

# The vocal behavior of the Brown-throated Wren (*Troglodytes brunneicollis*): song structure, repertoires, sharing, syntax, and diel variation

J. Roberto Sosa-López · Daniel J. Mennill

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**Abstract** Empirical descriptions of vocal behaviour are important for understanding avian biology. In this study, we provide the first detailed analysis of the vocal behaviour of the Brown-throated Wren (*Troglodytes brunneicollis*), a neotropical songbird found in oak forests in the highlands of Mexico and the southwestern United States. We quantify the fine structural characteristics of the song, and describe the size and structure of the song repertoire. Further, we describe diel variation, analyze song-sharing patterns among neighbors, and explore whether this species uses syntactical rules for creating their songs. Our analyses reveal that Brown-throated Wrens have complex songs and simple calls. They sing with eventual variety, repeating songs many times before switching to a new song type. Males combine syllables into phrases to create songs. We show that song repertoire size is not fixed; birds recombine their syllables to produce highly variable song types. Brown-throated Wrens sing with high vocal output after sunrise and song activity declines throughout the morning. Song sharing shows no variation with distance among our sampled individuals. We divide the syllables in Brown-throated Wren songs into 13 categories; birds sing some syllables more frequently than others, and some syllables are more likely to be found at the beginning, middle, or end

of the song. Transitions between syllable categories deviate significantly from random chance, and most males analyzed follow similar patterns of syllable transitions, revealing syntactical structure. This research, which provides the first empirical study of Brown-throated Wren song, expands our knowledge of the behaviour of this poorly-studied taxon, and contributes insight into the organization and composition of song in tropical birds.

**Keywords** Troglodytes · Diel variation · Repertoire · Syntax · Vocal behavior · Autonomous recorder

## Zusammenfassung

### Das Gesangsverhalten des Braunkehl-Zaunkönigs (*Troglodytes brunneicollis*): Gesangsstruktur, Repertoire, Syntax und tageszeitliche Variationen

Empirische Erhebungen des Gesangsverhaltens sind sehr wichtig für das Verständnis der Biologie von Vögeln. Mit dieser Studie legen wir die erste detaillierte Analyse des Gesangsverhaltens des Braunkehl-Zaunkönigs (*Troglodytes brunneicollis*) vor, eines neotropischen Singvogels aus den Eichenwäldern des mexikanischen Hochlands und des Südwesten der USA. Wir quantifizieren die Feinstruktur der Gesangsmerkmale und beschreiben Größe und Struktur des Repertoires. Ferner beschreiben wir tageszeitliche Variationen und Gemeinsamkeiten im Gesang von Reviernachbarn und untersuchen, ob diese Art bei der Ausprägung ihrer Gesänge Syntax-Regeln folgt. Unsere Analysen zeigen, dass Braunkehl-Zaunkönige sowohl einfache Rufe als auch komplexe Gesänge besitzen. Sie singen mit nur gelegentlichen Variationen, wobei sie ein Gesangelement oft wiederholen, bevor sie zu einem neuen überleiten. Bei der Zusammenstellung neuer Gesänge kombinieren die Männchen einzelne

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J. R. Sosa-López (✉) · D. J. Mennill  
Department of Biological Sciences, University of Windsor,  
Biology Building, 401 Sunset Avenue, Windsor,  
ON N9B 3P4, Canada  
e-mail: jrobertososa@gmail.com

Tonsilben zu Phrasen. Wir zeigen, dass die Repertoire-Größe nicht festgelegt ist; die Vögel setzen ihre Tonsilben zu immer neuen Gesangstypen zusammen. Die Braunkehl-Zaunkönige haben direkt nach dem Sonnenaufgang eine sehr hohe Gesangsproduktion, die im Laufe des Morgens dann nachlässt. Gemeinsamkeiten im Gesang von Nachbarn erwiesen bei unserer Stichprobe keine besonderen Variationen mit wachsendem Revierabstand. Wir teilen die Tonsilben in 13 Kategorien ein; die Vögel singen manche Tonsilben häufiger als andere, und einige Silben treten jeweils eher am Anfang, in der Mitte oder am Ende eines Gesangs auf. Die Übergänge zwischen den einzelnen Kategorien sind signifikant nicht zufallsverteilt, die meisten der untersuchten Männchen folgen ähnlichen Übergangsmustern, was auf eine syntaktische Strukturierung hinweist. Dies ist die erste empirische Untersuchung des Gesangs von Braunkehl-Zaunkönigen; sie erweitert unser Wissen vom Verhalten dieser nur wenig untersuchten Art und bietet weitere Einsichten in die Organisation und Zusammensetzung der Gesänge tropischer Singvögel.

## Introduction

Bird vocalizations are some of the most complex and well-studied acoustic signals in the animal kingdom (Marler and Slabbekoorn 2004). They can be analyzed at several levels of organization, from the simplest units of notes or syllables to higher levels of the composition of an entire song, to still higher levels of organization manifested in song repertoires and patterns of song delivery (Catchpole and Slater 2008). Bird species differ enormously in the variety of song styles and patterns of vocal organization. Traits that vary between avian taxa include the fine structural characteristics of songs and calls, the relative abundance of syllable types in the song (syllable composition), repertoires, daily vocal activity, syllables and song sharing, and rules that govern the position and order of the syllables within songs (e.g., Catchpole 1976; Kroodsmas 1977; van Horne 1995; Molles and Verhencamp 1999; Wright and Dahlin 2007; Valderrama et al. 2008; Camacho-Schlenker et al. 2011).

The description of bioacoustic traits is important because songs vary with the mode of acquisition (e.g., cultural or genetic inheritance) or with the form of selection they experience (e.g., habitat constrains, performance constraints, female choice, etc.; Catchpole and Slater 2008). To understand how these traits evolved and gain insight into their function, it is necessary to document and describe the precise vocal behavior for multiple taxa and evaluate them using a comparative approach. Careful descriptions of acoustic variation provide a foundation for

detailed research on the influence of selection on bird songs and song transmission between generations (Lynch 1996; Podos et al. 2004).

In this study, we provide the first comprehensive account of the vocal behavior of the Brown-throated Wren (*Troglodytes brunneicollis*). Brown-throated Wrens inhabit most of the mountains of Mexico and the extreme south of Arizona in the United States. They are found in open areas and forest edges of humid pine–oak forest and cloud forest (Howell and Webb 1995). They are a sedentary species, with occasional, limited movements between adjacent forest patches (Watson 2003). Many authors treat the Brown-throated Wren as a full species with two to three subspecies based on appearance, distribution, and habitat (Howell and Webb 1995; Brewer and MacKay 2001; del Hoyo 2005): *brunneicollis* from San Luis Potosi and Hidalgo south to the northern mountains of Oaxaca; *cahooni* from southern Arizona south to central Mexico; and *nitidus* isolated in the mountains of Sierra Madre del Sur of Guerrero and Oaxaca. Other authors consider Brown-throated Wrens to be a subspecies of the House Wren (*Troglodytes aedon*; American Ornithologists Union 1998). Species limits in the House Wren complex are, however, controversial (Brumfield and Capparella 1996; Rice et al. 1999), although a recent genetic analysis suggests that Brown-throated Wrens are indeed a distinct species (Martínez Gómez et al. 2005). A quantitative description of the vocal behavior of the Brown-throated Wren would provide a useful point of comparison for a better understanding of their taxonomy, yet their voices have never been analyzed.

We recorded Brown-throated Wrens in southern Mexico and conducted detailed bioacoustics analyses of their vocalizations. Our goals were: (1) to provide a description of the fine structural characteristics of the song and calls of Brown-throated Wrens, (2) to assess the repertoire characteristics in terms of both song types and syllable categories, and (3) to quantify how song output varies with time of day. We also sought to investigate (4) whether song-sharing varies with geographic distance, and (5) whether males deliver syllables in non-random order to create songs. We were motivated to conduct this investigation for several reasons. First, we wished to provide a careful bioacoustic description of this taxon's songs and singing behavior, and thereby facilitate comparisons to House Wrens, allowing us to explore the hypothesis that these taxa are distinct species (Howell and Webb 1995; Brewer and MacKay 2001; del Hoyo 2005). Second, we were interested in exploring repertoire sharing in Brown-throated Wrens, a behavior thought to be important in intra-sexual interactions in other songbirds (e.g., Beecher et al. 2000; Todt and Naguib 2000). Third, we sought to explore whether repertoire size may be the principal target

of selection in Brown-throated Wrens, as predicted by the Repertoire Size Hypothesis, which states that males should sing all the components of their repertoire with similar frequency, in order to best showcase their repertoire size (Lapierre et al. 2011). Finally, we wanted to test whether Brown-throated Wrens deliver syllables in a non-random order, exhibiting syntax, which is defined as the set of rules that govern the temporal arrangement of syllables (Hultsch and Todt 2004).

## Methods

We studied Brown-throated Wrens at San Mateo Río Hondo, Oaxaca, México (16°8'24"N, 96°26'26"W) from 3 to 17 May 2010 and from 5 to 17 June 2011. Both recording periods fell during the peak of the breeding season. We observed several of the recorded pairs building nests or rearing young, and during both recording periods wrens were actively singing and engaged in reproductive activities; therefore, we suspect that all birds were paired and at similar stages of breeding. During two field expeditions, we studied birds in 27 different breeding territories. In 2010, we studied Brown-throated Wrens in nine different territories. We caught at least one individual per territory using mist nets, banded them with a unique combination of color bands, and determined sex by inspection of the cloacal protuberance or brood patch; birds were deemed to be male if they exhibited a cloacal protuberance, or females if they showed feather loss, vascularization, or swelling of their abdomen (Ralph et al. 1993). In 2011, we studied Brown-throated Wrens in 20 territories, including 2 in which birds had been caught and banded in 2010, and 18 additional territories where we caught and banded at least one of the resident birds. Our analyses are based on the detailed recordings of males in 7 territories monitored in 2010 as well as 2 territories recorded in both 2010 and 2011, and complemented by additional observations of males from the 18 additional territories in 2011.

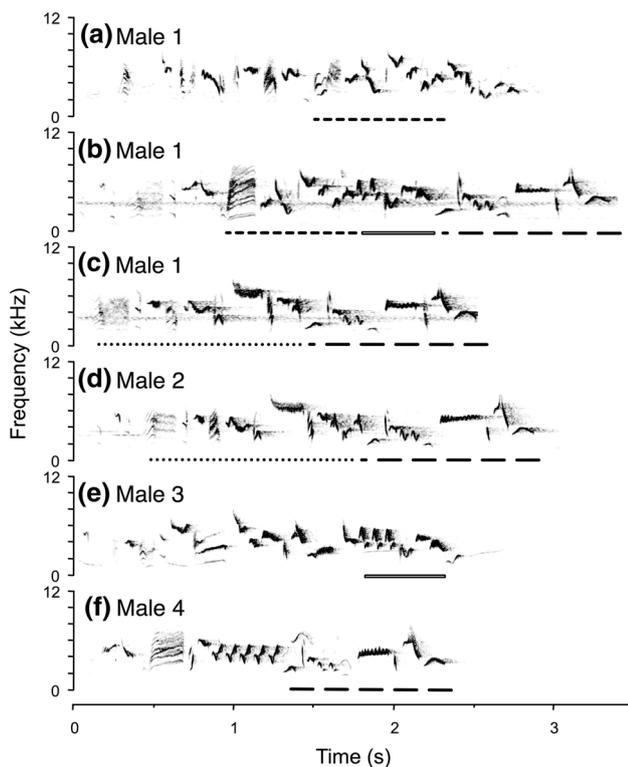
To ensure rigorous sampling of the repertoires of songs and to guarantee a high number of hours recorded in the field, we used two complementary recording techniques. First, we conducted focal recordings where a recordist followed the male and female as they traveled around their territory between 0600 and 1100 hours and between 1500 and 1800 hours, identifying the bird by its color bands whenever possible. Second, we recorded birds using autonomous digital recorders which allowed us to collect long, continuous recording in each bird's territory, thereby minimizing human disturbance and generating longer periods of recordings to provide more thorough estimations

of repertoire size. We chose the location for the autonomous recorders at the end of our focal recording sessions, placing them near a song perch where the male had performed his first song bout of the day and where he spent most of the time during the 2-h focal recording. Our observations suggest that these birds inhabit the same area over extended periods, and perform songs from the same or similar perches every morning (see "Results"). Our observations of interactions between neighboring males suggest that they are highly territorial birds with defined territorial boundaries; when two neighboring males engaged in counter-singing behavior, they did not cross the boundaries of their territories. Based on these observations, we are confident that our autonomous recording devices recorded the target birds and not birds in adjacent territories.

Our observations showed that Brown-throated Wrens occupied relatively large territories, where the widest dimension was  $82.0 \pm 13.5$  m (mean  $\pm$  SE;  $n = 15$ ; calculated as the maximum distance between the farthest points where a wren was detected). Territories had irregular shapes and usually did not overlap neighbors' territories (6 of 9 birds with neighbors had small regions of overlap at territory peripheries). Centers of the studied territories were separated by an average distance of 244.5 m (range 28.6–438.7 m).

Focal recordings were collected using three sets of equipment: a Marantz PMD660 with either a Sennheiser MHK67 shotgun microphone or a Telinga parabola with a Sennheiser K6/ME62 omnidirectional microphone, and a Nagra Ares-BB+ with a Telinga parabola and a Stereo Pro 6 Telinga microphone. Recordings were saved in WAV format at 44.1 kHz/16 bits and 48 kHz/24 bits, respectively. Autonomous recordings were collected using Wildlife Acoustics Song Meters (models SM1 and SM2), which include built-in, stereo microphones (see Mennill et al. 2012); recordings were saved in WAV format at 44.1 kHz/16 bits. We recorded males on every territory for a period of  $4.2 \pm 2.4$  days. Altogether, we collected a total of 255.5 h of recordings (7.7 h of focal recordings, and 247.8 h of continuous autonomous recordings) with an average of 28.3 h per territory in the nine territories recorded in 2010, or in 2010 and 2011 (range 9.2–79.75 h).

Previous studies on House Wrens (*T. aedon*) and Winter Wrens (*T. troglodytes*; Kroodsma 1977; Platt and Ficken 1987; van Horne 1995) suggest that *Troglodytes* wrens have very large repertoires and complex singing behavior. We assumed that extremely long field recordings would be required to rigorously sample each animal's behavioral repertoire. Consequently, in this study, we chose to maximize the recording time of a small number of birds, rather than collecting shorter recordings of many birds.



**Fig. 1** Sound spectrograms depicting songs recorded from five male Brown-throated Wrens (*Troglodytes brunneicollis*). Underlined sections highlight some of the phrases that are shared within males (a–c) and between males (c–f). c, d A song type shared between two males

## Bioacoustic definitions and classification

### Definitions

Brown-throated Wrens exhibit similar patterns to other wren species in their songs and singing behavior; therefore, we used the previously established criteria as a guideline to define syllables, phrases, songs, song repertoires, bouts of songs, and calls (van Horne 1995; Mennill and Vehrencamp 2005; Valderrama et al. 2008). We defined a “syllable” as the basic unit in the songs of Brown-throated Wrens. Syllables can be composed of one or more elements (i.e. one or more continuous tracings on a sound spectrogram; as defined by Catchpole and Slater 2008). We identified “syllable categories” by shape, using temporal and frequency characteristics to distinguish different categories (Platt and Ficken 1987; van Horne 1995); syllable categories were established a priori (details below). We defined a “phrase” as a combination of syllables in stereotyped order that was common across different birds or different vocalization bouts from the same bird (Catchpole and Slater 2008). For purposes of this study, we differentiate songs and calls based on their structure, rather than their function. We defined a “song” as long, complex

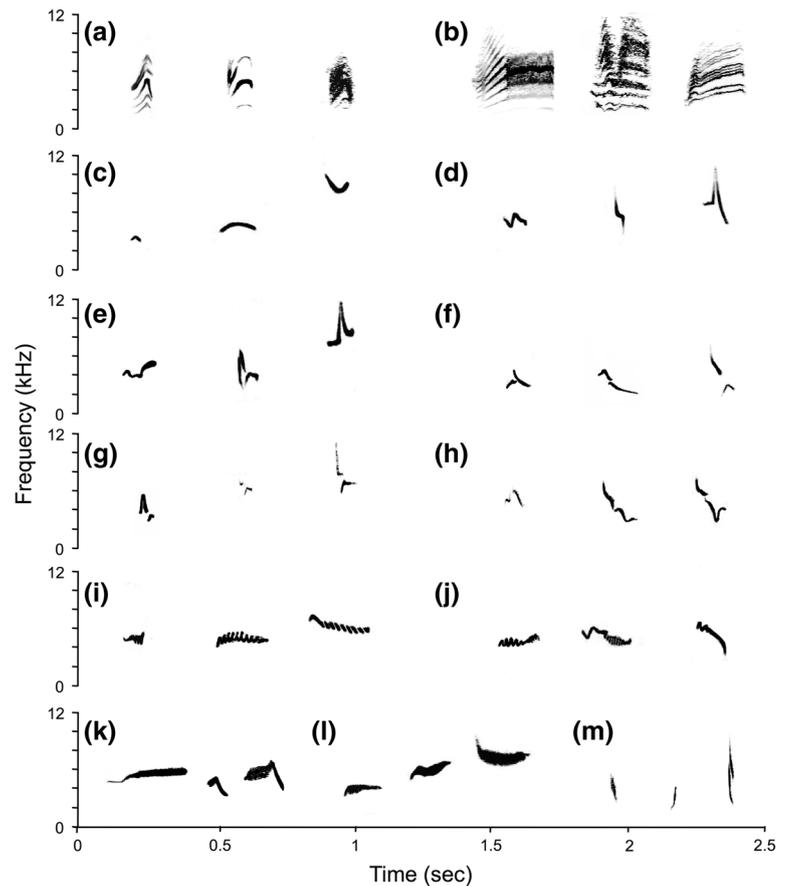
vocalizations produced by males and containing a series of syllables with no gaps of  $\geq 1$  s; we defined a “call” as a shorter, simpler vocalization delivered by both sexes (Catchpole and Slater 2008). The distinction between the study birds’ complex songs and simple calls was obvious in our recordings (see Figs. 1, 3). We defined “song repertoire” as the total number of song types recorded from each bird (Catchpole and Slater 2008). We defined a “bout of songs” as a period of singing activity with short gaps between songs. Typically, a song bout included one song type repeated at a regular pace. We considered a bout to end when a bird stopped singing, or when a bird changed to a different song type (following Borror 1956; Morton 1987). We defined a “trill” as a series of identical syllables, repeated three or more times in rapid succession within a song.

### Song, syllable, and call classification

After scrutinizing all songs recorded, we assigned all syllables into 13 categories based on the length of the syllable, its harmonic structure, and the number of inflection points in frequency-modulated syllables (Fig. 2). Syllables with harmonic structure were classified in two categories: “snarl syllables” were nasal sounds with narrowly spaced harmonic stacks less than 0.1 s length (e.g., Fig. 2a); and “mew syllables” were sounds with widely spaced harmonic stacks, longer than 0.2 s (e.g., Fig. 2b). Frequency-modulated syllables were sounds depicted in the spectrogram as a clear and continuous line with no overtones. We classified all syllables based on the number of elements and frequency modulations or inflections: one-element syllables having one inflection (e.g., Fig. 2c), two inflections (e.g., Fig. 2d), and three or more inflections (e.g., Fig. 2e); and two-element syllables having one inflection (e.g., Fig. 2f), two inflections (e.g., Fig. 2g), and three or more inflections (e.g., Fig. 2h). We classified syllables with more rapid frequency modulations in four categories: syllables with slow modulations (e.g., Fig. 2i), syllables composed of a section with slow modulations and a pure tonal section (e.g., Fig. 2j), syllables composed of a section with rapid modulations and a pure tonal section (e.g., Fig. 2k), and syllables made of rapid modulations (e.g., Fig. 2l). We classified syllables without inflections with one or two elements in a single category, all of which were short syllables (e.g., Fig. 2m). Acoustic signals produced by Brown-throated Wrens are very complex, and they may produce more than 13 syllable categories; our classification scheme is conservative and provided us an objective, repeatable method for studying the syllables in this species’ complex songs.

We define song types on the basis of being composed of the same categories of syllables in the same order

**Fig. 2** Sound spectrograms of the syllable catalogue of Brown-throated Wrens comprising 13 different syllable categories. *Letters* refer to the syllable identity



(following Mennill and Vehrencamp 2005; Valderrama et al. 2008). Two songs were considered as the same type if they shared  $\geq 75\%$  of the same syllables, in the same order. In the classification we considered the syllable category in a trill, but we did not take in account the number of repetitions of that syllable (i.e. a trill with four repetitions of a particular category of syllable was treated the same as a trill with five repetitions of that category of syllable).

We provided a classification and description of the different call types that Brown-throated Wrens produced during our field study. We classified call types based on qualitative traits like frequency modulation, presence or absence of harmonics, number of elements conforming the calls, and length. We also noted the context in which calls were performed.

#### Acoustic analyses

##### *Fine structural characteristics of the songs*

We described the fine structure of the song of the Brown-throated Wren in terms of frequency and time measurements. We measured six fine structural variables for each song: (1) song length (in seconds, measured from the

beginning of the first syllable to the end of the last syllable in the song, using the waveform as guideline to define the start and end of a syllable), (2) number of syllables, (3) number of trills, (4) maximum frequency (the highest frequency with energy in the song; in Hz), and (5) minimum frequency (the lowest frequency in the song; in Hz). Measurements were extracted from spectrograms visually, using Syrinx-PC (J. Burt, Seattle, WA, USA). Sound spectrograms were created using a 512 point fast Fourier transform (FFT; Blackman window setting), resulting in approximately 43 Hz frequency resolution and 4 ms time resolution.

##### *Song repertoire*

To assess song repertoire size, we used the time and frequency cursors in Syrinx-PC to highlight each song for each bird. Each new song was given a unique number and added to a digital catalogue, where we noted the identity of the singing bird and the song type. To assess song repertoire size, we plotted the cumulative number of song types detected against the number changes in song for every male (as described in Catchpole and Slater 2008; Valderrama et al. 2008). Brown-throated Wrens sing with eventual variety, where a song type is repeated many times before

switching to another song type. Hence, we used number of changes in song type to estimate song repertoire because short samples could under-estimate the actual repertoire size when using total number of songs (Catchpole and Slater 2008). We considered ourselves to have recorded the full repertoire of a male when the number of syllables or songs reached an asymptotic line (i.e. the line became horizontal). Two of the 9 birds recorded in 2010 were still alive in 2011. For these birds, the analyses of song repertoire included both sets of data from 2010 and 2011.

#### *Diel variation*

To study diel variation in vocal behavior, we calculated the total number of vocalizations, the total number of songs, and the total number of calls per hour, as well as the different number of song types sung per hour, for those birds with at least one continuous day of recording. Our analyses started at 0500 hours (sunrise occurred at 0605 hours) and ended at 1900 hours (sunset occurred at 1915 hours). Our field observations suggest that calls are not sex-specific and thus overall rate of calling was calculated on a per-pair basis. We tested whether vocal output differed with time of day by performing a nonparametric Friedman test using PASW statistics (v.18.0; Chicago, IL, USA).

#### *Song sharing and sharing-by-distance*

Assessing sharing is a challenge given the high variability in Brown-throated Wren songs, in which syllables are added or deleted between subsequent songs (a behavior also seen in other birds, such as some populations of Song Sparrows, *Melospiza melodia*; Lapierre et al. 2011). We followed previously established methods for comparing these variable songs to estimate the degree to which two song types matched (Lapierre et al. 2011). Using the catalogue of syllables in Fig. 2, and following a similar approach used to assess song repertoire, we scanned each song type within each male's repertoire for the presence of each syllable category. We chose songs with clear recordings, and with non-overlapping sounds that could obscure the categorization.

We assessed sharing between all pair-wise combinations of song types using the Jaccard's coefficient of similarity:  $J_{AB} = c/(a + b + c - d)$

Here,  $c$  is the number of syllables common to song types A and B;  $a$  is the number of syllables present in song type A but not song type B;  $b$  is the number of syllables present in song type B but not song type A; and  $d$  is the absolute value of the difference in number of syllables in song types A and B. We computed a single sharing coefficient by calculating an average of all coefficient values between two

males (*neighbor sharing coefficient*). We also calculated the degree to which a male shared syllables between songs within his own repertoire by computing all coefficient values between his different songs (*within male sharing coefficient*).

To understand the relationship between sharing and the physical distance between birds' territories, we performed a Mantel test (Quinn and Keough 2002). All matrices created for the Mantel test had pair-wise comparisons of every bird with every other bird. First, we created a matrix with *neighbor sharing coefficient* values. Then, we created a matrix with the actual distance between the centers of the birds' territories. The sharing matrix of *neighbor sharing coefficients* was created using Jaccard's coefficient of similarity (explained above). Mantel tests were performed using 10,000 permutations in PASSaGE software (v.2; Rosenberg and Anderson 2011). Distances between territories were calculated using the geographic coordinates at the centers of the territories with the program Geographic Distance Matrix Generator (v.1.2.3; New York, NY, USA; Ersts 2011), based on tracking of birds during collection of focal recordings.

#### *Temporal arrangement and syllable transitions*

We conducted three analyses of the temporal pattern of Brown-throated Wren singing behavior. First, we investigated whether birds preferentially produced some syllable categories more often than others by analyzing the relative frequency distribution of all syllable categories by bird. We ran a separate test for each of our nine most intensively-recorded males.

Secondly, we analyzed whether the temporal arrangements of syllables within a song were given at random by analyzing the relative frequency distribution of the relative position of each syllable category within a song. We ran a separate test for every syllable category across all songs and individuals. We ran Chi-square goodness-of-fit tests using relative values. Our data met the assumptions for these tests (see Krebs 1999).

Third, we tested whether syllable-to-syllable transitions within songs of Brown-throated Wrens deviated from random using lag sequential analysis (as in Wright and Dahlin 2007). Following Bakeman and Quera (2011), we calculated the probabilities of transitions between the observed syllable (first behavior; row) and the following syllable (second behavior; column) within the strings of specified events (a lag, or in this case a song), for each bird. We performed the analysis at two levels: at lag +1 measuring the frequency of transitions between syllables that were immediately adjacent within songs, and at lag +2 measuring the frequency of transitions between syllables with one intermediate syllable. We performed lag sequential analysis using the software SDIS-GSEQ (v.5.1).

We analyzed whether individuals had similar patterns of transitions between syllables by calculating the Bray–Curtis distance among all individuals. The Bray–Curtis coefficient takes into account abundant transitions and ignores missing transitions between two individuals, providing a distance value between 0 and 1, with 1 indicating that two samples are identical (Krebs 1999). We calculated Bray–Curtis distance using PAST software (v.2.17b; Hammer et al. 2001).

Throughout, values are presented as mean  $\pm$  SE. All tests are two-tailed with a significance threshold of  $P = 0.05$ .

## Results

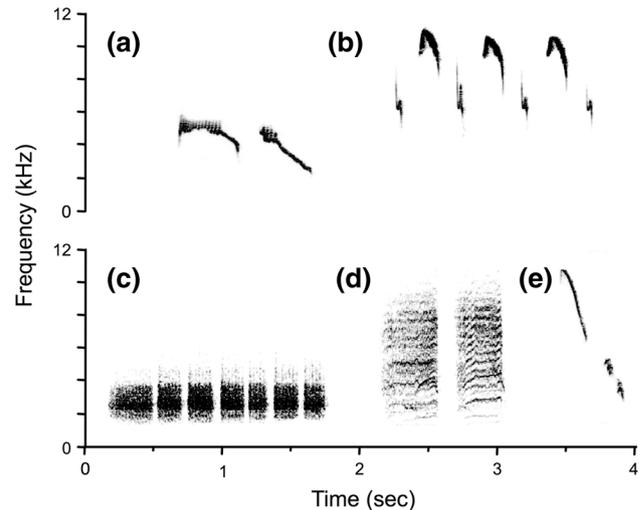
### Songs

We collected recordings of the vocal behavior of Brown-throated Wrens in southern Mexico, including observations of birds in 27 territories, with detailed recordings of birds in 9 territories. We only recorded males singing; during two field expeditions, we never encountered a female singing.

Songs of Brown-throated Wrens are, on average,  $2.2 \pm 0.1$  s long and have  $17.1 \pm 0.6$  syllables ( $n = 9$  males). Songs typically have  $1.4 \pm 0.01$  occurrences of trills, and a bandwidth ranging from a minimum of  $2,259 \pm 31$  Hz to a maximum of  $8,117 \pm 125$  Hz (minimum and maximum are the averages across all measured song types per male; average song types analyzed per male =  $735 \pm 142$ ).

Brown-throated Wrens sing with eventual variety, where a song is repeated many times before switching to a new song type. Bouts of song include  $35.2 \pm 20.1$  songs. Within song bouts, songs are separated by silent gaps of  $6.2 \pm 2.2$  s (based on measurements of the first bout of a morning for  $n = 9$  males).

Brown-throated Wrens compose songs by combining syllables. Songs often contain syllables given in stereotyped order, so that particular strings of syllables (“phrases”) were found frequently in different song types within the repertoire of a given bird, or across the repertoires of different birds. Birds varied where they inserted or substituted these phrases in their songs, producing complex patterns of repetition (see Fig. 1 for examples). Males often initiated a bout of songs by delivering an unusually long song followed by a short gap, and then continuing the remainder of the bout with shorter songs. Often the long, introductory song comprised two song types in rapid succession or one song type repeated twice with no break (e.g., AB...B B B B; or AA...A A A A).



**Fig. 3** Sound spectrograms of the calls of the Brown-throated Wren. **a** A two-element *whistle* call; **b** a series of *see* calls; **c**, **d** two examples of harsh calls; and **e** a downward series call

### Calls

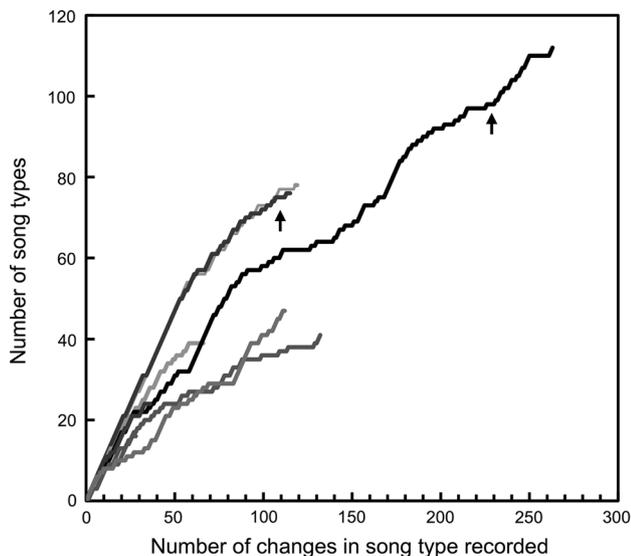
Both females and males produced a variety of tonal and atonal calls. We recorded four types of calls (Fig. 3; Table 1). The *whistle* call is a slow downward-modulated call, usually given as two notes with the first higher than the second. Both notes have rapid frequency modulations at the start (Fig. 3a). This was the most common call; we recorded 936 *whistle* calls produced by six pairs. We observed both sexes producing this call, and we recorded this call at all times of the day, although it seemed more common in the afternoon. Interestingly, we heard this call particularly often when following pairs with fledglings, but never during interactions between neighbors. These observations suggest that the *whistle* call may be a contact call and not an aggressive or alarm call.

The *see* call is comprised of very short high frequency notes (Fig. 3b). We recorded 105 *see* calls produced by 4 pairs. We believe the *see* call is given in aggressive interactions because often males exposed to playbacks of their own species’ song answered using these calls (J.R.S.-L., unpublished data). Although we never observed a female producing this call, we are not confident that males are the only sex that produces it.

We also recorded additional, varied calls that we were not able to quantify in detail, and for which the context is unclear. Many of these calls were harsh and unmelodic sounds, as is common for many wrens, including harsh broadband sounds (Fig. 3c, d). Occasionally, we observed one *whistle* call immediately preceding these harsh calls. We recorded such sounds on 33 occasions by 5 pairs. In addition, we recorded a broadband, downwards-modulated call (Fig. 3e) on four occasions by two pairs.

**Table 1** Description of the fine structural characteristics (mean  $\pm$  SE) of four call types of Brown-throated Wrens (*Troglodytes brunneicollis*)

Call type	Length (s)	High frequency (Hz)	Low frequency (Hz)	Bandwidth (Hz)
Whistle call	0.57 $\pm$ 0.04	5,610 $\pm$ 66	3,219 $\pm$ 93	2,391 $\pm$ 139
See call	0.28 $\pm$ 0.06	10,436 $\pm$ 385	7,110 $\pm$ 900	3,326 $\pm$ 695
Harsh call	1.24 $\pm$ 0.3	7,208 $\pm$ 679	2,528 $\pm$ 411	4,680 $\pm$ 1,001
Downward series call	0.55 $\pm$ 0.1	10,634 $\pm$ 1,114	3,678 $\pm$ 1,409	6,956 $\pm$ 2,523

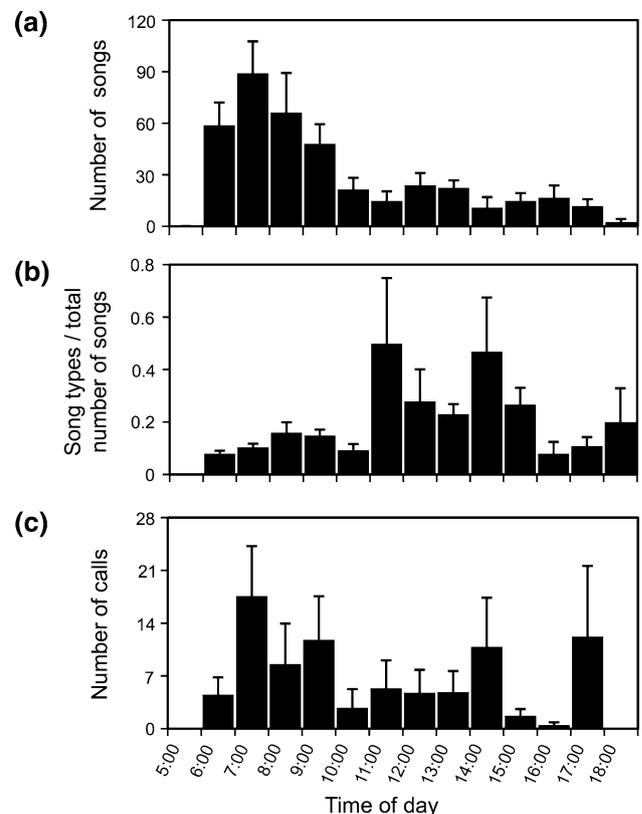
**Fig. 4** Repertoire asymptote accumulation curves showing the number of unique song types based on recording effort for nine male Brown-throated Wrens. Cumulative song repertoire size is plotted against the number of changes in song type recorded. *Arrows* show the repertoire asymptote accumulation curves for birds that were recorded in both 2010 and 2011

### Song repertoires

On average, we analyzed  $911.8 \pm 570.5$  songs and  $60.1 \pm 8.7$  changes in song type per male ( $n = 9$ ). The two males that we recorded in both years were recorded for additional periods of  $47.5 \pm 17.6$  h in the second year, annotating an additional  $618.5 \pm 229.8$  songs per male. Inspection of the repertoire asymptote curves (Fig. 4) showed that none of the asymptotic curves reached a plateau or showed any sign of leveling off in spite of our extensive recording, including those birds recorded in both years. This suggests that Brown-throated Wrens do not have a fixed song repertoire. We identified, on average,  $54.4 \pm 10$  song types per bird (range 16–112;  $n = 9$ ).

### Diel variation

Brown-throated Wrens started to sing around sunrise, with an average start time of 0640 hours (range 0630–0703 hours,  $n = 9$  birds recorded in 2010). Song rates declined

**Fig. 5** Vocal output of Brown-throated Wrens varies with time of day. **a** Mean number of songs per hour; **b** mean number of different song types divided by the number of songs sung per hour; and **c** mean number of calls per hour. *Error bars* indicate standard error. Sunrise occurred at 0605 hours, and sunset at 1915 hours

slowly during the morning and persisted at lower levels for the remainder of the day. In general, males initiated their first song bout of the morning at specific perches and moved around their territories, giving short flights and singing continuously as they did so. We monitored 12 males for at least two sequential days; all males chose the same perch to deliver their first song of the morning on subsequent days.

Vocal output varied with time of day (Fig. 5; analysis based on 7 males recorded extensively in 2010). In general, the highest peak of vocal activity fell between 0600 and 0900 hours, when all types of vocalizations were considered together. Song output varied significantly with time of

day, with the highest levels of activity occurring in the morning, after sunrise, and a peak between 0600 and 0900 hours (Friedman test:  $\chi^2 = 59.5$ ,  $df = 13$ ,  $P < 0.001$ ; Fig. 5a); song output remained low throughout the late morning and afternoon, with no sign of an increase at dusk. We found an interesting pattern in how often birds changed song types across the day, where birds changed song types more frequently (in relation to the total number of songs per hour) between 1100 and 1400 hours ( $\chi^2 = 24.4$ ,  $df = 13$ ,  $P = 0.02$ , Fig. 5b). Thus, our results show that the peak in song rate is related to the use of a low number of song types sung repeatedly, whereas a low rate of songs coincides with more frequent changes in song type. Calls were produced much less frequently than songs at all times of day. Calls showed significant variation across the day with a peak at 0700 hours and three peaks of similar intensity at 0900, 1400, and 1700 hours ( $\chi^2 = 29.4$ ,  $df = 13$ ,  $P = 0.006$ ; Fig. 5c).

#### Sharing and sharing-by-distance

We based our analysis of song sharing on nine males that we recorded extensively in territories that were in close proximity to one another. On average, we analyzed  $23.3 \pm 4.5$  song types per bird (range 4–42;  $n = 9$ ), and classified an average of  $521.8 \pm 105.7$  syllables per bird (range 89–995;  $n = 9$ ). The mean *within male sharing coefficient* ( $0.57 \pm 0.04$ ; range 0.52–0.64,  $n = 9$ ) did not differ from the mean *neighbor sharing coefficient* ( $0.55 \pm 0.03$ ; range 0.47–0.60,  $n = 36$ ; pair-wise comparisons, Kruskal–Wallis test 0.77,  $df = 1$ ,  $P = 0.3$ ). In other words, two song types produced by a single male shared the same amount of syllable categories compared to two song types sung by two different birds. We found no relationship between the physical distance separating male territories and their *neighbor sharing coefficients* (Mantel test:  $r = -0.2$ ,  $P = 0.1$ ;  $n = 9$ ). Figure 1 shows multiple examples of syllable sharing between birds.

#### Temporal arrangement and syllable transitions

The Chi-square analysis revealed that Brown-throated Wrens produce some syllable categories more often than others ( $\chi^2$  range = 56.2–211.8,  $df = 12$ ,  $P < 0.001$ ; see Fig. S1 in Online Resource). The Chi-square goodness-of-fit tests also showed that the relative position of different syllable categories within songs are not homogenous, with some syllables more likely to occur at a particular position within the song ( $\chi^2$  range = 5.4–194.5,  $df = 9$ ,  $P < 0.025$ ; see Fig. S2 in Online Resource).

Transition probabilities between syllables deviated from chance for all nine birds; this was true for both lag +1 (Pearson Chi-square:  $\chi^2$  range = 208–838, all  $P < 0.01$ ) and lag +2

( $\chi^2$  range = 213–713, all  $P < 0.01$ ) sequential analyses, except for lag +2 analysis of bird TB08 ( $\chi^2 = 128.9$ ,  $P = 0.8$ ; see Table S1 in Online Resource). The distance analysis between males showed an average Bray–Curtis index of 0.56 (range 0.32–0.74) for lag +1 analysis, and 0.54 (range 0.30–0.69) for lag +2 analysis. These results suggest that at least 50 % of abundant transitions are common among all individuals.

#### Discussion

Male Brown-throated Wrens produce elaborate, complex songs and simple calls. Males sing with eventual variety and have an apparently unlimited repertoire of song types. Brown-throated Wrens sing with the highest levels of output right after sunrise. Singing behavior varies with time of day, in terms of the number of songs, calls, and repetition of song types. In terms of syllable composition, two song types produced by a single male are as different to two songs produced by different males. There is no relationship between song sharing and geographic distance. Birds show a predilection to overproduce some syllables and underproduce others. The contribution of particular syllables to songs is non-random, where specific syllables are more prone to occur at the beginning, middle, or end of the song. Transitions between syllables are not given at random and all males analyzed followed similar patterns of transition between syllables. This first quantitative description of the vocal behavior of Brown-throated Wrens shows that these birds have complex and interesting patterns of vocal behavior.

Brown-throated Wren songs share similar features to House Wren songs from Wisconsin, USA (*T. aedon aedon*) and Alberta, Canada (*T. a. parkmanii*): songs are composed of highly frequency-modulated syllables, often including trills (Platt and Ficken 1987; Rendall and Kaluthota 2013); song length (Rendall and Kaluthota 2013) and song frequency are similar (Platt and Ficken 1987); songs are repeated several times before switching to a new song type (Kroodsmma 1977; Rendall and Kaluthota 2013), song repertoires are not fixed (but see Rendall and Kaluthota 2013), and both taxa use a finite repertoire of syllables to create an extensive song repertoire (Rendall and Kaluthota 2013). Our results, however, show that Brown-throated Wrens differ from House Wrens for some acoustic traits. For example, within songs, House Wrens repeat the same syllable several times before switching to a different syllable type and do not repeat it again (Rendall and Kaluthota 2013), whereas Brown-throated Wrens hardly ever repeat syllable types (except in trills). Prior studies reveal that House Wren singing behavior varies across the breeding cycle, and future comparisons between House Wrens and Brown-throated Wrens will be improved by controlling for

breeding stage (Johnson and Kermott 1991; Rendall and Kaluthota 2013).

Brown-throated Wren and House Wren songs show similarity with other closely related wrens' songs. Bewick's Wrens (*Thryomanes bewickii*) and Winter Wrens also compose songs by combining syllables in stereotyped order, creating phrases that are often found repeatedly in the repertoire of a given bird (Kroodsma 1977, 1980; van Horne 1995). Birds insert or substitute these phrases at the beginning, middle, or end of the song, suggesting that they consider these phrases the basic building blocks of song construction (Kroodsma 1977; Fig. 1). However, unlike House Wrens and Bewick's Wrens, whose phrases are composed of less variable syllables resulting in intermediate complexity, Brown-throated Wrens and Winter Wrens compose highly complex phrases with more variable syllables (Kroodsma 1977, 1980; van Horne 1995). The structural features we have described here for Brown-throated Wrens are intermediate between Winter Wrens and House Wrens. Interestingly, Martínez Gómez et al. (2005) suggest that Brown-throated Wrens are basal within the House Wren complex. Further detailed comparisons are needed in order to understand whether the vocal differences that we present here match the results of recent molecular studies showing that Brown-throated Wrens and House Wrens differ genetically (Rice et al. 1999; Martínez Gómez et al. 2005; but see Brumfield and Capparella 1996).

Empirical evidence suggests that high variability in song repertoire size is related to sexual selection through female choice (i.e. Repertoire Size Hypothesis; Catchpole 1976). The Repertoire Size Hypothesis predicts that, if repertoire size is the principal target of selection, then males should sing all the components of their repertoire with similar frequency, in order to best showcase their repertoire size (Lapierre et al. 2011). This strategy would decrease the chances of a listener underestimating the repertoire size of a singer (Lapierre et al. 2011). In contrast to this prediction, our results show that Brown-throated Wrens do not use all the syllables with similar frequency; certain syllable categories are over-produced, and some syllable categories are produced rarely. Therefore, our results do not provide support for the Repertoire Size Hypothesis. Alternatively, intra-sexual interactions may drive patterns of song repertoire delivery in birds (e.g., Beecher et al. 2000; Todt and Naguib 2000). Shared signals may be used for communicating different levels of threat, either escalating or de-escalating a conflict, explaining complex patterns of repertoire use during intra-sexual interaction (Beecher and Campbell 2005). Winter Wrens from Europe share most of their repertoire with neighbors when distances between territories are small (up to 500 m, similar to the distances in our study), but the pattern does not hold when territories

are located at more than 500 m (Camacho-Schlenker et al. 2011). Given that our analyses focus on nearby territorial males, we do not know whether sharing decreases with larger geographic distances in Brown-throated Wrens in a similar fashion. Further research is needed to clarify our understanding of the importance of song sharing during countersigning interactions in Brown-throated Wrens, and future playback studies may be particularly insightful to test whether males match components of playback stimuli.

The pattern of diel variation in Brown-throated Wren vocal output is consistent with the dawn chorus behavior known in many bird species (Staicer et al. 1996), with a peak at the beginning of the day and decreasing as the day progresses. We found that the peak in song rate is associated with low song type diversity, whereas a low rate of songs coincides with more frequent changes in song type. Interestingly, our field observations suggest that the peak in vocal activity, which coincides with infrequent changes in song type, occurred after sunrise when males were signing from exposed perches with few movements through their territories; in contrast, periods of low vocal activity, which coincide with frequent changes in song type, occurred throughout the afternoon when most of the interactions among territory owners and neighbors were observed. In several species of songbirds (e.g., Spector 1991, 1992), males sing with little variety early in the morning, and much greater variety during the day; this difference corresponds to apparent differences in context and function, where early morning songs are given with an emphasis on attracting females and daytime songs are given in interactions with other males, where song-type matching may be especially important (Todt and Naguib 2000). In addition, the pattern of song delivery we describe for Brown-throated Wrens suggests that females cannot easily assess repertoire characteristics early in the morning, but females might instead assess other song features, such consistency between multiple renditions of each song (Price 2013).

Calling behavior, in contrast to singing behavior, showed multiple peaks of activity during the day. Most of the calls were recorded with automated systems and we therefore do not have observational data to accompany these recordings. Our field observations suggest that pairs produced *whistle* calls more often when fledglings were nearby and when they were feeding on the ground, suggesting that these vocalizations function as contact calls or in attracting conspecifics to food sites (Kondo and Watanabe 2009). Other calls, including *see* calls, *harsh* calls, and *downward* series calls, were observed to occur more often during playback trials (J.R.S.-L., unpublished data), suggesting an antagonistic function (e.g., Kondo and Watanabe 2009). It is worth noting that songs and calls may serve different functions at different breeding stages,

and this may influence patterns of repertoire use and song structure (e.g., Johnson and Kermott 1991); future analysis with recordings that extend across multiple breeding stages would be required to test these ideas.

Our recordings reveal that Brown-throated Wrens deliver some syllables more frequently than others, and that some syllables are given preferentially at specific positions within songs. This suggests that Brown-throated Wrens deliver syllables in a non-random order, providing evidence for the idea that this species has vocal syntax. Evidence for syntactical rules in *Troglodytes* wrens have been presented in two other studies. The first is a descriptive analysis by van Horne (1995) of North American Winter Wrens, showing a non-random temporal arrangement of syllables within songs and transition probabilities differing from expected values. The second comes from an experimental playback study conducted by Holland et al. (2000) showing that European Winter Wrens are able to discriminate between songs with typical syntax versus modified syntax. This type of syntax, known as combinatorial syntax (Leger 2005), has also been reported in nonpasserine birds (e.g., Blue-throated Hummingbird, *Lampornis clemenciae*; Ficken et al. 2000), suboscine birds (e.g., Flammulated Attila, *Attila flammulatus*; Leger 2005), and other oscine birds (e.g., Bengalese Finches, *Lonchura striata*; Okanoya and Yamaguchi 1997).

Empirical studies have shown that song types are the salient unit of interaction for birds (e.g., song-type matching in Song Sparrows; Beecher et al. 2000). However, a study by Kroodsma (1977) suggested the idea that phrases are the basic building blocks of song production in some members of the Troglodytidae family. There are at least two lines of empirical evidence suggesting that phrases are the functional units of song production (reviewed in Suthers 2004). First, empirical evidence suggests that the avian brain stores song information as syllables or packages of syllables (Hultsch and Todt 1989; Suthers 2004), and that muscular movements and the respiratory system are programmed to respond synchronously when producing these components of song. Thus, in complex singers, animals may learn strings of syllables (phrases) as a unit, and then use these phrases to compose their song repertoire. Second, when repertoires are large, receivers are unlikely to count entire repertoires and may rely on other cues, such as phrase detection probabilities (Garamszegi et al. 2005). The fact that Brown-throated Wrens combine syllables in a stereotyped order to create phrases, and that these phrases are shared between individuals (see Fig. 1 for examples of shared phrases), supports the idea that phrases, rather than whole songs, are the basic building blocks of song production in Brown-throated Wrens.

In summary, our study provides the first comprehensive description of the vocal behavior of the Brown-throated

Wren. We show that this species has a non-fixed song repertoire, and that this species combines syllables to create phrases, using particular rules for syllable placement, creating highly complex songs. These findings are valuable additions to the variety of song organization strategies already known, but also provide a baseline for further comparisons with other *Troglodytes* wrens for a better understanding of their taxonomy and their behavioral biology.

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