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Individual differences in the vocalizations of the buff-throated woodcreeper (*Xiphorhynchus guttatus*), a suboscine bird of neotropical forests

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Abstract

Unlike in temperate forests, bird communities in neo-tropical forests are largely composed of species of Tyranni, or suboscines, a suborder of passeriform birds that do not learn their songs. Thus, songs of suboscines are typically acoustically simple compared to the complex songs of Passeri, the oscine passeriforms. While a great deal is known about oscine song, few descriptions of the repertoires of tropical suboscines have been published, and relatively little is known about the use and function of song in suboscines. Additionally, whether suboscines can recognize individuals by voice alone has received little attention. One representative of these tropical suboscines is the buff-throated woodcreeper (*Xiphorhynchus guttatus*, Dendrocolaptinae), a bird commonly found in the forests of the tropical Americas. To investigate the possibility for individual variation in songs of this species, we recorded buff-throated woodcreepers at dawn and dusk in Amazonian Perú. From these recordings, we document two long-range song types, describe their acoustic parameters, and examine their occurrence at different times of day and across two seasons. Quantitative analysis of frequency, timing, and pattern of songs revealed that woodcreeper vocalizations varied significantly among individuals. A discriminant function analysis of song parameters successfully assigned a majority of songs to the correct individual. Despite their relatively simple structure, the vocalizations of buff-throated woodcreepers vary consistently among individuals but apparently not so distinctly as those of many oscines. Questions remain regarding whether the buff-throated woodcreeper can use these differences for individual recognition and how the two song types function in communication.

Keywords

individual differences, birdsong, woodcreeper, neotropics, suboscines, song types.

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1. Introduction

While a great deal is known about the songs of temperate zone birds (Catchpole & Slater, 2008), fewer aspects of behavior and song have been thoroughly studied in tropical species. A number of key differences between the two regions places further importance on investigating whether temperate patterns hold true in the tropics. Less pronounced seasonality in the wet tropics creates a prolonged breeding season, and birds tend to live longer (Stutchbury & Morton, 2001). Consequently, there is a premium on space, and tropical birds often must defend their territories year-round. Perhaps because territorial defense is a high priority, members of both sexes commonly defend territories, and females engage in territorial disputes with broadcast songs as males do. Indeed female song is much more common in the tropics than in temperate regions (reviewed by Farabaugh, 1982).

Whereas oscines, members of the suborder Passeri, make up most of the species in temperate regions, it is the suboscines of the suborder Tyranni that constitute over 60% of the bird species in some Neotropical forests (Morton, 1996). Although highly speciose, little is known about tropical suboscines, especially about their songs and social behavior. The difference in the phylogenetic composition of neotropical avifaunas has important implications for the acquisition of song by birds in the two regions, as oscines always learn some features of their songs, while evidence suggests that suboscines develop their vocalizations without learning (although evidence suggests limited learning in some Cotingidae; Saranathan et al., 2007). Experiments with several tyrannids show that these birds develop normal vocalizations in acoustic isolation (Kroodsma, 1984, 1985; Kroodsma & Konishi, 1991) and show no signs of subtle learning in the field (Wiley, 2005). These phylogenetic differences in acquisition of song result in differences in structural characteristics of the songs themselves (Gaunt, 1983). In learning their songs, members of Passeri go through stages of memorization and crystallization which often result in a complex song or set of songs (Marler, 1981; Marler & Peters, 1982). Conversely, birds that do not learn their songs often produce a smaller repertoire of vocalizations with fewer types of notes. Furthermore, in comparison to the oscines, suboscines have simpler muscular control of the syrinx, which also contributes to the simpler forms of their notes and syllables (Müller, 1878; Ames, 1971; Gaunt, 1983). The Tyrannidae have the most complex syringes of the suboscines, and they have correspondingly the most complex note structures (Ames, 1971; Baptista & Trail, 1992). Despite the relatively complex note structure in Tyrannidae, in general the songs of suboscines exhibit a feature that indicates little influence of learning in the development of song, which is limited individual differences in vocalizations.

Past research on oscines confirms that many species have consistent individual differences in their complex songs, and these acoustic differences enable birds to identify individuals such as mates, neighbors, or strangers, and gauge their aggressive responses accordingly (Brooks & Falls, 1975; Wiley, 2013). Furthermore, oscines can use their repertoires to communicate escalation or de-escalation of aggression (reviewed by Searcy & Beecher, 2009). Suboscines also face the challenges of territorial encounters, but an understanding of song variation, use of song in territorial disputes, and capabilities for individual recognition remains lacking.

All birds, including non-passerine species such as terns and owls, appear to have some degree of individual variation in their vocalizations (Hutchison et al., 1968; Miller, 1978; Wooller, 1978; Moseley, 1979; Cavanagh & Ritchison, 1987; Galleotti et al., 1993; Robisson et al., 1993; Peake et al., 1998; Delport et al., 2002; Lovell & Lein, 2004, 2005; Wiley, 2005). Indeed, there is no reason to expect less individual variation in behavior, such as birdsong, than in morphology. Nevertheless, in the absence of learning, individual variation in song is usually limited. Learning, a form of behavioral plasticity, includes both imitation (with attendant copying errors) and improvisation, and can lead to cultural evolution and geographic variation, as well as differences among individuals (Janik & Slater, 2000). Learning can also lead to similarity among individuals as a result of copying or selective attrition (Nelson, 2000). Suboscine birds in general show neither the degree of individual variation in some features, nor the precise matches between individuals in other features, that characterize the songs of most or all oscines.

In recent years information about the vocalizations of suboscine birds has increased. There is now evidence that their vocalizations have adapted to environmental conditions (Seddon et al., 2005; Tobias et al., 2010), have diversified under morphological constraints (Derryberry et al., 2012), and that their vocalizations include individual differences which, in some cases, are recognized by conspecifics in the field (Bard et al., 2002; Lovell & Lein,

Figure 1. Photograph of a buff-throated woodcreeper caught at the Madre Selva Biological Station in Perú. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1568539x.

2004, 2005). There are descriptions of the repertoires and uses of vocalizations of a number of tyrannids (Smith & Smith, 1996). Nevertheless, our knowledge of suboscine vocalizations is still rudimentary.

Of the suboscines, the woodcreepers, subfamily Dendrocolaptinae (SACC: Remsen et al., 2012), are among the least well studied. Little is known about their mating systems, territoriality, or vocalizations. In the present study we focus on a widespread species, the buff-throated woodcreeper, *Xiphorhynchus guttatus* (Figure 1). This sexually monomorphic species is common throughout forests of the tropical Americas, and both sexes produce broadcast songs (Marantz et al., 2003). As is typical of suboscines, this woodcreeper has structurally simple songs and, thus, is a candidate for investigating individual differences and recognition of vocalizations in a suboscine. In this study, we describe the long-range vocalizations of the buff-throated woodcreeper, including two complex song patterns. In addition, we document diurnal patterns of the use of these songs and their occurrence in behavioral interactions. Finally, we investigate the nature of individual differences in these songs.

2. Material and methods

2.1. Recording and identification of song patterns

We studied the behavior of buff-throated woodcreepers in July and August of 2002 at the Madre Selva Biological Station on the Río Orosa in Amazonian Perú (3°37′2″S, 72°14′8″W). Woodcreepers were common throughout terra firme forests around the station, and we focused on a part of the population near a clearing along a low bluff about 100 m from the river. In order to determine the locations of individual birds, we created an east-to-west transect about 175 m long with markers every 25 m and mapped nearby landscape features. At dawn and dusk, two to four observers stood at different positions along the transect, tape recorded the songs, and dictated their compass directions and distances. With these data we triangulated the locations of calling birds and mapped the territories of 10 different individuals (2 probable male–female pairs and 6 lone individuals) based on their regular use of distinct positions for vocalization.

These observations were carried out from 5:00–6:30 and 17:00–18:30 for a period of six weeks. Recordings were made with a Sony TC-D5M professional cassette recorder and a Sennheiser K6U/ME62 cardioid microphone. Approximately 24 h of tape were digitized using the sound analysis program WildSpectra (Wiley & Wiley, 2002), at sampling rate 22 100 Hz, transform size 128, frequency resolution 172 Hz, temporal resolution 5.80 ms and panel height 128 pixels.

From our recordings, we identified two distinct categories of vocalizations. Type I songs consisted of a rapid series of similar notes, a ‘trill’, that sometimes ended with a distinct terminal note (Figure 2a). Type II songs consisted of a sequence with several distinct types of notes. In addition, this species produces a loud vocalization consisting of a single note (Figure 2b). Notes are continuous vocal utterances separated from others by at least 6 ms, and syllables are combinations of two notes (in Type II songs) separated by less than 1 s (see Lemon, 1965).

2.2. Song use

To determine the how singing varied throughout the day, we sampled singing rates of buff-throated woodcreepers throughout the morning between the hours of 5:45–9:00 AM in July 1999 and 2002 and in March 2006. These recordings were made with Sennheiser ME62/K6 omnidirectional microphones 2.0 m (±10%) above ground at 12 sites in mature terra firme forest

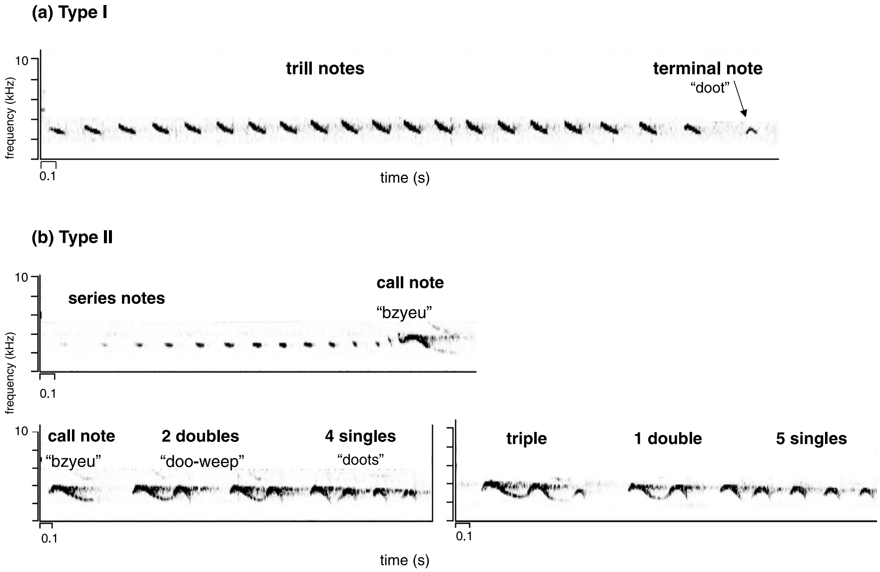

Figure 2. Spectrograms of buff-throated woodcreeper vocalizations: of Type I (a) and Type II (b). Type II vocalizations included more complexity in patterning than Type I songs.

along the Río Orosa. Eight sites were on property of the Madre Selva Biological Station, but 1–2 km from the site at which the individual recordings were made and, thus, did not include the same individuals. Recordings were processed in the same manner as above, and vocalizations were identified to song type or call. Because we could not always determine how many individuals called at each site, we counted every minute in which a vocalization of this species occurred. We divided these counts into three periods of the morning: (1) 5:45–6:45 AM, (2) from 7:00–7:59 AM and (3) from 8:00–9:59 AM. Civil sunrise at this time was approximately 6:00 AM. Roughly 255 h of recordings were used to calculate rates of singing for each vocalization type per hour.

2.3. *Analysis of song for individual differences*

We analyzed individual differences among the ten individuals that were repeatedly sampled at the Madre Selva site (as described in Section 2.1 above). Recordings varied in quality because of background noise, distance from the bird, direction of the microphone, and occurrence of other species calling at the same time. We selected clear recordings of 5–10 songs for each individual as identified by habitual locations for singing. Because the songs had

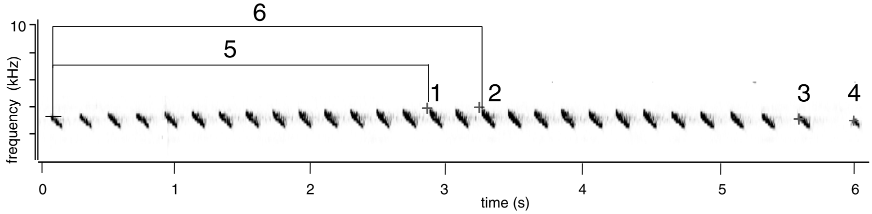

Figure 3. Six frequency and timing measurements used in ANOVA of Type I vocalizations.

a relatively narrow range of frequencies and were recorded from distances of 10–20 m, there were no indications that frequency-dependent attenuation affected the appearance of the full range of frequencies on spectrograms. We selected songs that were recorded at least 11 h apart when possible. In no case did we use more than three songs from any one individual from one recording session. For Type I and Type II songs, three and seven individuals, respectively, met conditions for this analysis.

To make acoustic measurements of the songs, we used standardized windows in WildSpectra, at the settings noted above. To capture the variation in Type I songs, we measured seven features as follows (Figure 3): (1) the highest frequency of the fifteenth note (approximately the mid-point of a song), (2) the highest frequency overall, (3) the highest frequency of the last note, (4) the frequency difference between the fifteenth and first notes, (5) the frequency difference between the last and first notes, (6) the frequency of the single note at the end if it occurred, and (7) the number of notes per second.

For Type II songs we measured time and frequency at eight points (Figure 4): (1) the highest frequency of the first note of the first and (2) second double syllables, (3) the highest frequency of the first single syllable, (4) the frequency of the second note of the first double syllable, (5) the frequency difference between the first note and second note of the first double syllable, (6) the interval between the initial peak of the first and second double notes (between the *doo*-'s of the first two *doo-weep*'s), (7) the interval between the first and second double syllable, (8) the interval between the first and second single notes. We also included two features of the overall pattern, (9) the number of double syllables and (10) the number of single syllables.

We used ANOVA (JMP version 3) to assess variation within and between individuals for each of these parameters. In order to correct for multiple tests, we used a sequential Bonferroni correction to determine statistical significance. We then selected the parameters with the highest F-ratios for use in a

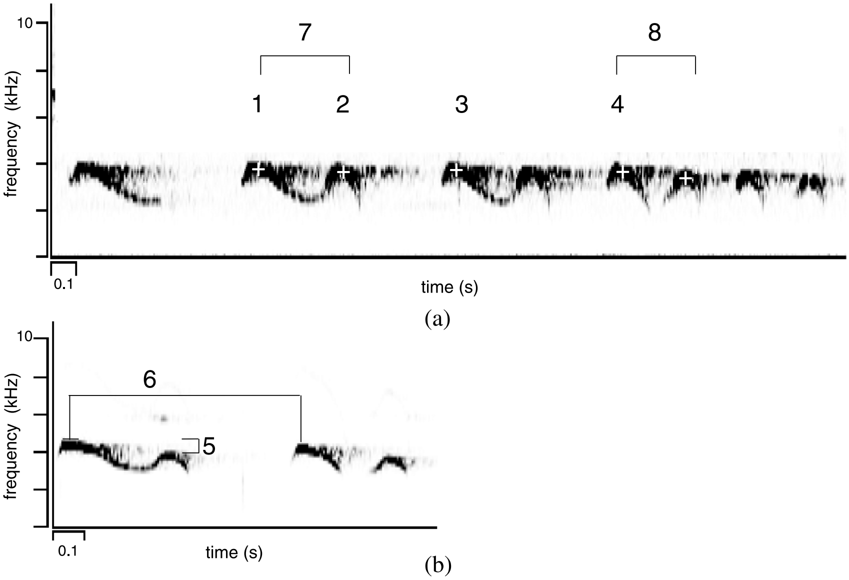

Figure 4. Seven frequency and timing measurements used in ANOVA of Type II vocalizations. In describing song pattern, parameters 9 and 10 would be recorded as two doubles and four singles for spectrogram a, and two and zero respectively for spectrogram b.

discriminant function analysis (DFA), which provided a model for assigning calls to individuals. For Type I songs, the two parameters with the greatest individual variation were parameters 1 and 3. For Type II songs, we used six parameters: 1, 2, 3, 5, 9 and 10. All parameters used in the DFA for both Type I and II songs retained statistical significance after sequential Bonferroni corrections, except the terminal which was only sung occasionally.

Introductory notes sometimes preceded single-note *bzyeu* calls and Type II songs. These notes occurred in series but appeared different in shape and sound from the notes of Type I songs. To determine whether or not these introductory notes differed from the those in Type I songs, we performed one-way ANOVAs on the same parameters as those measured for Type I songs, i.e., parameters 1–3. We compared 45 total songs from six individuals total, three individuals singing Type I songs and three singing introductory notes preceding Type II notes. Next, in order to determine if the introductory notes preceding the *bzyeu* call and those preceding Type II songs differed, we compared the same measurements. For this analysis we used 15 songs preceding the bzyeu call and seven songs that preceded the regular Type II notes from four individuals.

3. Results

3.1. Song description

The two song patterns appeared to be used by different individuals. A single individual never switched from one type to the other. Our maps of the singers' locations indicated that the two patterns never came from exactly the same location. Furthermore, one song type was often answered by the other song type from a different location, sometimes apparently a neighboring territory but sometimes apparently a different location within the same territory (as both males and females produce song). It, thus, seemed possible, but not confirmed, that paired males and females often sang different song types.

Type I songs included two different kinds of notes: a short ascending note repeated on average 25 times in a sequence and a single terminal note that rapidly ascended and descended in pitch (Figure 2a). The notes rose slightly in spectral frequency over the course of the song and were repeated at a regular rate of about five notes per second.

Type II vocalizations, apparently not described previously, were sung primarily at dawn and dusk, and only rarely after the first three hours of the morning. When this song pattern was given during the middle of the day, it was usually sung only once. For the Type II songs we identified six syllables types, as follows (Figure 2b): a sudden call that dropped in pitch (*bzyeu*), a double syllable (*doo-weep*), a single note symmetrically concave downwards in pitch (*doot*), quiet notes usually in a short series, and a rare triple syllable similar to a double note but with a soft final element. These syllables were usually combined in a pattern that began with the double syllable and continued with the single notes. *Bzyeu* calls often occurred alone or preceding one of these combinations. The introductory notes always preceded Type II songs or *byzeu* calls.

3.2. Song pattern variation

Type I songs varied according to the number of notes included. The notes were repeated 5 to 39 times, and an average call included 25 notes at 4.7 notes/s. Each note rose in pitch, either a straight ascent or slightly concave upward, whereas the terminal note, if it occurred, was concave downward.

Type II songs were sung in a variety of patterns. The variation came from the numbers of each syllable sung rather than the sequence of the syllables, which almost always progressed as follows: introductory notes, *bzyeu*, triple, double and single notes. Only one recorded song did not follow this order but instead included a triple after a double syllable. Most Type II songs lacked introductory notes, and when they did occur they often preceded the *bzyeu* call note. Most Type II songs began with one to three double syllables (*doo-weep*s). The songs did not always include the single syllables, for instance, a common pattern consisted of only two double syllables, while other songs contained as many as seven single syllables.

Introductory notes that preceded Type II songs varied in number from 5 and 19. These notes increased only slightly in frequency and were slightly faster (5.0 notes/s) than Type I notes. Each note was shorter than those in Type I songs and either sloped only slightly downward or was slightly concave downward, similar to the single syllable *doot*. If a call consisted of only introductory notes and either a *bzyeu* call or Type II song, then the number of introductory notes was also always less than 20. Introductory notes preceding either *bzyeu* or typical Type II song differed statistically in frequency from Type I notes (one-way ANOVA, $F = 10.31$, df = 5, 40, $p = 0.0058$, for highest frequency, and $F = 21.45$, df = 5, 40, $p = 0.0003$, for the frequency difference between the last note and the first note). On the other hand, introductory notes preceding *bzyeu*s were not statistically different from those preceding Type II song for the same two frequency measures (one-way ANOVA, $p > 0.05$). Thus, introductory notes preceding a *bzyeu* call were consistently similar to those preceding Type II song but were significantly different from the notes in Type I songs.

3.3. Song use

From 255 h of recording this species across 12 sites, we found most of the singing to occur between 5:45 and 6:45 (Figure 5). During that first hour in July of 1999 and 2002, 61% of the songs recorded were Type I and 39% were Type II. Later in the morning, between 7:00 and 9:00, this ratio was reversed (37% Type I: 63% Type II). However, in March of 2006 Type I song was nearly absent during all three hours of the morning. In addition, overall singing rates of both song types and *bzyeu* calls were significantly lower in March than in July (t-test, $p = 0.044$). Calls with introductory notes, however, showed the opposite pattern occurring more often in March than in July (t-test, $p = 0.046$).

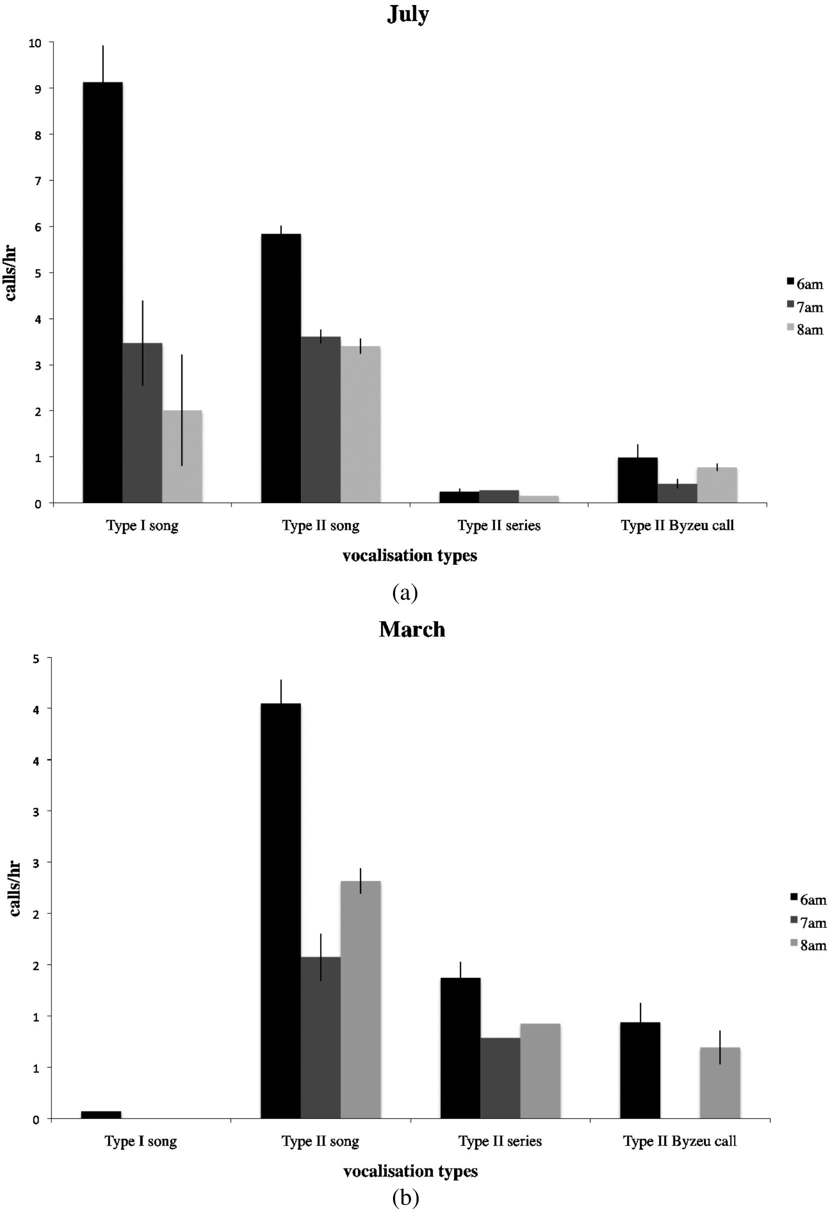

Figure 5. Singing behavior of the buff-throated woodcreeper recorded between 5:45–9:00 AM in July 1999 and 2002 (a) and March 2006 (b): mean rates of vocalization with standard deviations for two song types and two long-range calls.

3.4. Individual differences

Type I songs differed significantly among individuals in frequency parameters (Table 1). The measure of notes/s, in contrast, did not differ among individuals. Parameters 1 and 3 (the highest frequency of the 15th note and last notes) were used in the DFA (Figure 6a). For the three individuals with Type I songs in the analysis, the DFA attributed 56 ± 12% of the vocalizations to the correct individual.

Type II vocalizations were more complex than Type I and included a variety of patterns of syllables. Individuals sang distinctive patterns of double and single syllables, and these pattern parameters (9 and 10) differed significantly across individuals (Table 2). All frequency measures (parameters 1–5) of Type II songs also differed significantly among individuals as well. Parameters 1, 2, 4 and 5 showed the greatest differences among individuals. None of the temporal measures, however, differed significantly among individuals.

A DFA with parameters 1, 2, 3, 5, 9 and 10 correctly classified 74 ± 8% of the calls to the observed individual (see Table 2 and Figure 6b). For individuals 1, 3 and 7, 100% of the songs were assigned correctly. Two calls of individual No. 2 were misclassified and attributed to a close neighbor, individual No. 1. Individuals No. 4 and No. 5 were also neighbors, and calls of each bird were misclassified to the other.

4. Discussion

4.1. Song description, pattern and use

The buff-throated woodcreeper has three broadcast vocalizations, two song patterns that consist of sequences of notes and a single call note. The two song types are sung primarily during the first hour of daylight and become less frequent as the morning proceeds, as is typical of many bird species (Figure 5). The striking variation in singing rate of Type I songs by season, with a lower rate in March than in July, leads to questions about the function of this song type in relation to the mating system of the species. The *bzyeu* and the introductory series vocalizations are less common than the more complex songs overall and do not vary as much in rate of use with time of day or season. Perhaps they serve primarily as otherwise undifferentiated contact calls.

Table 1.
Type I songs vary significantly among individuals for frequency but not for timing parameters in one-way ANOVA.

Parameter		N	Range	Mean	SD	F ratio	p	Corrected α
	Frequency (Hz)							
1	15th note	30	1507–1894	1703	90.7	7.55	0.002*	0.008
2	Highest note	30	1378–1679	1577	90.1	6.84	0.004*	0.01
3	Last note	30	172–603	412	106.4	13.78	<0.001*	0.007
4	Terminal note	14	12–473	284	94.7	3.97	0.048*	0.025
	Frequency difference (Hz)							
5	15th note–1st note	30	1593–1981	1831	107	4.39	0.022*	0.017
6	Last note–1st note	30	1679–1981	1880	84	5.68	0.009*	0.013
	Rate							
7	Notes per second	30	4.35–5.18	4.69	0.17	1.04	NS 0.368	0.05

Three individuals are used for this analysis, degrees of freedom for the F ratios are 2 and $N - 3$. Values of α include sequential Bonferroni corrections.

* Significant difference ($p < 0.05$).

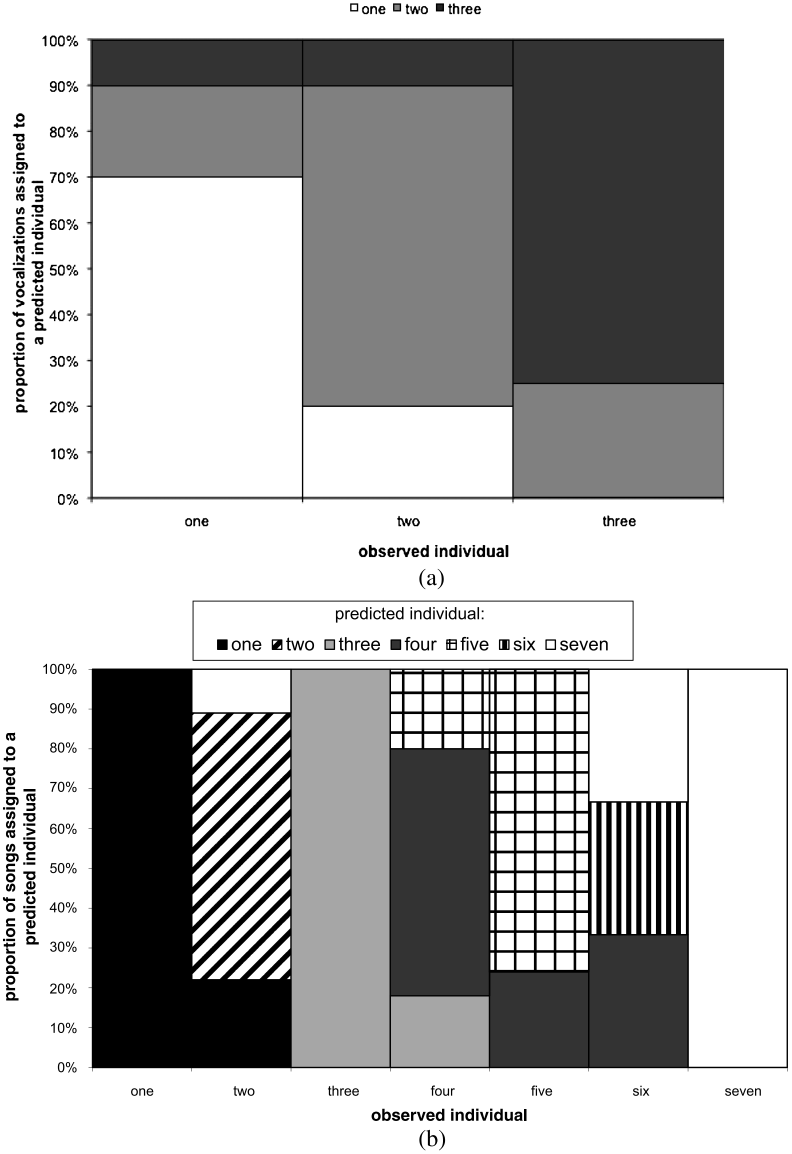

Figure 6. Assignment of observed songs to predicted individuals by the DFA. The columns along the x-axis represent the songs of observed individuals. The y-axis shows the assignments of proportions of those songs to predicted individuals (indicated by different shadings). (a) DFA of Type I vocalizations classified 56 ± 12% of songs to the correct individual. (b) DFA of Type II vocalizations classified 74 ± 8% of songs to the correct individual.

Table 2.
Type II songs vary significantly among individuals for both frequency differences and pattern differences, but not for timing in one-way ANOVAs.

Parameter		N	Range	Mean	SD	F	p	Corrected α
	Frequency (Hz)							
1	1st note of 1st double	47	1808–2196	2014	120.3	41.27	<0.0001*	0.005
2	2nd note of 1st double	47	1765–1981	1882	78.9	7.99	<0.0001*	0.006
3	1st note of 2nd double	43	1808–2153	1963	105.5	17.18	<0.0001*	0.006
4	1st single syllable	41	1722–2067	1847	80.1	3.31	0.0113*	0.013
	Frequency difference (Hz)							
5	1st and 2nd note of 1st double	47	43–302	128.5	68.4	19.75	<0.0001*	0.0071
	Time intervals (ms)							
6	Between 1st and 2nd double	43	616–1103	800.5	98.6	1.36	NS 0.256	0.05
7	Duration of 1st double	47	250–494	323.3	40.4	1.87	NS 0.109	0.017
8	Between 1st and 2nd single	29	134–330	249.8	41.3	1.57	NS 0.207	0.025
	Pattern							
9	No. of double syllables	47	1–3	2	1	4.16	0.0024*	0.01
10	No. of single syllables	47	0–6	2	2	5.92	0.0002*	0.0083

Seven individuals are used for this analysis, so degrees of freedom for the F ratios are 6 and $N - 7$, where N is the number of songs. Values of α include sequential Bonferroni corrections.

* Significant difference ($p < 0.05$).

All these vocalizations have the characteristics of long-range signals with high amplitude and species-specific pattern. What little that is known of their use suggests that they might serve for communication between the sexes as well as for territorial advertisement. The loud complex vocalizations of suboscines have been termed ‘loudsongs’ (Willis, 1967; Isler et al., 1998) rather than ‘songs’, the term often used for such vocalizations of oscines, although it is not clear that these vocalizations of suboscines differ substantially from those of oscines in their function in communication.

The presence of two distinct broadcast vocalizations seems less common among birds that do not learn their songs, but this arrangement occurs in other woodcreepers. At least one other woodcreeper, the Plain-brown woodcreeper, *Dondrocincla fuliginosa*, also produces two distinct songs each composed of sequences of notes (Willis, 1972). Other members of the genus *Xiphorhynchus*, including *X. obsoletus*, *X. ocellatus* and *X. elegans*, also appear to have two complex songs (J. Diaz, pers. commun., and personal observations). Other species of suboscines, outside the woodcreeper family, have sex-specific vocalizations which are often used in duets (Morton & Derrickson, 1996).

The roles in communication of the two song types of buff-throated woodcreepers remain unknown. These vocalizations are possibly each produced by one sex. Our observations of singing locations and the coordination of the two song types by two individuals within a territory suggest the possibility of sex differences. In the tropics the occurrence of female song is much more common than in temperate regions. The possibility of sex-specific vocalizations in this species opens the door for further investigation of territorial defense by both sexes and intrasexual selection among females (Tobias et al., 2011). In addition, the mating system of this species needs more investigation (see below). The difficulty of observing vocalizing woodcreepers and of determining sex even in the hand makes it a challenge to confirm the sex of vocalizing birds.

The trend for Type I vocalizations to predominate at dawn and Type II vocalizations during late morning suggest a parallel with the dawn and day songs of many tyrant flycatchers, although none of the *Xiphorhynchus* woodcreepers sings with the rapidity and persistence of tyrannids at dawn (Lein, 2007). The occurrence of two song types is also common in many oscines such as warblers (Spector, 1992). Long-term observations of *X. guttatus* at six nests have provided no evidence that more than one adult feeds nestlings at each nest (Skutch, 1996). This indication of single parental care by female *X. guttatus* (Skutch, 1996), if confirmed, might indicate that the Type I songs come from males on traditional display sites, like the vocalizations of some cotingas that lack pair-bonds. The absence of clear sexual dimorphism in *Xiphorhynchus* species suggests not, however. The two vocalizations might also depend on the pairing status of males or females, as has been shown in nightingales (Naguib et al., 2011), although both types seem to be too frequent for vocalizations associated with unpaired individuals in a species with year-round residence.

Other insights into the function of the two song types come from our behavioral observations of interactions between individuals and six preliminary playbacks that we conducted in late July. We recorded bouts of counter-singing of Type I songs but no such interactions involving Type II vocalizations. In addition, we performed three playbacks each of Type I and Type II songs on the boundaries of territories as determined by triangulation of locations of vocalizations. Playback of Type I elicited increased rates of singing Type I songs from the 3 individual subjects. Playback of Type II vocalizations, however, did not elicit responses of either song type. While further study is needed to confirm these preliminary observations, the data suggest the two types differ in function. Furthermore, the responses suggest a potential sex difference if one sex is more likely to engage in territorial signaling more often.

4.2. Individual differences

Our analyses of buff-throated woodcreeper vocalizations revealed consistent, if slight, individual differences (Tables 1 and 2, Figure 6a, b). The two song types differ significantly among individuals in frequency and also, for Type II songs, in pattern, but not timing. Thus, buff-throated woodcreepers could use both frequency and pattern to distinguish individuals by voice. The timing of song features could play a role in species-recognition, especially the rate of note production in Type I songs (Derryberry et al., 2012).

The degree to which songs differed among individuals varied between the two song types. Only about 56% of Type I songs were classified to the correct individual in DFA as compared to 74% correct classification of Type II songs. The relatively large numbers of errors in classifying individuals by their Type I songs was particularly remarkable considering the small numbers of individuals in our analysis. Any procedure for discriminating categories within a finite range of variation becomes more difficult on average the larger the number of categories. Hence, the 56% accuracy in classification of Type I songs in DFA is probably an overestimate of the accuracy if the number of individuals were greater. The seven individuals in our analysis of Type II songs seem closer to the number of conspecifics that a woodcreeper might regularly encounter.

The simpler structure of Type I songs probably accounts for the errors in assigning these vocalizations to particular individuals. For Type II songs, incorrect assignments of songs were often attributed to a bird's neighbor. Another source of possible error comes from counter-singing, during which songs could be misclassified. There were also two cases in which we suspected that individuals formed a mated pair, as they vocalized regularly from within the same area. The four individuals of the two putative pairs regularly sang, answering each other, at the boundary of their territories, one of each pair singing Type I, and one of each pair singing Type II. The DFA incorrectly assigned a proportion of these individual's songs to the corresponding member of the neighboring pair. These similarities in calls suggest that a bird's location was occasionally misidentified or that one bird occasionally visited another territory, perhaps while defending a boundary. Also these findings raise the question of the extent to which neighbors' songs are more similar in pattern or frequency than non-neighbors.

As discussed earlier, individual differences are not in themselves unexpected in any behavior, including vocalizations. The differences in this woodcreeper fit the pattern for other suboscines and nonpasseriform birds. Variation in their songs combines (1) less pronounced differences among individuals and (2) more variation in the repetition of exemplars of any one type of vocalization than occurs in the songs of oscines. Both of these features could prove generally true of species that do not learn their songs. Learning, as previously mentioned, involves both imitation and improvisation during development and promotes both individuality and stereotypy.

The less conspicuous individual differences in the vocalizations of suboscines presumably increases the difficulty members of the species would face in recognizing individuals. In tyrannid flycatchers, playback experiments have suggested that species vocalizing above vegetation do indeed recognize these slight individual differences (Lein, 2007). In contrast, a similar species in the understory of tall forests does not differentiate individuals in their responses to playbacks, unless the playbacks were prolonged (Wiley, 2005). Suboscines in the understory of tropical forests might also have difficulty in recognizing individuals' vocalizations (Bard et al., 2002). Difficulty in individual recognition could have consequences for the evolution of social interactions, both cooperative and aggressive (Wiley, 2013). On the other hand, most suboscines in tropical forests occupy year-round territories and, once they have a territory, have high survival rates (Morton, 1996). The more prolonged opportunities for interaction with neighbors and mates might compensate for the greater difficulty in their distinction by voice. Clearly questions regarding social interactions, the function and recognition of song, the occurrence and role of female song need further study, especially for the residents of tropical forests.

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