different song syllables during the production of their songs, (3) determine whether males share flight song syllables and whether there is a relationship between syllable sharing and geographic distance, (4) quantify whether Ovenbirds are repeatable in their flight song features, and (5) examine whether flight song versatility (i.e. an index for syllable diversity within a song; Gil and Slater 2000) and song length significantly covary at the among- and within-individual levels.

We more specifically predicted that the syllable repertoire of males would be larger than the number of syllable types within a song so that flight songs could be variable in composition, length, and song versatility both among and within males. As we expected that males would differ in their syllable repertoires, we also expected males to differ in how they transitioned between syllables during song production. We predicted that syllable sharing in flight songs would be related to geographic distance, as song sharing has been demonstrated in other warbler species (e.g. Byers 1996b). Individuals were expected to be significantly repeatable in flight song features but, as negative relationships between song features have been previously reported (Ballentine 2004; Podos et al. 2004), we expected that flight song versatility and length would negatively covary at the level of the individual if there are limits to augmenting both of these song features in synchrony. Males in a population may specialise by maximising one song feature over the other (negative covariance among-individuals) where, for example, some males have high song versatility but shorter songs, and vice versa. It is also possible that males plastically alter which song feature to express (negative covariance within-individuals) where a male may sing different types of songs that focus on increasing one song feature or the other based on intrinsic or extrinsic factors. Relationships between traits may be similar or different at the among- and within-individual levels (van de Pol and Wright 2009; Careau and Wilson 2017) and therefore, differentiating and quantifying how individual song features vary at multiple levels is necessary to develop a more comprehensive understanding of the variation that exists in song behaviour. As of yet, relationships between song features have not been explored using a multilevel approach, and we therefore did not make predictions about whether a negative covariation would occur among or within individuals.

Methods

Field recordings

We deployed twenty-nine Song Meter automated recorders (model: SM2; Wildlife Acoustics, Maynard, MA, USA) in Hiawatha Highlands Conservation Area and Kinsmen Park, in Sault Ste Marie, Ontario, Canada (46° 35′ 25″ N, 84° 16′ 13″ W; Figure S1A) between May 16 and 21 July 2013. Each Song Meter was equipped with two omnidirectional SMX-II microphones placed on the left and right sides of the recorder. Recorders were set to record for 59 min and pause for 1 min (to write files to the memory card) from 2 h before nautical twilight until 2 h after sunrise. Recordings were made at 22,050 Hz, 16bit and stored as WAV files.

Song extraction

We scanned all recordings in Syrinx PC (John Burt, Seattle WA) from the start of each recording up until the start of the Ovenbird dawn chorus. This period is when Ovenbird flight songs are sung most frequently and also are less likely to be overlapped by other singing species (Perrault et al. 2014; Pearse 2018). All Ovenbird flight songs that were clearly visible (all notes were visible in the spectrogram) were clipped from the recording. Next, we sorted the songs into twelve collection sites (groups of recorders that were within close proximity and would detect the same individuals). We then identified the songs clipped from these recorder sites to individuals using visibly distinct variation in the primary syllables within the flight songs (N = 23 individuals; Lein 1980; Ehnes and Foote 2015). To confirm that our method of assigning songs to the same individual was consistent with automated methods, we calculated spectrogram cross-correlations among primary syllables from 5 clearly recorded flight songs (good signal:noise ratio) of 10 randomly selected males in the dataset. Because the number of primary syllables varies among songs (Figure 1), we extracted two primary syllables from these 50 songs. We calculated spectrogram cross correlations in Raven Pro with the following settings: normalised spectrograms, band-pass filter (1000–10,000 Hz), Hamming window, 512 fast fourier transform (FFT), and 87.5% overlap (Ehnes and Foote 2015). We compared among male to within male cross-correlation scores using an unpaired t-test. Primary syllables had mean within-individual spectrogram cross scores (41.9 ± 1.7%) that were significantly higher than values for among individuals (20.9 ± 1.3%; unpaired t-test: t = 13.3, df = 52, $P < 0.0001$). We show examples of eight songs from a single individual (Figure 1(a)) and eight songs from different individuals (Figure 1(b)), illustrating the visual differences between primary notes.

Song analysis

From among the Ovenbirds for which we had flight song recordings, we included all individuals with at least 10 clearly recorded flight songs for intra- and inter-individual variation in song analysis. In total, the songs of 23 males recorded with 29 recorders (Figure S1A) were used in this study for a sample size of 396 songs (17 ± 2.0 songs/male; range: 10–45). We analysed the note structure of the flight songs using Raven Pro
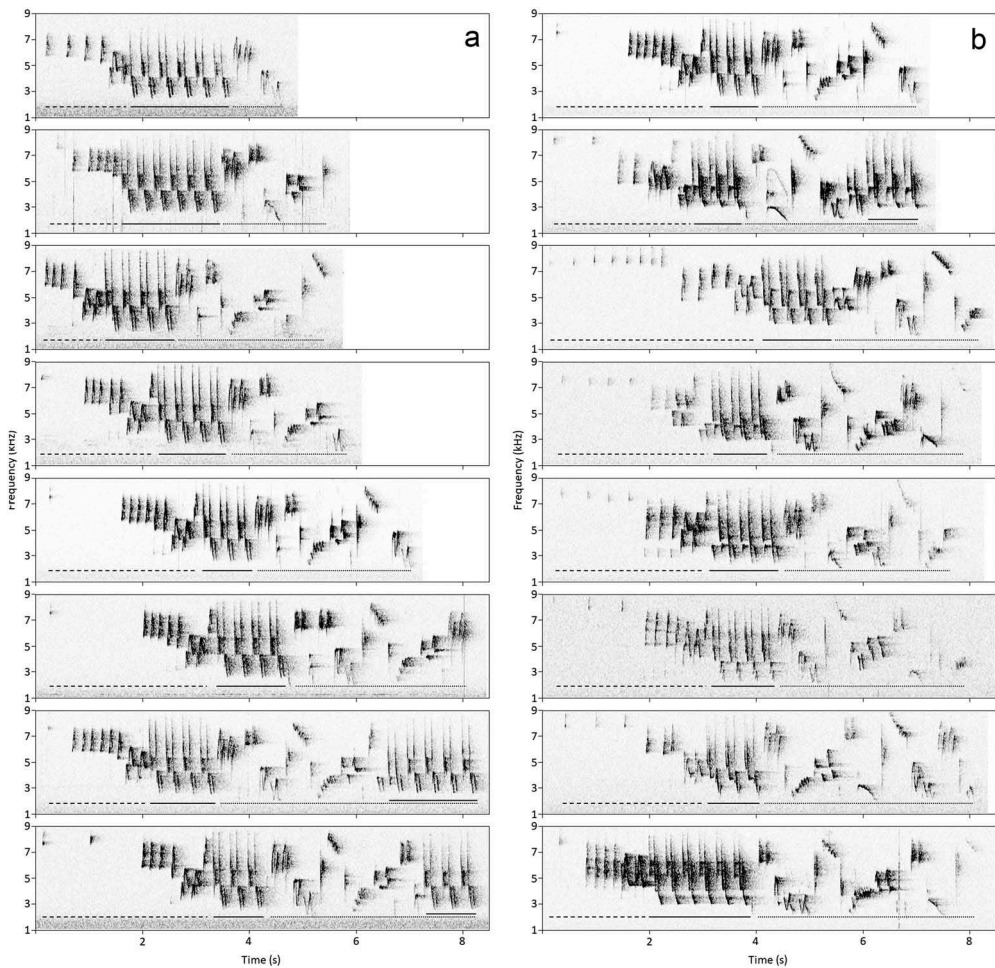
Figure 1. Spectrograms of eight flight songs sung by (a) a single male and (b) by different males. Note that for the third song in (b) extra soft-tsips (syllable A) were trimmed from songs for figure scaling. Introductory segments are indicated with a dashed line, primary syllables (Syllable S in Figures 2–3) are indicated with a solid line, and terminal segments are indicated with a dotted line. Songs with primary syllables in the terminal segment are additionally indicated with a solid line above the dotted line.

(Cornell Lab of Ornithology, Bioacoustics Research Program, Ithaca NY). We defined syllables as units of songs with the same duration, shape, and bandwidth (following Catchpole and Slater 2008; Dos Santos et al. 2016; Saldívar and Massoni 2017). We identified and labelled each syllable from each song using the time and frequency cursors in Raven, and assigned each syllable type a letter code (A-Z then AA-AN; Figure S2). This generated a syllable sequence for each song in Raven's table feature. After a new syllable was discovered and assigned a letter, we searched through all 396 songs for that particular syllable and assigned it the same letter as it was first identified with. Each syllable of the 396 songs were characterised in the same way to form a total syllable repertoire among

the male Ovenbirds. All syllable identifications were performed by one observer (NP) and blindly confirmed with 96% concordance by JRF (Saldívar and Massoni 2017).

Full syllable repertoires appeared to be captured by the tenth song (Figure S3A). To confirm that syllable repertoires were well captured, we examined the relationship between note repertoire size and number of songs sampled and found no significant relationship (linear model: estimate ± SE = 0.032 ± 0.057, t = 0.54, P = 0.60; Figure S3B). We also annotated the start to the end of each flight song to measure song length.

Statistical analysis

Flight song syllable transitions

We next examined song syllable sequences by looking at the order in which different syllable types were sung in each song. We restricted this analysis to songs with a single primary sequence because we were interested in whether there was a relationship between syllables within the introductory and terminal portions of the song and the second primary sequence is typically part of the terminal segment of flight songs (Lein 1981; Ritchison 1991). We generated transition matrices which calculated the number of transitions from each syllable to the next, which were used to calculate transition probabilities (e.g. B syllable proceeded A syllable 54% of the time). We generated two types of transition matrices to describe the Ovenbird flight song. Our first flight song matrix was generated using natural transitions of flight song syllables which included instances where the same song syllables were repeated consecutively. As certain syllables were found to be repeated at a high probability in the Ovenbird flight song (e.g. probability of repeating syllable A = 0.59), transitions between the same syllables constrained our ability of evaluating transitions between different syllable types. Our other type of flight song matrix was therefore modified so that all of the diagonal transitions of the matrix (i.e. instances where syllables were repeated) were set to zero so that transitions between different syllables could be examined more closely. Using the natural and modified transition matrix approaches, we examined song syllable transitions at the (1) population level which included recorded songs from all individuals, and (2) individual level where only songs from each individual were included. The population-level transition matrices controlled for the number of songs included per individual by dividing each individual's syllable transitions (elements in each individual matrix) by the number of songs they sang (mean = 11, range = 1–34). We then took the average of the syllable transitions (elements) across all individual matrices to generate the population matrix and converted the syllable transitions into probabilities. Network analysis was used to visualise syllables into communities so we could examine which syllables were more closely clustered in our syllable network. Community detection is a way of grouping together nodes (e.g. individuals, syllables, etc.) based on their interconnectedness and strength of connections in a network to more closely examine structure. Here we apply this approach to examine the structure of syllable transitions and clustering of syllable types within the Ovenbird flight song. Following previous studies (Deslandes et al. 2014; Hedley 2016; Samotskaya et al. 2016; Saldívar and Massoni 2017; Potvin et al. 2019), transition matrices were generated using the markovchain package (Spedicato 2017) and syllable networks were visualised using the igraph package (Csardi and Nepusz 2006). We

constructed community networks using the spin glass community detection algorithm (Reichardt and Bornholdt 2006) by including natural syllable transitions that occurred at a probability >0.1.

Syllable sharing

We calculated the distances between all recorder locations in BaseCamp (Garmin, Schaffhausen, Switzerland). We calculated syllable sharing between each pair of males by using the equation 2Ns/(R1+ R2) to determine whether neighbouring males shared more syllable types than distant males, where *Ns* is the number of shared syllable types among two males and *R1* and *R2* are the repertoire sizes of each male, respectively (Mcgregor and Krebs 1982). We then used a Mantel test (10,000 permutations) to compare the number of shared syllables between each male and the distance between recorders using the vegan package (Oksanen et al. 2019). We repeated the Mantel test again once removing 10 syllables that were sung by all 23 males and once removing 4 syllables sung by 22 of 23 males. We included this second analysis to remove the possibility that songs shared by 96–100% of males might mask patterns of sharing of rarer syllables.

Individual variation in flight song features

To examine more closely how individuals consistently differed among each other in their song composition, we calculated unadjusted repeatability estimates for the total number of syllables and the number of unique syllables in both the introductory (before intermediate primary syllables) and terminal segments (after intermediate primary syllables) of individual flight songs. We also generated a repeatability estimate for the number of primary syllables individuals sang within their flight songs (intermediate portion). We estimated individual repeatability using mixed-effects models (intraclass correlation repeatability; Nakagawa and Schielzeth 2010) which allowed estimation of variation at the among-individual and within-individual residual levels so that repeatability estimates represent the proportion of phenotypic variation among individuals by the variation within individuals. Repeatability was estimated under a gaussian error structure, as opposed to a poisson, because the distribution of the variables of interest followed linear distributions rather than skewed counts. Repeatability estimates are unadjusted as we accounted for only male identity as a random intercept effect. Repeatability was calculated with 1000 parametric bootstraps in the rptR package (Stoffel et al. 2017).

We calculated song versatility and song length repeatabilities with a bivariate mixed model in the MCMCglmm package (Hadfield 2010). A bivariate mixed model includes two response variables (multivariate) that can have unique model structures, which allows examination of the covariance (i.e. relationship) between response variables at multiple levels (e.g. among and within individuals) while also simultaneously examining how the response variables may be independently affected by different fixed and random effects (Dingemanse and Dochtermann 2013). We chose to calculate these repeatability estimates within a multivariate model as we were also interested in the relationship between song length and song versatility metrics at the among- and within-individual levels and, by partitioning variance of both traits within the multivariate framework, we avoid the possible misinterpretation of this relationship and allow comparison at multiple levels (as advised in Careau and Wilson 2017; Houslay and Wilson 2017; Berberi and Careau 2019). As of yet, multivariate mixed modelling software is not freely

available under a Frequentist framework and we therefore use a Bayesian approach for this particular analysis. We fit a simple bivariate model where both response variables were modelled under a linear error structure with an uninformative gamma prior and Male ID as a random intercept effect. We calculated a song versatility index (SVI) for each song to represent a song's syllable diversity, which is a measure that may be informative for species with variable songs composed from a syllable repertoire (Trainer and Plltz 1996; Gil and Slater 2000; Dos Santos et al. 2016). We also measured the length of all songs. Our response variables were song length and the number of syllable types in each song. SVI for each song is generally calculated prior to analysis by dividing the number of syllable types by the total number of syllables per song (Dos Santos et al. 2016). However, as the number of syllables per song and song length were highly correlated (r = 0.79, df = 394, $P < 0.001$), a comparison between a SVI ratio and song length violates the assumption of independence. We therefore included the number of syllables per song as a fixed effect in our model which was regressed onto number of syllable types but not song length. This approach generated residuals (BLUPs) that represented an SVI measure without causing non-independence between our response variables. We found a high correlation between an individual's SVI BLUPs generated from the model and when calculating each individual's mean SVI index using the ratio approach (r = 0.934, df = 21, $P < 0.001$), which confirmed that generating an SVI index within the model was appropriate. The model was run for 420,000 iterations with a burn-in of 20,000 and a thinning interval of 100 which produced unbiased traces of each estimate. All statistical tests were done in R v.3.5.3 (R Core Team 2019). All results were considered significant at an alpha level of 0.05 and repeatability estimates were considered significant by likelihood ratio tests or if their 95% confidence intervals excluded zero.

Results

Characterisation of the flight song

We identified a total of 40 syllable types in the flight songs of 23 male Ovenbirds. Some notes were found in all males' repertoires while others were unique and only found in one or two male's repertoires (Figure S2). Individual syllable repertoires averaged 23.7 ± 0.13 syllables (range: 19–28). We found that individual flight songs (n = 396) had on average 28.3 ± 0.26 syllables (range: 12–46) and were 7.7 ± 0.08 s long (range: 3.8–18.8 s); however, the average number of syllable types sung in one flight song was 16.0 ± 0.13 (range: 2–24).

Sixty-five per cent of flight songs had a single primary sequence that divided the song into introductory and terminal segments. However, the remaining 35% of songs had more than one primary sequence with the second sequence found either within the terminal segment (58%) or at the end of the terminal (42%) segment (Figure 1). One song had two additional primary sequences and one song had no primary sequences. For songs with a single primary sequence (n = 255), the introductory segments had 9.9 ± 0.17 (range: 3–20) syllables composed of on average 5.5 ± 0.10 unique syllables (range: 2–11), while terminal segments had 13.3 ± 0.25 (range: 4–25) syllables of 9.7 ± 0.16 unique syllables (range: 2–16). Males included on average 3.8 ± 0.06 primary syllables (range: 2–6) between the introductory and terminal segments.

Flight song syllable transitions

From the analysis of 396 flight songs, we discovered that Ovenbirds vary the order in which they use syllables within their flight songs. Some songs, for example, have a rather long introduction portion of short, high-frequency notes while other songs contain more primary syllables throughout the flight songs, or had a longer and more variable terminal segment (Figure 1). Some syllables were exclusively found in either the introductory ($n = 5$) or terminal segments ($n = 5$) while others were more likely (greater than a 3:1 ratio) to be found in the introductory ($n = 8$) or terminal segments ($n = 10$) of the song (Figure S2).

The natural flight song syllable transition network showed that many song syllables were repeated consecutively throughout the flight song (Figure 2) and, when modifying the matrix to remove consecutively repeating syllable transitions, we unsurprisingly see more transitions occurring at a higher probability between different syllables (Figure S4). In both natural and modified flight song matrices at the population-level, many song syllable transitions occurred with transition probabilities >0.1 (Figure 2(a) & S4A) with fewer transitions occurring with a probability >0.25 (Figure 2(b) & S4B). Population- and individual-level song transition networks were found to visually differ demonstrating that individuals vary among each other in how they transition between song syllables (Figure 2 (c) & S4C). Syllables were grouped into five distinct communities where syllables appeared to be grouped depending on whether they were sang before or after the intermediate primary syllables (introductory or terminal segments) of the flight song (Figure 3).
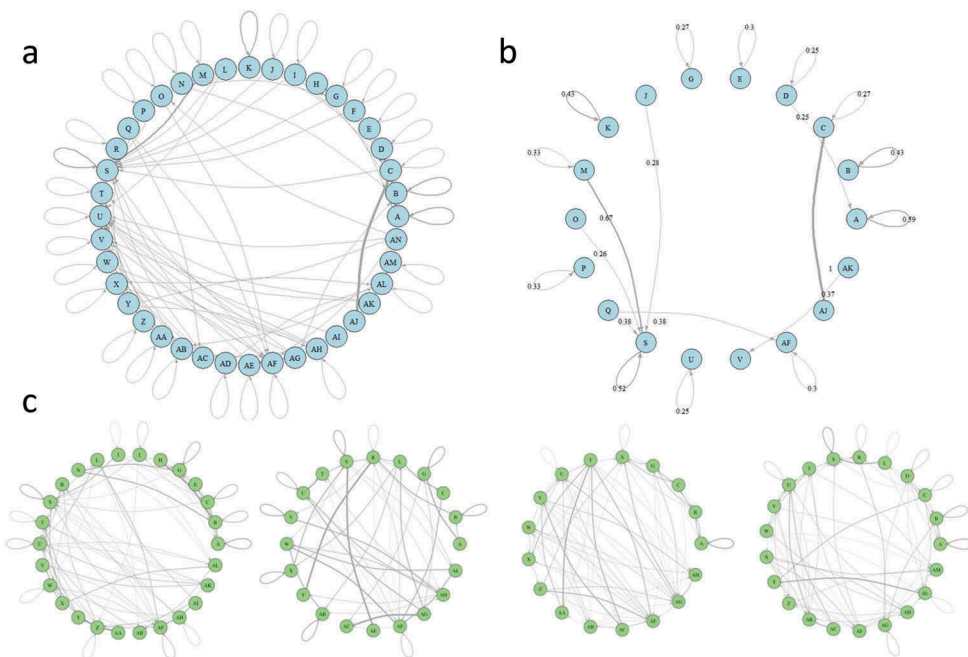

Figure 2. Ovenbird flight song syllable transition sequences for (a) all individuals sampled in the population where transition edges >0.1 probability are shown, (b) all individuals sampled in the population where transition edges >0.25 probability are shown and labelled, and (c) four selected individuals where transitions >0.1 probability are shown for comparison with the population sequence in (a). Node letter codes (A-AN) represent unique song syllables described in Figure S2 and line thickness represents the probability of transitioning (thicker lines = higher probability).
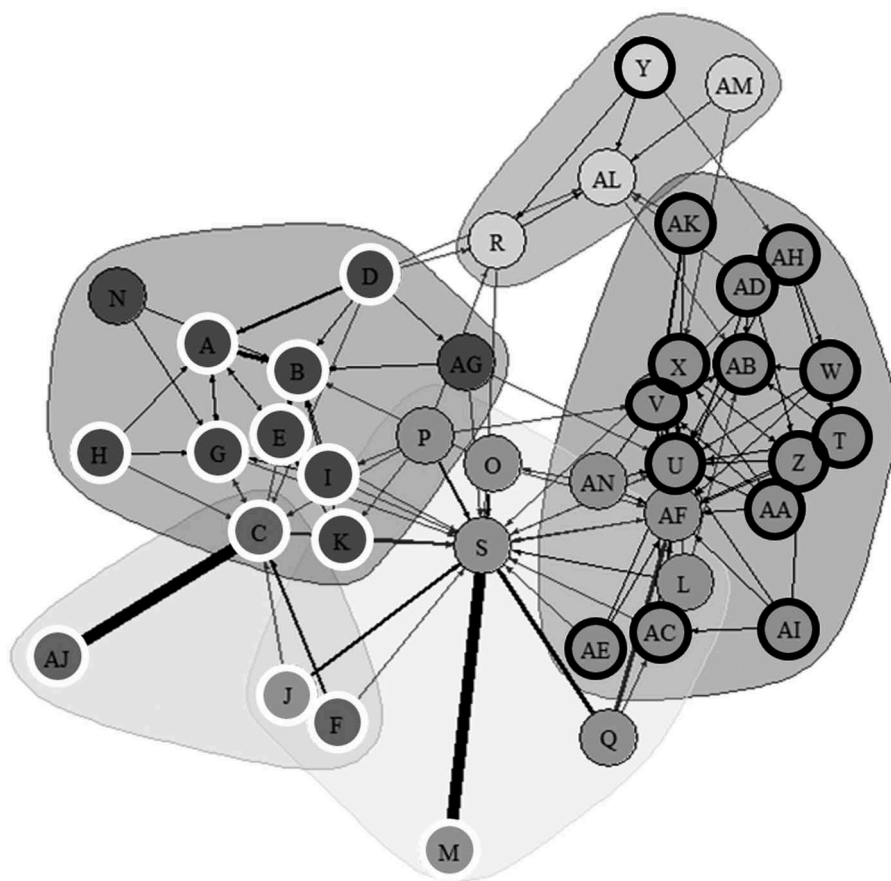
Figure 3. Community network of flight song syllables (nodes; see Figure S2) coloured by their temporal positions within flight songs. White = occurred more often (>3:1 ratio) in the introductory segment (before primary syllables – "S") and black = occurred more often (>3:1 ratio) in the terminal segment. Weighted edges that connect syllable nodes are shown where thicker edges represent larger transition probabilities.

Syllable sharing

There was no relationship between syllable sharing and distance between males (Mantel test: $r = 0.069$, $p = 0.21$, 10,000 permutations). When we calculated syllable sharing and excluded syllables shared by at least 22 of 23 males, there was also no relationship between syllable sharing and distance between males (Mantel test: $r = 0.0049$, $p = 0.49$, 10,000 permutations). Rare syllables were not confined to neighbourhoods but were often dispersed throughout the study area (Figure S1B-D).

Individual variation in flight song features

The mean number of syllables per male varied for introductory (range: 6–14.3), primary (intermediate; range: 2.9–5.5), and terminal (range: 8–17.3) segments of the song. The number of syllable types also varied among males in introductory (range: 3–9.7) and

terminal (range: 6–11.8) segments. Individual males were significantly repeatable in the total number of syllables used and the number of syllable types used within the introductory and terminal segments of their flight songs (Table 1(a–d)). They were also significantly repeatable in the number of primary syllables they used within their flight songs (Table 1(e)). Individuals had lower repeatability estimates for the number of syllables and the number of unique syllables in the terminal segment of their flight songs compared to the introductory segment, and this was likely an artefact of the residual within-individual variance being larger in terminal segments (V_e; Table 1).

There was also significant among- and within-male variation in both song length and versatility, which were both significantly repeatable (length: $R = 0.39$ [0.25–0.57]; versatility: $R = 0.32$ [0.18–0.49]; Table 2). Song length and versatility negatively correlated at the among-individual level but this was found to be non-significant as the confidence interval was wide and crossed zero ($r_{ind} = -0.38$ [−0.70–0.11]; Table 2; Figure 4). At the within-individual level, the correlation between song length and versatility was also negative ($r_e = -0.16$ [−0.31 − −0.006]; Table 2), but this estimate was considered weakly significant as the confidence interval was close to zero but did not overlap it. We therefore find weak evidence for a negative relationship between song length and versatility within individuals where individuals either sing longer or more versatile songs, but do not find evidence for a similar relationship at the among-individual level.

Discussion

We characterised the flight song and syllable repertoire of Ovenbirds. We found that individual Ovenbirds differed from one another in which syllables their flight songs contained and also in how they transitioned between syllables while signing. Contrary to our predictions, we found no relationship between the syllable repertoires and spatial distribution of individuals which does not support a clear pattern of syllable sharing by neighbours in our population; however, there were many syllables that were shared among individuals within our site. Ovenbirds were moderately repeatable in their flight song features suggesting that individuals differ consistently in how they express these song features over time and contexts. We examined the relationship between flight song versatility and length at both the among- and within-individual levels. Although song

Table 1. Variance components for the calculation of repeatability ($n = 23$ individuals) for (a) the number of syllables used within the introduction portion, (b) the number of syllables used within the terminal portion, (c) the number of unique syllables used within the introduction portion, (d) the number of unique syllables used within the terminal portion, and (e) the number of primary syllables used throughout the entire duration of flight songs. Variance (V) of traits at the among- ($_{ind}$) and within-individual residual ($_e$) levels were used to calculate repeatability (R) for each trait and its significance via likelihood ratio tests (P). Repeatability estimates are unadjusted as all models included only male ID as random intercepts under a gaussian error structure.

Source	(a). Intro syllables	(b). Terminal syllables	(c). Unique intro syllables	(d). Unique terminal syllables	(e). Primary syllables
V_{ind}	3.56	4.10	1.88	1.34	0.48
V_e	5.01	12.03	1.31	5.08	0.56
R [CI]	0.42 [0.23–0.56]	0.25 [0.10–0.39]	0.59 [0.39–0.72]	0.21 [0.067–0.35]	0.46 [0.25–0.61]
P	<0.001	<0.001	<0.001	<0.001	<0.001

Table 2. Variance components for the calculation of repeatability and correlation estimates ($n= 23$ individuals) for (A) song length and (B) song versatility (SVI = number of syllables regressed onto number of unique syllables) generated in a bivariate mixed-effects model. Variance (V) of both traits and the covariance (COV) between traits were used to calculate repeatability (R) for each trait and the correlation between traits at the among- ($_{ind}$) and within-individual ($_e$) levels.

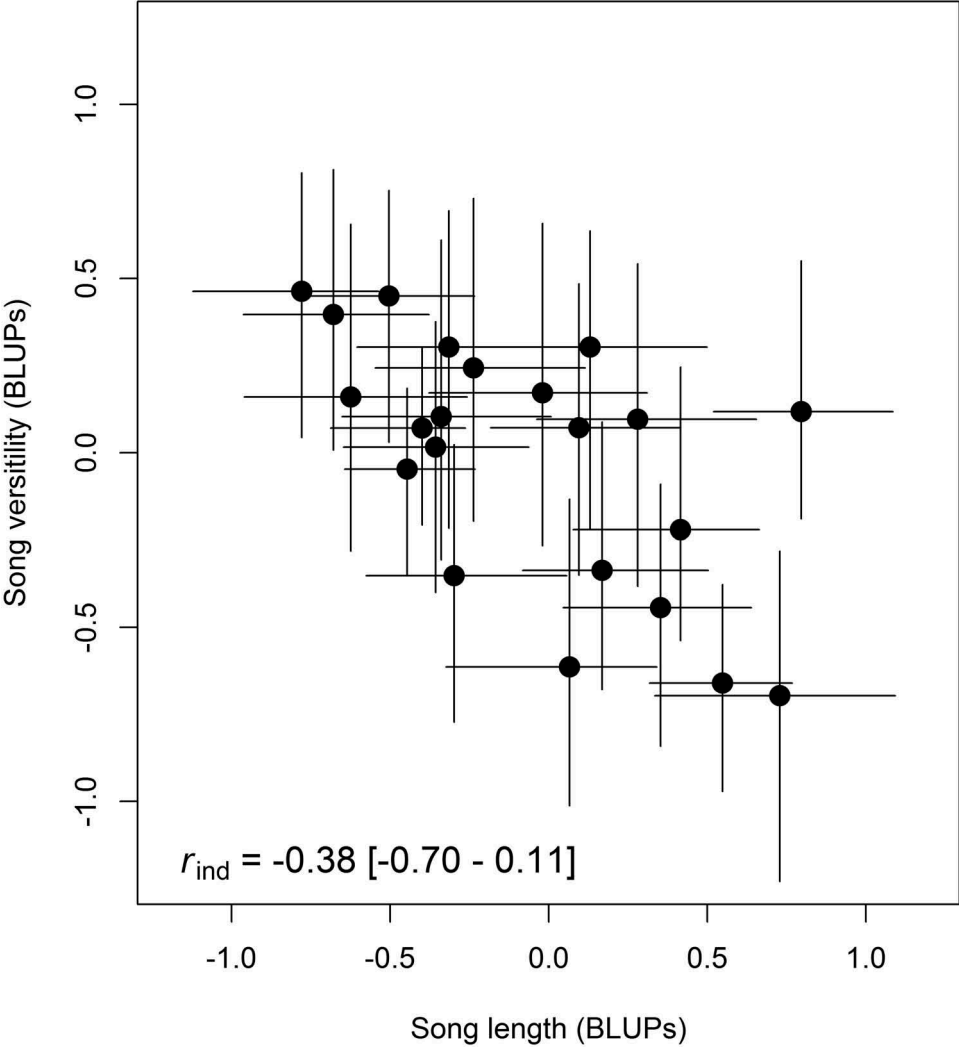| Source	A. Song length		B. Song versatility (SVI)	
	Estimate	95% CI	Estimate	95% CI
V_{ind}	0.47	0.19 – 0.81	0.41	0.16 – 0.74
V_e	0.65	0.56 – 0.74	0.72	0.61 – 0.82
COV_{ind}	−0.24	−0.50 – −0.033		
COV_e	−0.21	−0.29 – −0.14		
R	0.39	0.25 – 0.57	0.32	0.18 – 0.49
r_{ind}	−0.38	−0.70 – 0.11		
r_e	−0.16	−0.31 – −0.006		

$$r_{ind} = -0.38 \; [-0.70 - 0.11]$$

Figure 4. Among-individual ($n = 23$) covariation between model-estimated BLUPs for song versatility and song length. Confidence intervals around each individual's estimated residuals are shown.

versatility and length were negatively related at both levels, we find that this relationship was non-significant among individuals and only weakly significant within individuals. Overall, we find that individuals differ from one another in how they sing their flight songs, through their syllable repertoires and in their expression of song features, but also provide evidence that individuals plastically adjust how they sing this song type.

Characterisation of the flight song

Individual males varied their flight songs by using different syllable types from their repertoire and by varying the number of repeats of syllables. Ovenbirds typically used 16 syllable types per song though repertoires averaged 24 syllable types, and as such songs were typically not sung with maximum versatility. Some syllables were commonly repeated consecutively while others were rarely repeated, and some terminal segments included additional primary sequences either within or at the end of the sequence. The only other species for which the flight song has been well characterised is the Common Yellowthroat (*Geothlypis trichas*), which also included additional primary song sequences in their flight songs (Ritchison 1991). Compared to the Common Yellowthroat, the Ovenbird has more syllables and more syllable types within their flight songs. The order of syllables was not reported to vary in Common Yellowthroats but did vary in both introductory and terminal sequences of Ovenbird flight songs (see next section).

Flight song syllable transitions

One of this study's objectives was to descriptively explore how Ovenbirds use different syllables within their flight songs. To do this, we generated song syllable transition matrices for natural and modified songs at both the population (average of all individuals) and individual levels. We found that transitions occurred both between the same syllable (consecutively repeated) and between different syllables, but show that there were only some transitions that occurred with a probability >0.25. Ovenbirds show moderate probabilities of repeating syllables consecutively within their songs unlike the Saffron Finch (*Sicalis flaveola pelzelni*) that rarely repeats syllables within their songs (Saldívar and Massoni 2017). When modifying the transition matrices to exclude instances when the same syllable was repeated consecutively, there were more transitions >0.25 as expected. Additionally, there were particular syllables that were more often or exclusively found in introductory or terminal song segments. This suggests that Ovenbirds use some syntactical rules when composing flight songs but still demonstrate considerable plasticity.

To examine this further we generated syllable communities that were found to broadly represent how syllables grouped into temporal segments of flight songs. Syllables were grouped into five communities: a larger and smaller community for both the introductory and terminal portions of the song, and an intermediate community containing the 'S' or primary syllable. The smaller communities likely include syllables that were sung less frequently during introductory (e.g. syllables AJ, C, F) and terminal (e.g. syllables AL, Y, AM) segments, whereas the larger communities contain syllables that were sung more regularly together in these temporal segments. The S or primary syllable was well connected in the syllable community network as it was frequently used, occurred in the middle of all flight songs, and was identified to be highly connected to syllables both within its

community and other communities. The placement of the S primary syllables within the intermediate or middle community of the song network confirms the observation that these intermediate syllables separate introductory and terminal segments of flight songs (Lein 1981; Ritchison 1991; Spector 1992; this study). Previous studies examining song syllables or phrases also identified that bird songs contained community structures where certain syllables were grouped (Hedley 2016; Potvin et al. 2019). We additionally show that our syllable communities seemed to be broadly related to the temporal structure of songs.

Although we found general syntactical patterns at the population-level where syllables generally grouped in introductory, intermediate, or terminal positions of flight songs, we also found that individual-level syllable transition networks were visually different from each other. This demonstrates that individual Ovenbirds showed variation in which syllable types they used and which syllables they transitioned between more commonly, while still likely following general syntactical patterns where certain syllables were sung in certain temporal segments of their songs. In the future, song syllable structures at the individual-level can be examined further by generating network estimates for each node (e.g. individual or syllable level) which can be used in subsequent analyses. This exciting avenue of research is expected to allow a closer examination into how individual differences in song structure may affect other aspects of an individual's ecology including their sociality, behaviours, and fitness (Potvin et al. 2019).

Syllable sharing

We found no relationship between syllable sharing and distance between individuals. There was a high degree of syllable sharing among individuals, including syllables shared by all birds; however, rare syllable types did not cluster. Patterns of syllable or song sharing among individuals often relate to distance in species that learn songs (e.g. Wilson et al. 2000; Koetz et al. 2007) when individuals settle near song tutors (e.g. Beecher et al. 1994). It may be that sharing of flight song notes with neighbours is not advantageous in Ovenbirds such that we do not see a pattern of sharing with distance within our study site. Similarly, other studies of song learning birds have not found a pattern of song or syllable sharing with distance (e.g. Whitney and Miller 1987) while in some species, the pattern is not consistent across populations (e.g. Hughes et al. 1998; Hill et al. 1999; Wilson et al. 2000; Foote and Barber 2007) or across song types (Byers 1996b). In other cases, there is no clear pattern of sharing with distance within a population but there is a relationship between sharing and distance among populations (Marova et al. 2010).

When comparing the flight songs we recorded to those that Lein (1981) recorded over four decades ago in Massachusetts and New Hampshire, there are different note types present in that population that we do not observe. Lein (1981, Figures 3–4) reports that flight songs may contain non-song vocalisations such as the 'whink' and 'pe-bleep' notes or vocalisations (Lein 1980). We did not find any syllables that are clearly similar in songs from our population. However, we did find that many songs began with a number of 'soft sip' notes and often included notes that may be the 'chep' and 'whip' vocalisations (Lein 1980). It is possible that inclusion of non-song vocalisation types may vary among populations or that these vocalisations may themselves be considerably variable among populations. We do not have recordings of any independently sung non-song vocalisations from our population for comparison. With respect to other syllables within the

songs of Ovenbirds, it is challenging to compare with just several spectrograms, however, the up sweeping syllable W common in our population also appears in Lein (1981, Figures 3 and 4). Most other notes and syllables have no clear match between the two locations suggesting that dialects may exist. With the increased use of automated recorders across North America that may capture flight songs across populations, a macrogeographic comparison of flight song characteristics may be possible and perhaps a pattern similar to that found by Marova et al. (2010) for Blyth's Reed Warbler (*Acrocephalus dumetorum*) may exist also for Ovenbird flight songs.

Individual variation in flight song features

Male Ovenbirds showed significant repeatability in the syllable composition of their flight songs. We find significant differences between males in the number of syllables, number of syllables types, and number of primary syllables a male sang within their flight songs. Previous work on Common Yellowthroats also found that males varied in the number of syllables found in the three temporal segments of flight songs (Ritchison 1991). Additionally, the flight song of Ovenbirds appear to be more variable within individuals than the Common Yellowthroat's flight song (Ritchison 1991), which is described as including minor variation. Lein (1981) also observed variation within and among individuals, however, this variation was not quantified.

Repeatability estimates were lower when considering syllable composition within the terminal segments compared to the introductory segments of flight songs. The residual within-individual variance was high compared to the among-individual variance for the terminal segment measures, which resulted in lower repeatability estimates for terminal segments in comparison to the introductory segments. This likely reflects that individuals are less consistent in how many and which syllables they sing during the final portion of their flight songs compared to the beginning of their songs. Terminal variation is likely even greater than estimated here given that these analyses were restricted to songs with one clear primary sequence, and not all songs included just one primary segment (see above). Syllable transition patterns were less uncertain in the introductory segment of Willow Warbler songs (*Phylloscopus trochilus*, Gil and Slater 2000), which may indicate that individuals of this species are more consistent and vary less among one another in how they sing at the beginning of their songs. Sparrows may also be less repeatable in the terminal composition of their songs as there is evidence that some species vary the terminal trill notes at the end of their songs depending on context (*Melospiza melodia*, Borror 1965; *Zonotrichia leucophrys pugetensis*, Nelson and Poesel 2011). To our knowledge, we provide the first estimates showing that individuals may differ in their repeatability during different temporal segments of a song. Introductory portions of flight songs may convey more consistent information about the signaller (higher repeatability) while the terminal segments may be used more flexibly depending on context or motivation (lower repeatability). Further examining the consistency in which individuals may sing temporal portions of their songs may improve understanding on both the function and the information contained within these songs. This is highly speculative and more work is required to validate our assumptions. Nonetheless, we encourage others to examine how individual repeatability may compare across song segments.

We found a negative association between song versatility and song length at both the within- and among-individual levels. However, we find that the within-individual association was only weakly significant while the among-individual association was non-significant. These findings suggest individuals tended to behave plastically and altered whether they sang longer or more versatile songs between contexts but did not seem to specialise significantly in the types of songs they sang. The weakly significant within-individual correlation may have resulted from either correlated plasticity at the population level if an unaccounted for factor affects both traits (e.g. morphology, condition) or at the individual level if individuals are similar in how they perform in different contexts (due to an environmental variable; Careau and Wilson 2017). By partitioning covariance to the within-individual level, we conclude that plasticity (either correlated at the population or individual level) likely plays a part in this association. Further work will be needed to determine what drives plasticity within individuals. Tradeoffs between vocal features have been shown previously in bird song and are suspected to be a result of selection being opposed by the motor constraints of producing difficult song features in synchrony (reviewed in Podos et al. 2004; but see Kroodsma 2017). As of yet, previous work has not examined these song feature associations at multiple levels and our work therefore brings a new perspective showing that correlated performance tradeoffs may occur within individuals as a result of plasticity for some song features.

Furthermore, despite individuals plastically adjusting whether they sang more versatile or longer songs, we importantly found that individuals were significantly repeatable in both these song features. Individuals were consistently different from each other in the versatility and length of their flight songs over time and contexts, but still plastically adjusted which feature to maximise within each of their songs. There has been a recent emphasis on the need to more closely examine the complex relationship between consistent individual differences and individual plasticity (Dingemanse et al. 2010). It is a possibility that we lacked power to detect a significant among-individual correlation and our weak within-individual tradeoff was partially an artefact of correlated measurement error (Dingemanse and Dochtermann 2013). We provide an initial framework for partitioning variation in song features at the individual level, but future work should aim to sample the song behaviours of many individuals (>125; Dingemanse and Dochtermann 2013), potentially through collaborative efforts, to validate our findings. Our results highlight the importance of examining song features of individuals at multiple levels, which may further understanding of how associations between different song features, and thus different song structures, may arise.

Conclusions

Our study demonstrates that there is still much to learn about the extended flight songs of warblers and that these songs are considerably more variable than previously thought. The flight song of Ovenbirds shows considerable plasticity and information content compared to the primary song, which has a limited capacity to vary. The function of the Ovenbird flight song and its impact on reproduction is still unknown (Foote et al. 2017, 2018) but, as we find that individuals express repeatable differences in both this song's syllable composition, versatility, and length, we provide evidence that this song likely provides consistent information about the signaller. As we also find that individuals may show correlated plasticity in

how they express certain features within their songs, we provide weak evidence that these songs may not indicate signaller quality as transparently as assumed. The close examination of song characteristics and features is still in its early stages and by exploring variation among and within individuals, knowledge concerning the function and information that these songs convey may be improved. There is a growing number of studies that utilise analytical techniques that make this possible (e.g. markovian/hierarchical models, bivariate multilevel models, network analysis), which will further allow estimation of how variation in song features and characteristics may associate with other aspects of ecology and fitness.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

The data that support the findings of this study are openly available in figshare at DOI:10.6084/m9.figshare.11591544.v1.

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