

Vocal behaviour of the island-endemic Cozumel Wren (*Troglodytes aedon beani*): song structure, repertoires, and song sharing

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Abstract Documenting the diversity of vocal behaviour across different avian taxa is key to understanding the ecology and evolution of complex behaviours. Unique to Cozumel Island in the Mexican Caribbean Sea, the Cozumel Wren (*Troglodytes aedon beani*) provides an opportunity to investigate how isolation influences complex cultural traits. Most aspects of the biology, natural history, and taxonomy of Cozumel Wrens are unknown. In an attempt to better understand the Cozumel Wren's biology, we provide the first description of the songs and the vocal behaviour of this island-endemic bird. Based on more than 700 h of recordings, including more than 36,000 songs, we describe the fine structural characteristics of male Cozumel Wrens songs, and explore patterns of repertoire organization and song sharing. Cozumel Wrens sing songs composed of highly variable syllables, with prominent trills at the end of each song. Each bird has a limited repertoire of songs, which they create by recombining a restricted number of syllable and trill types. They repeat a song type several times before switching to a different one, with some variation in the number of times they repeat specific elements. Cozumel Wrens share more song types with neighbours than distant individuals. Syllable sharing, however, is equivalent between neighbours and distant individuals. Our results provide important data for future research on the ecology, evolution, and behaviour of this

island-endemic songbird, and for helping to clarify the taxonomic status of Cozumel Wrens.

Keywords Cozumel Wren · Song repertoire · Song sharing · Syllable repertoire · *Troglodytes* · Vocal behaviour

Zusammenfassung

Stimmverhalten des inselendemischen Cozumelzaunkönigs (*Troglodytes aedon beani*): Gesangsstruktur, Lautrepertoires und Strophenverteilung

Die Dokumentation der Diversität des Stimmverhaltens über verschiedene Vogeltaxa hinweg spielt eine Schlüsselrolle beim Verständnis von Ökologie und Evolution komplexer Verhaltensweisen. Der Cozumelzaunkönig (*Troglodytes aedon beani*) kommt nur auf der Insel Cozumel in der Mexikanischen Karibik vor und bietet somit eine Gelegenheit zu untersuchen, inwieweit Isolation komplexe kulturelle Merkmale beeinflusst. Die meisten Aspekte der Biologie, der Naturgeschichte und der Taxonomie des Cozumelzaunkönigs sind noch unbekannt. Für ein besseres Verständnis der Biologie des Cozumelzaunkönigs stellen wir hier die erste Beschreibung der Gesänge und des Lautverhaltens dieser inselendemischen Vogelart vor. Auf der Grundlage von über 700 Stunden Aufnahmematerial, darunter mehr als 36.000 Gesänge, beschreiben wir die Feinstruktur der Gesänge männlicher Cozumelzaunkönige und untersuchen die Muster von Repertoireaufbau und Strophenverteilung innerhalb der Population. Die Gesänge der Cozumelzaunkönige bestehen aus hochgradig variablen Silben, und jeder Gesang endet in einem markanten Triller. Jeder Vogel hat ein limitiertes Gesangsrepertoire, das durch die Kombination einer

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begrenzten Anzahl von Silben- und Trillertypen gebildet wird. Ein Strophentyp wird mehrmals wiederholt, bevor zu einem anderen gewechselt wird; dabei variiert die Anzahl der Wiederholungen spezifischer Elemente. Cozumelzaunkönige haben mehr Strophentypen mit ihren Nachbarn gemeinsam als mit weiter entfernten Individuen. Allerdings haben Nachbarn ähnlich viele Gesangselemente gemeinsam wie weiter voneinander entfernt lebende Individuen. Unsere Ergebnisse liefern wichtige Daten für die weitere Erforschung von Ökologie, Evolution und Verhalten dieses inselendemischen Singvogels und können zur Klärung des taxonomischen Status des Cozumelzaunkönigs beitragen.

Introduction

The diversity in vocal behaviour across the songbirds provides a rich source of material for biologists interested in the ecology and evolution of complex cultural traits (Catchpole and Slater 2008). To understand variation in these complex characters, it is necessary to document and describe the vocal behaviour and song structure for each species (e.g. Mann et al. 2009). Quantitative research on avian vocal behaviour also helps to inform taxonomists, conservation biologists, and wildlife managers interested in characterizing and protecting biodiversity, particularly in the tropics, where biodiversity is poorly surveyed and under increasing anthropogenic threat (Kroodsma et al. 1996; Tubaro 1999).

In this study, we analyze the vocal behaviour of Cozumel Wrens (*Troglodytes aedon beani*). These small, active birds are restricted to Cozumel Island in the Caribbean Sea

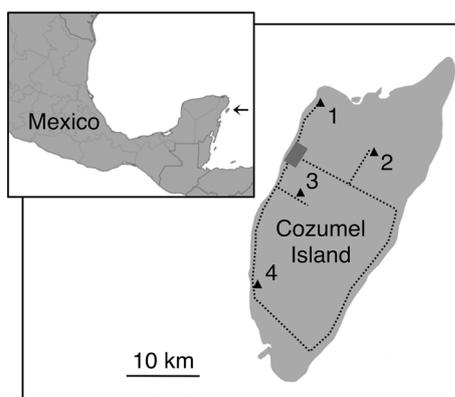


Fig. 1 Map of Cozumel Island, Mexico, with four triangles showing the locations where recordings of Cozumel Wrens were collected during this two-year field study: 1 north of San Miguel de Cozumel, 2 6 km north of kilometre 5.5 of Carretera Transversal, 3 Pueblo Fantasma, and 4 near the southwestern edge of the island. Map at upper left shows the location of Cozumel Island, 18 km off the eastern coast of the Yucatan Peninsula

off the northeastern coast of the Yucatan Peninsula in Mexico (Fig. 1). Cozumel Wrens are common in the forest habitat on this island, wherever there are cavities suitable for nesting (Sosa-López, pers. obs.), and they adapt well to low-density human settlement (Brewer 2001; Kroodsman and Brewer 2005). Despite their restricted distribution, they do not hold a threatened status (Brewer 2001; Kroodsman and Brewer 2005). The isolated, island-endemic status of Cozumel Wrens makes them an interesting subject for studying vocal behaviour.

Animals that live on islands often express different traits compared to their mainland counterparts (Mirsky 1976; Baptista and Johnson 1982; Catchpole and Komdeur 1993; Päckert and Martens 2004; Baker 2006; Baker et al. 2006). For the complex songs of birds, this is manifest in multiple ways, where island-living birds sometimes exhibit patterns that contrast with mainland-living species. Some island populations have songs with a simple and highly variable structure (e.g. *Certhia familiaris*, Baptista and Johnson 1982); some have unusually small repertoire sizes (e.g. *Meliphaga virescens*, Baker 1996); some have large repertoire sizes and sing novel songs unknown on the mainland (e.g. *Gerygone fusca*, Baker et al. 2003); and others have songs with simpler structures, but with larger repertoires (e.g. *Acrocephalus sechellensis*, Catchpole and Komdeur 1993). Due to the complex vocalizations of the wrens—a group that exhibits some of the most complex voices of any organism on Earth (Van Horne 1995; Mann et al. 2006, 2009)—research on island-living wrens provides an intriguing opportunity to understand how isolation influences complex cultural traits.

Most aspects of the biology of Cozumel Wrens, including their vocal behaviour, are undescribed. A few anecdotal descriptions of their vocalizations exist. Some authors suggest that Cozumel Wren songs are similar to Northern House Wren and Southern House Wren songs, but “fuller” or “richer”, and without trills (Howell and Webb 1995; Brewer 2001; Kroodsman and Brewer 2005). The lack of behavioural data is not restricted to Cozumel Wrens; among the ten recognized species in the genus *Troglodytes* in North and South America (American Ornithologists’ Union 1998; Banks et al. 2006; Chesser et al. 2010; Remsen et al. 2013), quantitative descriptions exist for only Northern House Wrens (*T. aedon*) and Pacific Wrens (*T. pacificus*; Platt and Ficken 1987; Van Horne 1995). The dearth of quantitative studies of *Troglodytes* vocal behaviour may be due to their elaborate songs (Platt and Ficken 1987; Kroodsma 1980; Van Horne 1995). For example, male Northern House Wrens attach different introductory notes to songs, presenting challenges to attempts to classify song types (Platt and Ficken 1987; Johnson 1998), while Pacific Wrens create new song types continuously, so estimating an exact song repertoire size is

very difficult (Van Horne 1995). Thus, it is unclear whether *Troglodytes* wrens have fixed song repertoires, or whether they use a repertoire of syllables to create their variable and complex songs, or whether both types of repertoire are evident in different species.

Like their songs, the taxonomy of Cozumel Wrens is enigmatic. Cozumel Wrens are thought to belong to a group known as the House Wren complex, together with Northern House Wrens (*T. aedon*), Southern House Wrens (*T. a. musculus*), Brown-throated Wrens (*T. a. brunneicollis*), and wrens restricted to Lesser Antilles islands (American Ornithologists' Union 1998). Cozumel Wrens share morphological similarities with Southern House Wrens (the taxon understood to be their closest mainland relative), but there are marked differences in size and colour: Cozumel Wrens are larger and their plumage is lighter in colour (Howell and Webb 1995; Navarro-Sigüenza and Peterson 2004). These morphological differences have raised questions regarding whether Cozumel Wrens should be considered full species (Howell and Webb 1995; Stotz et al. 1996; Navarro-Sigüenza and Peterson 2004). The lack of behavioural and genetic data limits our ability to answer these questions. Thus, a detailed study of the Cozumel Wren's song structure and vocal behaviour can inform their taxonomic classification.

Our study is the first to provide a detailed bioacoustic analysis of the song and vocal behaviour of Cozumel Wrens. Based on 2 years of field research, we describe the fine structural characteristics of Cozumel Wren songs. We estimate both song repertoire size and syllable repertoire size, and we assess repertoire sharing among neighbours, testing whether geographic distance is related to song and syllable sharing.

Methods

Study area

Cozumel Island is located in the Mexican Caribbean Sea, 18 km off the northeastern coast of the Yucatan Peninsula (Fig. 1). The island is 53 km long and 16 km wide, covering an area of approximately 470 km². The terrain is flat, with an average elevation of 5 m above sea level and a highest peak of 15 m (Muckelbauer 1990). The vegetation is dominated by tropical semi-deciduous forest, low tropical deciduous forest, mangroves, and coastal dune vegetation (Romero-Nájera et al. 2007).

Field techniques

We recorded and observed Cozumel Wrens from May 19 to 31, 2010, and from May 17 to 31, 2011. Both recording

periods fell during the breeding season, and wrens were actively singing and engaged in reproductive activities throughout both field expeditions. In total, we followed the vocal behaviour of 23 males: 9 males recorded only in 2010, 12 males recorded only in 2011, and 2 males recorded in both 2010 and 2011. We recorded wrens at four locations on the island (Fig. 1): (1) one bird north of the "San Miguel de Cozumel" (20°32'N, 86°55'W; recorded in 2010); (2) two birds 6 km north of kilometre 5.5 of "Carretera Transversal" (20°30'N, 86°51'W; recorded in 2011); (3) 18 birds at "Pueblo Fantasma" (20°27'N, 86°57'W; recorded in 2010 and 2011); and (4) two birds near the southwestern edge of the island (20°18'N, 86°58'W; recorded in 2010).

To distinguish individuals, we caught birds using mist nets and banded them with a unique combination of coloured leg bands. We assigned sex by inspecting the cloacal protuberance or brood patch. We banded 16 birds: 14 males and two females. Of the 14 banded males, at least 5 were paired: 1 was observed with an unbanded partner who was incubating eggs, and he was observed bringing food to the nest, helping to clean the nest, and later attending to fledglings; a second male was also observed with a partner (a banded female) who was incubating eggs, and this male was also observed bringing food to the nest; a third male was observed with a partner (a banded female) and fledglings; the two remaining males were observed affiliating with an unbanded partner. Our observations of the banded males confirmed that they remained within their territories for the duration of our field study, and were even found in the same territory between years (all three of the banded males that were present in 2010 and 2011 occupied the same territory in both years). Therefore, we distinguished the unbanded birds based on their territory position. Our observations of the unbanded males confirmed that at least two of those males were paired: one was observed with a partner and fledglings, and the other was observed affiliating with a partner. In summary, of the 23 males included in this study, we are certain that 7 were paired, and 4 of these males were observed to have a nest or to have fledglings. We were not able to determine the pairing status or breeding stage of the remaining males due to the challenges of observing birds through the thick vegetation at the study site, but we suspect that all birds were paired and at similar stages of breeding.

Sound recording

To ensure rigorous sampling of repertoires of songs, and to guarantee a high number of recording hours in the field, we used two complementary recording techniques. First, we collected focal recordings where a recordist followed the male around his territory between 0500 and 1100 hours and

between 1500 and 1700 hours (CST), identifying the bird by its colour bands whenever possible. We followed one or two birds per day. Focal recordings were collected using three sets of equipment: (1) a Marantz PDM660 digital recorder (WAV format; 44.1 kHz; 16 bits) with a Sennheiser MHK67 shotgun microphone; (2) a Marantz PMD660 digital recorder (WAV format; 44.1 kHz; 16 bits) with a Telinga parabola and a Sennheiser ME62/K6 omnidirectional microphone; or (3) a Nagra Ares-BB+ digital recorder (WAV format; 48 kHz; 16 bits) with a Telinga parabola and a Stereo Pro 6 Telinga microphone.

Second, we recorded birds using autonomous digital recorders, which allowed us to collect a long, continuous recording in each bird's territory from 0400 to 2000 hours. These autonomous recordings minimized any disturbance to the birds' behaviour caused by the presence of the human recordist, and generated longer periods of recordings to facilitate thorough calculations of repertoire size and quantitative descriptions of diel variation in vocal behaviour. These recordings were collected using song meters (Wildlife Acoustics; model SM1 and SM2; WAV format; 44.1 kHz; 16 bits; see details in Mennill et al. 2012). One autonomous recorder was placed in the area where the male spent most of the time singing during a preceding focal recording. Our behavioural observations of Cozumel Wrens, and other *Troglodytes* species, confirmed that these wrens are territorial and that territories are well defined, with little or no overlap between them. Therefore, we are confident that our autonomous recordings reliably sampled the targeted individuals.

We collected recordings in every male's territory for an average recording period of 4.5 ± 0.6 days (here, and

hereafter, values are shown as the mean \pm SE), with a range of 1–11 days. Altogether, we collected a total of 700.5 h of recordings (22.5 h of focal recordings plus 678 h of autonomous recordings) with an average of 30.4 ± 6.9 h per territory (range 0.1–96.7 h). Within these recordings, we sampled a total of 36,271 songs ($1,577 \pm 424.2$ per male; range 6–7,943; $n = 23$).

Definitions

Following Catchpole and Slater (2008), we defined a “syllable” as the basic unit in Cozumel Wren songs; each syllable can be composed of one to several “elements”, which we defined as a distinct continuous tracing on a sound spectrogram. We defined a “trill” as a section of the song composed of a series of the same syllable repeated three or more times. We defined a “song” as a long, complex vocalization containing a series of syllables with no silent gaps of ≥ 1 s (silent gaps within songs were always much smaller). We defined “song repertoire size” as the total number of unique song types recorded from each bird. We defined “syllable repertoire size” as the total number of unique syllable types and trill types recorded by each bird.

Song and syllable classification

Songs of Cozumel Wrens are composed of two sections. The introductory section is composed of a variety of low-amplitude and broadband noisy, nasal, harmonic, or tonal sounds; the terminal section is composed of a variety of mostly tonal sounds, and typically begins with the first trill

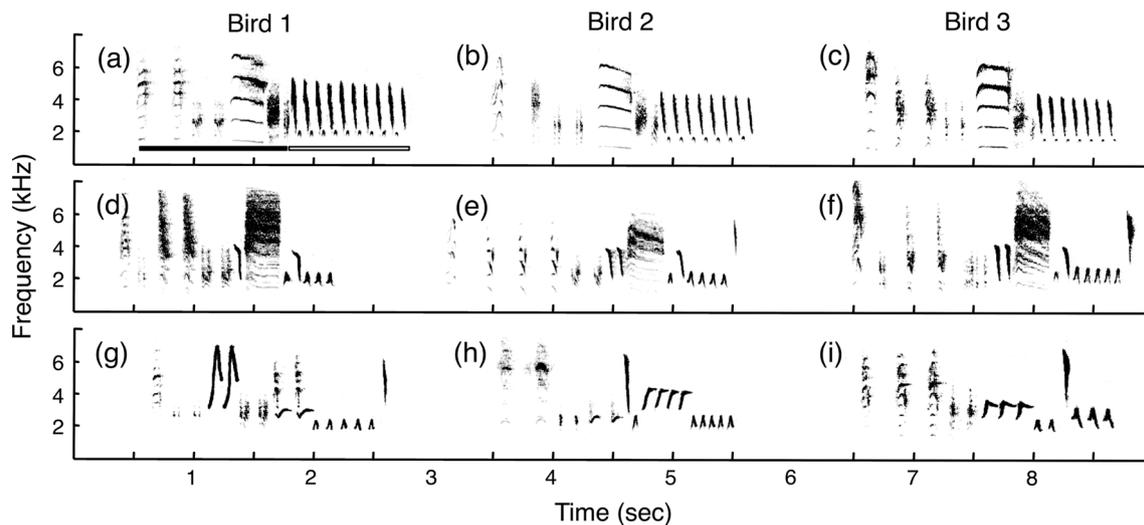
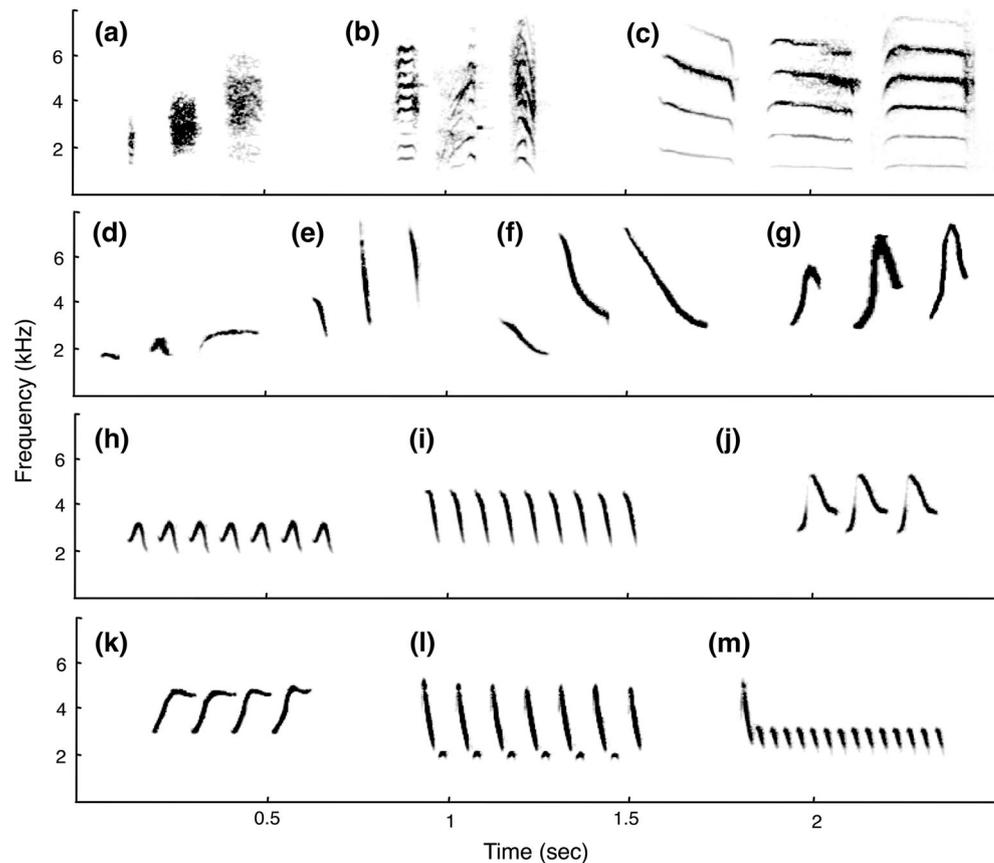


Fig. 2a–g Sound spectrograms showing three songs for each of three male Cozumel Wrens. Each column shows a subset of the repertoire for three different males (three songs per male). Songs are arranged to show song types that are shared in common between the three males

in examples a–c and d–f, whereas non-matched songs are shown for g–i. For song a, the solid bar shows the introductory section of the song, and the open bar shows the terminal, trilled section of the song

Fig. 3a–m Catalogue of sound spectrograms showing examples of the different syllable and trill types produced by male Cozumel Wrens: **a** waah syllables, **b** snarl syllables, **c** mew syllables, **d–g** frequency-modulated tonal syllables, and **h–m** trills. The spectrograms depict three examples for each syllable type and one example for each trill type



in the song (Fig. 2). After scrutinizing all of the songs recorded, we classified seven types of syllables and six types of trills (Fig. 3). We classified three categories of broadband and nasal sounds: waah syllables were variable, broadband noisy sounds (Fig. 3a); snarl syllables were nasal sounds with narrowly spaced harmonic stacks that were less than 0.2 s in length (Fig. 3b); and mew syllables were sounds with widely spaced harmonic stacks that were longer than 0.2 s (Fig. 3c).

Frequency-modulated tonal syllables were sounds depicted in the spectrogram as a clear and continuous line with no overtones (Fig. 3d–g). We classified four different categories of tonal syllables: frequency modulated syllables with frequencies below 4 kHz, which were quite variable (Fig. 3d); short downslurred syllables with a wide bandwidth and a length shorter than 0.1 s (Fig. 3e); slower downslurred syllables that were longer than 0.1 s (Fig. 3f); and upslurred syllables with a frequency modulation occurring at the highest point (Fig. 3g).

We classified six different trills based on the shape and sound of the syllables, regardless of the number of times that the syllable was repeated (Fig. 3h–m): trills with relatively narrowband chevron-shaped syllables below 4 kHz (Fig. 3h); trills with quick downslurred syllables (Fig. 3i); trills with broadband upslurred syllables ending in a

chevron shape (Fig. 3j); trills with upslurred syllables that reached a plateau at the end of each syllable (Fig. 3k); trills with double elements made up of downslurred broadband syllables alternated with short low elements (e.g. Fig. 3l); and trills with downslurred syllables below 4 kHz, where sometimes the first syllable was longer and of higher frequency (Fig. 3m). In some instances, wrens added 1–3 extra syllables to the end of a trill, as shown in Fig. 2e, f, but we still considered these to be the same trill type. Series of repeated waah, snarl or mew syllables were rare and were not considered trills.

We classified songs as being of the same type if they shared the same mew and tonal syllables in the introductory section and the same trill type in the terminal section, as well as the order of the syllables and trills (Fig. 2). We used these three song components (mew syllables, tonal syllables, and trills) to define similar songs because they are relatively stereotyped, they are a prominent feature of the songs, and they are found across birds. We did not include frequency-modulated syllables below 4 kHz when classifying song types, because these syllables showed high variability (e.g. Fig. 3d). When songs had the same mew, tonal, and trill syllables, but included additional different syllables, we considered them to belong to the same song type (e.g. Fig. 2d–f).

Repertoire size assessment

To assess song repertoire size, we annotated all of our recordings in Syrinx-PC (J. Burt, Seattle, WA, USA) using the time and frequency cursors to highlight every recorded song in our focal and automated recordings. Each new song was added to a digital catalogue, where we noted the identity of the singing bird and the song type. We followed the same procedure to assess syllable repertoire by highlighting each syllable and trill in each song. Each new category of syllable or trill was given a unique number and added to a digital catalogue, where we noted the identity of the singing bird and the syllable type or trill type. We annotated syllables and trills using the catalogue of song types obtained in the song repertoire analysis. These analyses were carried out using spectrograms with a 512-point fast Fourier transform (FFT) and a Blackman window.

We tested whether our sampling of Cozumel Wren song repertoires was exhaustive by plotting the number of changes in song type recorded against the total number of song types detected (i.e. song type changes were counted chronologically from the start to the end of an individual's recording). Similarly, we tested whether our sampling of syllable and trill repertoires was exhaustive by plotting the number of song types recorded against the total number of syllable and trill types detected (Baker 1996; Catchpole and Slater 2008).

Song and syllable sharing

In many bird species with repertoires, males share some of their songs, or song subcomponents, with neighbours (e.g. Vehrencamp 1999). We assessed the proportion of songs, as well as syllables and trills, shared between pairs of males by calculating a sharing coefficient (McGregor and Krebs 1982; Vehrencamp 1999; Molles and Verhencamp 1999). We calculated both song sharing indices and syllable/trill sharing indices as $S = 2Ns/(R1 + R2)$, where Ns is the number of shared songs or syllables and trills, and $R1 + R2$ is the total repertoire size of the two males. A value of $S = 0$ indicates that two males share no songs or syllables/trills, and a value of $S = 1$ indicates that all songs or syllables/trills are shared by both individuals.

We tested whether song and syllable/trill sharing indices varied with geographic distance by conducting Mantel tests. Mantel tests were performed using 10,000 permutations in the Passage 2 software package (Rosenberg and Anderson 2011). The geographic distance matrix was calculated using the coordinates at the approximate center of every male's territory, based on handheld GPS data collected during focal recordings in the field. We calculated the pairwise distances between the territories of every pair

of males using the Geographic Distance Matrix Generator V.1.2.3 software package (American Museum of Natural History, Chicago, IL, USA).

Song structure

We quantified the fine structural characteristics of Cozumel Wren songs in terms of frequency, time, and syllable and trill types. For this analysis, we randomly selected up to five single exemplars of different song types from each male's catalogue. In total, we measured 86 songs from 23 males for this analysis (3.9 ± 0.26 song types per male). Each song was saved into a separate sound file with at least 0.5 s of silence at the beginning and the end of the song. Then, we filtered the sound files with a 1-kHz high-pass filter and normalized songs to a peak amplitude of -1 dB using the Audition software package (Adobe Systems, San Jose, CA, USA). We then created a spectrogram for every song using a 1024-point FFT, 93.75 % overlap, a Blackman window, 22 Hz frequency resolution, and 2.9 ms temporal resolution in SASLab Pro (version 5.2.04; Avisoft; R. Sprecht, Berlin, Germany). We quantified a total of seven fine structural variables for each song: (1) song length (in s); (2) minimum frequency (in Hz); (3) maximum frequency (in Hz); (4) bandwidth (in Hz); (5) total number of syllables in the song; (6) number of unique syllable types; and (7) number of trills. Measurements were performed using the automatic parameter measurement feature in Avisoft-SasLab Pro, with a threshold setting of -20 dB and a hold time of 10 ms. Automatic detection always identified the start and the end of a trill, but it could not always distinguish the first syllables of the introductory section due their low amplitude. In these cases, we selected the onset of the introductory section manually, by looking at the first syllables on the spectrogram. We calculated an average value for all structural measurements for each male.

Results

Song structure

Cozumel Wren songs are composed of two sections, an introductory section with diverse types of syllables that start at a low amplitude and crescendo, and a terminal section with a trill (Fig. 2). Songs had an average length of 1.6 ± 0.04 s (range 1.3–2.0, $n = 23$), a minimum frequency of $1,650.5 \pm 56.1$ Hz (range: 1,090–2,133), a maximum frequency of $6,704 \pm 117$ Hz (range 5,643–7,793), and a bandwidth of $4,050 \pm 187$ Hz (range 2,998–6,350). Songs had 14.1 ± 0.4 syllables and trills (range 10.6–18.5) with 3.9 ± 0.1 different syllable types

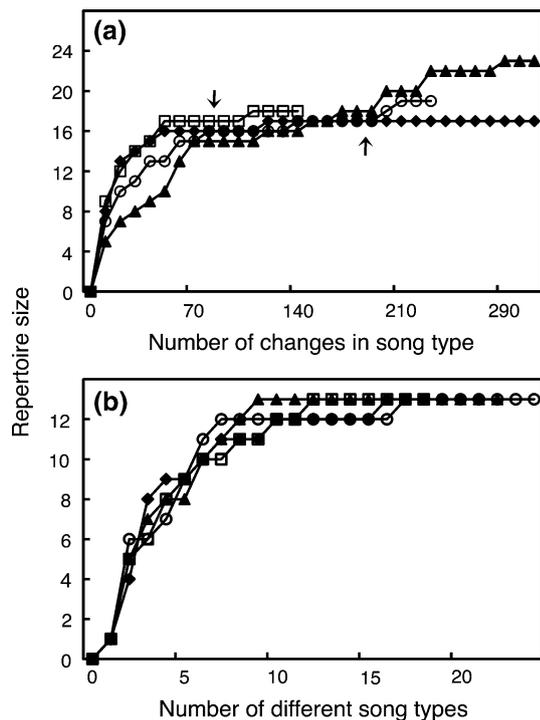


Fig. 4 Repertoire asymptote curves for **a** song types and **b** syllable and trill types of Cozumel Wrens. For both songs types and syllable and trill types, Cozumel Wrens have a fixed repertoire size given sufficient sampling. Examples of asymptotic curves are shown for four birds. Asymptotic curves with *filled symbols* correspond to two birds recorded in 2010 only. Asymptotic curves with *open symbols* show data for birds recorded in both years of the study; *arrows* indicate changes between years for those birds recorded in 2010 and 2011

(range 3.0–5.2) and 1.2 ± 0.06 different trill types (range 0–3) per song. During 28 days of field research over 2 years, and based on more than 22.5 h of focal recordings, we only recorded males singing; we only observed female Cozumel Wrens producing calls, not songs.

Song and syllable repertoire size

Cozumel Wrens repeat the same song type many times before switching to a new song type. However, when repeating the same song type, males alter the number of times they repeat specific syllables that constitute the song type, suggesting that Cozumel Wrens sing with a pattern that is intermediate between “eventual” and “immediate” variety. Inspection of the repertoire asymptotic curves for song types showed that 10 of the 23 Cozumel Wrens recorded reached the asymptotic line (all 10 were recorded in Pueblo Fantasma; Fig. 4a). Using data from birds that reached the asymptotic curve, we found a total of 50 different song types among all individuals analyzed. Individually, birds had an average repertoire size of 18.7 ± 0.6 song types (range 15–23; $n = 10$). For the remaining

males, we recorded between 2 and 16 song types and none reached an asymptote. The total number of songs analyzed for males that reached the asymptote was on average 3,302.3 (range 1,240–7,943), and the number of songs analyzed for males that did not reach the asymptote was 249.8 (range 6–671).

We found that Cozumel Wrens had an average syllable and trill repertoire of 12.8 ± 0.1 (range 12–13, $n = 10$; Fig. 4b). All birds had waah, snarl, and mew syllables in their repertoires. On average, the birds had a repertoire of 3.9 ± 0.1 tonal syllables (range 3–4, $n = 10$) and 5.9 ± 0.1 trill types (range 5–6, $n = 10$). Most waah, snarl, mew, and tonal syllables occurred in the introductory sections of songs, although tonal syllables also occurred in the terminal sections of songs, sometimes between trills and at the end of the song (Fig. 2).

Repertoire comparison between years

There were two Cozumel Wrens recorded in both 2010 and 2011. We found only subtle differences in song repertoire size between years. The song repertoire sizes for the two birds in 2010 and 2011 were 19 and 12 song types (bird TAB 03), and 17 and 14 song types (bird TAB 05), respectively. When both 2010 and 2011 data were plotted together, the song repertoire sizes were 20 and 18 song types, respectively (Fig. 4a). Both of the birds recorded had the same pool of syllable and trill types in both years. The asymptote lines for the song repertoire and the syllable and trill repertoire showed similar patterns when both years were computed either separately or together, and in both cases the males reached an asymptotic curve (Fig. 4). In 2011, the birds repeated 57.8 % (i.e. 11 of 19 song types for TAB 03) and 76.4 % (i.e. 13 of 17 song types for TAB 05) of the song types that were recorded in 2010.

Song and syllable sharing

We evaluated sharing between eight males recorded in 2011 for which we were confident that we had recorded most of their repertoires based on their asymptote curves. The distance between the centers of the territories of the tested males was, on average, 600.1 ± 124.3 m (range 102.8–1,388.6 m; $n = 8$). These wrens shared, on average, 60 % of their song repertoires (song sharing index 0.6 ± 0.03 ; range 0.4–0.7; see examples in the top two rows of Fig. 2) and 90 % of their syllable and trill repertoires (syllable/trill sharing index 0.9 ± 0.01 ; range 0.8–1). Mantel tests revealed a significant relationship between song-type sharing and geographic distance ($r = -0.3$; one tailed $P = 0.03$; $n = 8$). Conversely, the syllable and trill sharing index showed no pattern with geographic distance ($r = -0.1$; one tailed $P = 0.1$).

Discussion

Cozumel Wrens sing complex songs that are a conspicuous component of the soundscape of Cozumel Island, Mexico. Males sing the same song type many times before switching to a new song type, subtly varying the number of times they repeat specific elements during successive repeats of the same song type. Songs are composed of four different categories of syllables with a prominent trill near the end of the song. Cozumel Wren males have fixed repertoires of songs, and of syllables and trills. They create their songs by combining a restricted number of syllable and trill types that are shared among most individuals in the population. Song-type sharing between males decreases with distance, whereas syllable and trill sharing between males is consistently high, even for non-neighbours.

Cozumel Wrens sing, on average, 18 song types, and song type repertoires are finite and quantifiable. Every song type comprises, on average, 4 different syllable types and 1 trill type from a repertoire of approximately 13 syllable and trill types. These song characteristics are similar to those of mainland Northern House Wrens, where a restricted number of song types are built based on a restricted number of syllable types (Platt and Ficken 1987). Anecdotal evidence from our observations of two birds recorded in two consecutive years supports the idea of fixed repertoires of songs, syllables, and trills; in 2011, these birds used the same pool of syllable and trill types and most of the song types recorded in 2010, showing little change between years. During song bouts, Cozumel Wren males sing the same song type many times before switching to a new song type. During successive renditions of the same song type, however, males alter the number of times they repeat specific elements that constitute the song type, suggesting that Cozumel Wrens sing with a style that is somewhat intermediate between “eventual” and “immediate” variety. This style of song, which adds versatility to song bouts, is a behaviour observed previously in Northern House Wrens (Platt and Ficken 1987).

Interestingly, given the number of syllables and trills in a Cozumel Wren’s repertoire, it would be possible for these birds to build a larger song repertoire than they actually manifest. We found that the Cozumel Wrens have a restricted number of discrete songs that are stereotyped in syllable and trill composition and length. It is possible that the occurrence of songs that are stereotyped in both syllable and trill composition and length arises due to the use of syntactic rules where syllable and trill types are produced in non-random order. Such a pattern has been seen in other bird species (e.g. Leger 2005; Wright and Dahlin 2007; Ivanitskii et al. 2012). We are not aware of any study conclusively demonstrating the use of syntactic rules in members of the family Troglodytidae. However, previous

studies confirm that some compositional rules are important in wren song (Van Horne 1995; Holland et al. 2000; Camacho-Schlenker et al. 2011). This is an important area for further investigation.

Stereotyped songs and high degrees of sharing can arise due to learning and imitating strategies (Kroodsma 2004). Our results show that Cozumel Wrens combine syllables to create song types that are shared only at a local level. Local song sharing is known to occur when birds copy the details of songs from their parents and neighbouring adults, a behaviour known as imitative learning (Kroodsma et al. 2002; Kroodsma 2004). Our results that reveal high local sharing of song types are consistent with the idea of imitative learning in Cozumel Wrens. Furthermore, it is thought that one of the consequences of imitative learning is the formation of dialects (Kroodsma 2004). Dialects—groups of nearby animals that share more acoustic similarity to each other than to different groups—have been shown to occur in several songbird species, including some members of the Troglodytidae family (Verner 1975; Morton 1987; Węgrzyn and Leniowski 2010; Camacho-Schlenker et al. 2011).

We found that syllable and trill types of the Cozumel Wren are widespread across Cozumel Island. A common library of syllables and trills are used to build songs that vary geographically around the island. Similar patterns have been reported in Swamp Sparrows (*Melospiza georgiana*, Marler and Pickert 1984) and Indigo and Lazuli Buntings (*Passerina cyanea* and *P. amoena*; Baker and Boylan 1995). Baker and Boylan (1995) suggest that syllables could be the fundamental unit of cultural evolution in species where syllables are widely distributed among populations and are stable in their acoustic traits across generations. Further research across space and time in Cozumel Wrens could help us to understand the relationship between songs and syllables, and their significance in the evolution of cultural traits.

Several prior investigations have reported differences in vocal behaviour between island and mainland bird populations (e.g. Baker 2006; Baker et al. 2006; Aleixandre et al. 2013; Potvin 2013). Our observations suggest that there are also significant vocal differences between Cozumel Wrens and continental populations of Northern and Southern House Wrens (Sosa-López and Mennill, unpublished data). Several bioacoustic studies on members of the family Troglodytidae have shown that vocal characters are useful as taxonomic characters (e.g. *Hylorchilus navai* vs. *H. sumichrasti*, Gómez de Silva 1997; *Thryothorus nicefori* vs. *T. rufalbus*, Valderrama et al. 2007; *Troglodytes pacificus* vs. *T. hiemalis*, Toews and Irwin 2008, 2012; across the *Thryothorus* wrens, Mann et al. 2009; *Henicorhina l. leucophrys* vs. *H. l. hilaris*, Dingle et al. 2010); including the recent recognition of Cobb’s Wren (*T. cobbi*) as a full

species (Campagna et al. 2012; Remsen et al. 2013). A careful and detailed comparison performed across the geographic range of the House Wren complex is needed to improve the taxonomy of Cozumel Wrens.

What is the function of song in Cozumel Wrens? Prior observational and experimental studies of Northern House Wrens demonstrate that male song is important in both mate attraction and territory defence (Johnson and Kermott 1991; Johnson and Searcy 1996; Cramer 2013). Our observations of Cozumel Wrens suggest the same functions are at play. During the early morning, all males performed their singing activities from a single perch area, repeating their loud songs for an extended period; later in the morning, males moved around to produce song in punctuated bouts throughout their territory. We conducted playback experiments as part of a separate investigation, and found that territorial male Cozumel Wrens reacted aggressively when conspecific songs were played, approaching the loudspeaker and singing at a heightened rate (Sosa-López and Mennill, unpublished data). These patterns are consistent with a territorial function of Cozumel Wren song. In order to understand whether Cozumel Wren song also plays a role in mate attraction, future research should focus on male singing behaviour early in the breeding season, prior to pairing, and on the link between male song and female choice. We speculate that songs in Cozumel Wrens play a role in both mate attraction and territory defence, as is common in many other songbirds (Catchpole and Slater 2008).

Our study is the first to provide a detailed study of the vocal behaviour of Cozumel Wrens. They sing complex songs made up of variable syllables and trills. Each bird has a limited repertoire of stereotyped songs, which they create by recombining a restricted number of syllable and trill types. Our results provide behavioural information for ornithologists to better understand the relationship between Cozumel Wrens and other *Troglodytes* wrens. Our results also provide a foundation for future research on the ecology, evolution, and behaviour of Cozumel Wrens and island-living animals.

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