J Ornithol
DOI 10.1007/s10336-015-1237-y

ORIGINAL ARTICLE

Vocal behaviour of White-eared Ground-sparrows (*Melozone leucotis*) during the breeding season: repertoires, diel variation, behavioural contexts, and individual distinctiveness

Luis Sandoval[1,2] · Carolina Méndez[2] · Daniel J. Mennill[1]

Received: 7 March 2014 / Revised: 9 October 2014 / Accepted: 13 May 2015

Abstract There are relatively few quantitative descriptive studies of the vocalisations and vocal behaviour of tropical bird species, in spite of the tropic's rich avian biodiversity and the extensive variety of vocalisations produced by tropical birds. This lack of information inhibits our understanding of tropical animals, including our ability to perform comparative analyses on vocal behaviours from an evolutionary perspective. In this study, we present the first quantitative description of the vocal repertoire and daily vocal activity of White-eared Ground-sparrows (*Melozone leucotis*), using focal and autonomous recordings collected during two consecutive breeding seasons in Costa Rica. We classified vocalisations into categories based on their visual appearance on sound spectrograms to create a library of vocalisations for this species. We found that White-eared Ground-sparrows produce three main categories of vocalisations: solo songs, calls, and duets. Solo songs were produced only by males. Each male sang a repertoire of solo song types, which all shared the same general structure with short introductory notes, a frequency-modulated middle section, and a terminal trill. Both sexes produce calls and coordinated vocal duets. We quantified patterns of diel variation in each category of vocalisation, and found that the Ground-sparrows produced all three vocalisations at higher output at dawn (between 0500 and 0600 hours) compared to the rest of the day. This study allowed us to conduct the first comparisons of vocalisations between White-eared Ground-sparrows and North American species in the genus *Melozone*, and revealed both similarities and differences between the species groups. Our investigation also showed that vocalisations related to communication within pairs and to territory defence (calls and duets) exhibited lower levels of individual distinctiveness than vocalisations related mainly to female attraction (male solo songs). Our observations suggest that each of the three types of vocalisations have multiple functions in White-eared Ground-sparrows, revealing diverse communication functions with a small vocal repertoire in this tropical songbird.

Keywords Calls · Diel variation · Duets · Emberizidae · Songs · Tropics

Zusammenfassung

Gesangsverhalten von Weißohrammern (*Melozone leucotis*) während der Brutzeit: Repertoires, Tagesvariation, Verhaltenskontext und individuelle Charakteristik

Trotz des Vogelartenreichtums der Tropen und der großen Vielfalt an Lautäußerungen tropischer Vögel, gibt es verhältnismäßig wenige quantitativ-beschreibende Studien zu Vokalisation und Gesangsverhalten tropischer Vogelarten. Dieser Mangel an Informationen vermindert unser Verständnis tropischer Vögel, einschließlich der Fähigkeit, vergleichende Analysen zum Gesangsverhalten aus Sicht der Evolution durchzuführen. In dieser Studie präsentieren wir

---

Communicated by C. G. Guglielmo.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-015-1237-y) contains supplementary material, which is available to authorized users.

✉ Luis Sandoval
biosandoval@hotmail.com

[1] Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B3P4, Canada

[2] Laboratorio de Bioacústica Escuela de Biología, Universidad de Costa Rica, San Pedro, Montes de Oca, Costa Rica

erstmals eine quantitative Beschreibung des Stimmenrepertoires und der täglichen Gesangsaktivität von Weißohrammern (*Melozone leucotis*) mittels gezielter und unabhängiger Aufnahmen, die in zwei aufeinander folgenden Brutsaisons in Costa Rica gesammelt wurden. Wir teilten die Lautäußerungen in Kategorien ein, um auf Basis des Aussehens der Klangspektrogramme eine Sammlung der Lautäußerungen für diese Art anzulegen. Weißohrammern erzeugen drei Hauptkategorien von Lautäußerungen: Sologesang, Rufe und Duette. Sologesänge werden ausschließlich von Männchen erzeugt. Jedes Männchen sang ein Repertoire aus Sologesangstypen, die alle die gleiche Grundstruktur hatten mit kurzen Einleitungstönen, einem frequenzmoduliertem Mittelteil und einem abschließendem Triller. Beide Geschlechter erzeugen Rufe und aufeinander abgestimmte Stimmduette. Wir quantifizierten Muster in der täglichen Variation der einzelnen Lautäußerungskategorien. Dabei konnten wir feststellen, dass Grundammern in der Morgendämmerung (zwischen 5:00 und 6:00) eine höhere Gesangs- und Stimmäußerungsleistung erbringen im Vergleich zum Rest des Tages. Mit Hilfe dieser Studie können die ersten Vergleiche von Lautäußerungen zwischen Weißohrammern und anderen nordamerikanischen Arten der Gattung *Melozone* angestellt werden, um sowohl Gemeinsamkeiten als auch Unterschiede zwischen den Artengruppen aufzuzeigen. Unsere Untersuchungen zeigen auch, dass Lautäußerungen im Zusammenhang mit der Kommunikation zwischen Brutpartnern und zur Revierverteidigung (Rufe und Duette) ein geringeres Maß an individueller Charakteristik aufweisen, als solche, die vor allem der Weibchenanwerbung (Sologesänge der Männchen) dienen. Unsere Beobachtungen lassen erkennen, dass jeder der drei Lautäußerungstypen verschiedene Funktionen bei Weißohrammern hat, was wiederum darauf hin deutet, dass das kleine Stimmenrepertoire eines tropischen Singvogels diverse Kommunikationsfunktionen haben kann.

Introduction

A vocal repertoire is the complete library of vocalisations an individual or species can produce (Catchpole and Slater 2008). Oscines learn their vocalisations, and the result of this learning process is that each population or individual produces new vocal characters by learning, making mistakes, or improvising (Beecher and Brenowitz 2005). Oscines in the tropics exhibit several vocal behaviours that are rare or absent in the north temperate zone, including female solo songs (Langmore 1998; Beecher and Brenowitz 2005), duets (Hall 2004, 2009), and choruses (e.g. Baker 2004, 2009; Hale 2006).

The number of quantitative descriptive studies that have been conducted on the vocalisations of tropical birds is limited considering the impressive diversity of tropical bird species. Moreover, with the recent importance assigned to vocalisations as a tool for resolving taxonomic issues between closely related taxa (Price and Lanyon 2002; Stiles 2009; Cadena and Cuervo 2010; Millsap et al. 2011), studies of this type are becoming increasingly informative. Our restricted information on the vocal behaviour of birds also limits or delays the ability to perform comparative analyses on vocal behaviours that could enhance our understanding of taxonomic relationships (e.g. Price and Lanyon 2002; Cadena and Cuervo 2010) and facilitate better modeling of the evolution of diversity in tropical birds (Price et al. 2011). For example, if singing behaviour, repertoire size, and patterns of diel variation are consistent between individuals across a species distribution, this may reflect close genetic relationships (Price and Lanyon 2002; Cadena and Cuervo 2010).

In this study, we present the first quantitative description of the vocal repertoire, singing behaviour, and pattern of diel variation in White-eared Ground-sparrows (*Melozone leucotis*), a species found between 500 and 2000 m a.s.l., from Chiapas, Mexico, in the north, to Costa Rica's Central Valley in the south (Stiles and Skutch 1989; Howell and Webb 1995). Across their disjunct distribution, this Ground-sparrow inhabits thickets, secondary forest edges, and shaded coffee plantations (Stiles and Skutch 1989; Howell and Webb 1995; Sandoval and Mennill 2012). White-eared Ground-sparrow pairs use vocalisations to defend their territories throughout the year (Sandoval and Mennill 2012; Sandoval et al. 2013). They are one of seven recognized species in the genus *Melozone* (Chesser et al. 2010), and one of three species in the genus where our knowledge of vocal behaviour is restricted to brief and anecdotal descriptions (Stiles and Skutch 1989; Howell and Webb 1995; Sandoval and Mennill 2012; see Sandoval et al. 2014, for an exception). Historically, the *Melozone* genus included only three Mesoamerican species—Prevost's Ground-sparrow (*M. biarcuata*), Rusty-crowned Ground-sparrow (*M. kieneri*), and White-eared Ground-sparrow (*M. leucotis*)—but the taxonomy has recently been changed as a result of genetic studies (DaCosta et al. 2009; Chesser et al. 2010; Klicka et al. 2014). Four Towhee species formerly categorized as part of the *Pipilo* genus (Tweit and Finch 1994; Howell and Webb 1995; Johnson and Haight 1996; Benedict et al. 2011) are now classified as *Melozone*: Abert's Towhee (*M. aberti*), California Towhee (*M. crissalis*), Canyon Towhee (*M. fusca*), and White-throated Towhee (*M. albicollis*). All four of these species inhabit dense brush and understories as well as areas of semi-arid montane shrubland in Mexico and the southeastern United States (Tweit and Finch 1994; Howell and Webb 1995; Johnson and Haight 1996; Benedict et al. 2011). The three Mesoamerican Ground-sparrows inhabit mainly dense habitats such as thickets, young secondary forest, and the montane forests of shaded coffee plantations (Stiles and Skutch 1989; Howell and Webb 1995). In contrast with the more northerly species of *Melozone*, the natural history, behaviour, ecology and description of these three tropical *Melozone* species is limited to anecdotal descriptions (Stiles and Skutch 1989; Howell and Webb 1995; Rising 2011).

To expand our knowledge on the vocalisations of White-eared Ground-sparrows, we had five objectives in this paper: (1) to quantitatively describe their vocal repertoire; (2) to study the behavioural contexts in which different types of vocalisations are used; (3) to describe the pattern of diel variation in vocal output for each of these vocalisations; (4) to compare differences in vocal characteristics between territorial pairs; and (5) to analyse whether the solo types within a male's repertoire are delivered in a predictable or random order.

Methods

Recording techniques

We collected recordings from birds in four populations of colour-banded White-eared Ground-sparrows in Costa Rica: Monteverde, Puntarenas Province (10°18′N, 84°48′W; altitude 1600 m), North Heredia, Heredia Province (10°01′N, 84°05′W; elevation: 1200–1500 m), University of Costa Rica campus, San Jose Province (09°56′N, 84°05′W; elevation 1200 m), and Lankester Botanical Garden, Cartago Province (09°50′N, 83°53′W; altitude 1400 m). We used two recording techniques. First, we directly recorded vocalisations during two consecutive breeding seasons (from April to August 2011 and from March to July 2012) by following and continuously recording focal birds during a 1-h period, starting just before sunrise. These recordings were collected using a shotgun microphone (Sennheiser K6/ME66) and a digital recorder (Marantz PMD 661 or PMD 660; recording format: WAVE; sampling rate: 44.1 kHz; 16 bit accuracy). We recorded 50 different pairs with this approach: 20 pairs were recorded in 2011 on two occasions ($n = 14$) or three occasions ($n = 6$), and 45 pairs were recorded in 2012 on one occasion ($n = 43$) or two occasions ($n = 2$). From the 45 pairs recorded in 2012, 15 were also recorded in 2011. Whenever possible, we noted the sex of the singer, although the thick vegetation and secretive nature of the birds made sex identification challenging. Therefore, some of the comparisons between vocal characteristics were made between pairs and not between individuals.

To quantify the diel pattern of vocalisations produced by pairs of White-eared Ground-sparrows, we also recorded birds using autonomous digital recorders (Wildlife Acoustics' Song Meters; Wildlife Acoustics, Concord, MA, USA; recording format: WAVE; sampling rate: 44.1 kHz; accuracy: 16 bits). Each recorder was positioned in the centre of a pair's territory, to minimize the chance of recording neighbouring birds. Comparison of the vocal repertoires collected during focal recordings confirmed that our autonomous recordings sampled the intended birds, because we found the same song types as in our focal recordings. We collected autonomous recordings from 0450 hours (10 min before sunrise) until 1800 hours. We recorded 3 pairs for 5 days and 12 pairs for 2 days during 2011 for the analysis of diel variation.

Vocal measurements

Vocalisations were classified visually according to their appearance on sound spectrograms in Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, NY, USA) following an approach similar to that used by Franco and Slabbekoorn (2009). The vocal repertoire we recorded fit neatly into distinctions of calls, solo songs, and duets. We defined calls as short-duration vocalisations (duration ≤ 1 s) produced by both members of the pair (Fig. 1); solo songs as vocalisations produced solely by males (duration >1 s) and with 2 or more element types (Fig. 2); and duets as vocalisations produced by both members of the pair (duration >1 s) involving the production of several elements that overlapped in time and frequency (Fig. 3). Contrary to the majority of duetting species that have been studied in detail (Hall 2004), White-eared Ground-sparrows duets are made up of vocalisations that are markedly different from their solo songs (Fig. 3), a pattern that appears to hold true across other *Melozone* and *Aimophila* species (e.g. Collins 1999; Benedict and McEntee 2009; Sandoval and Mennill 2014). Occasionally, the vocalisation that birds produce during duets was given by a lone

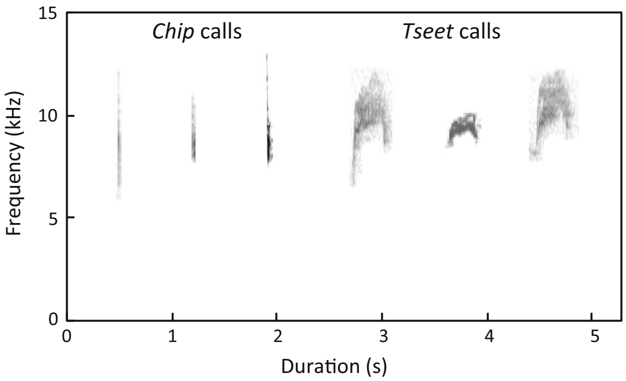

Fig. 1 Sound spectrogram showing three examples of the two call types, *chip* and *tseet*, produced by both sexes of White-eared Ground-sparrows (*Melozone leucotis*). Spectrograms were generated with a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz

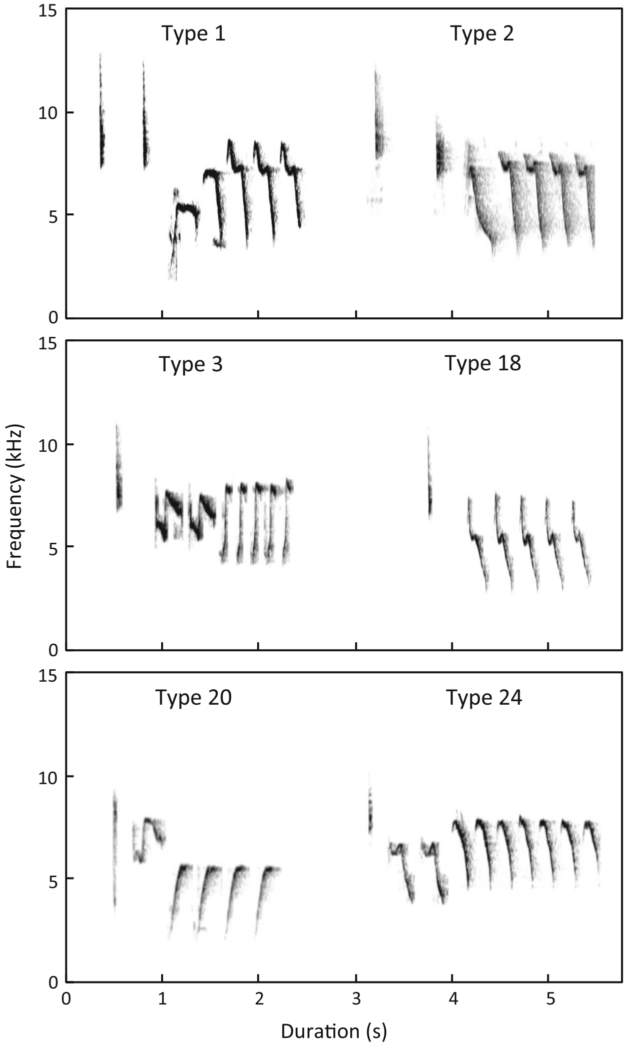

Fig. 2 Sound spectrograms showing six common male solo song types recorded from White-eared Ground-sparrows at four study sites in Costa Rica. Spectrograms were generated with a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz

individual and the partner did not respond; we refer to these vocalisations as "incomplete duets".

The recordings used to produce the spectrograms in Figs. 1, 2 and 3 are available from the Animal Sound Archive at the Museum für Naturkunde Berlin (http://www.animalsoundarchive.org; see Electronic Supplementary Material).

We extracted vocalisations from our recordings and measured the following spectro-temporal details: duration (s), minimum frequency (Hz), maximum frequency (Hz), and frequency of maximum amplitude (Hz). We collected measurements using multiple visualisations of each vocalisation, including the spectrogram (to identify sounds), the power spectrum (to measure frequency features), and the waveform (to measure temporal features) in Raven Pro 1.4. Spectrograms were constructed using a Hann window with 50 % overlap and 256 Hz transform size, resulting in a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz. We conducted these measurements only on vocalisations with high signal-to-noise ratio and without overlap by other sounds.

We annotated the total number of unique song types produced by each male, to estimate each male's song repertoire, using all recordings for each individual. Song types were classified visually according to the number of different solo song elements and their appearance on spectrograms. Solo songs that showed only subtle variation in the number of elements in the first part or final part of solo songs were classified as the same song type, as in Sandoval et al. (2014). We estimated song repertoire sizes using a curve-fitting method by applying the equation proposed by Wildenthal (1965). The estimation was conducted in Excel 2007 on individuals with ≥80 recorded songs recorded during the focal and autonomous recordings combined.

We analysed diel variation in vocal output by annotating the number of each type of vocalisation recorded from 0450 to 1800 hours from the autonomous recorders. Birds typically produced their first vocalisation of the day around 0500 hours, although occasionally just prior to 0500 hours, as early as 0450 hours. We grouped the vocalisations from 0450 to 0500 hours with the vocalisations produced from 0500 to 0600 hours for this analysis. All other vocalisations were grouped into 1-h intervals from 0600 to 1800 hours.

Statistical analyses

We tested whether calls and duets showed distinctiveness between pairs using a discriminant function analysis (DFA). Rather than focusing on individuals for this analysis, we focused on pairs, because the dense habitat of our study animals meant it was difficult or impossible to observe the birds as they vocalised, making it very difficult to distinguish the male from female in a pair. In this analysis, we used the four spectro-temporal measurements as response variables, and pair identity as the independent variable. The accuracy of classification by pair was estimated using a Jackknife cross-validation method, using the software Systat (v.11.00.01; SYSTAT Software, Chicago, IL, USA). We conducted this analysis separately for the two types of calls that we found in our recordings (see "Results") and for complete duets. We used a binomial test to analyse the probability that the classification accuracy of the DFA is higher than the classification expected by chance (one divided by the number of pairs included in each DFA). We evaluated whether the fine structural details of complete and incomplete duets differed from

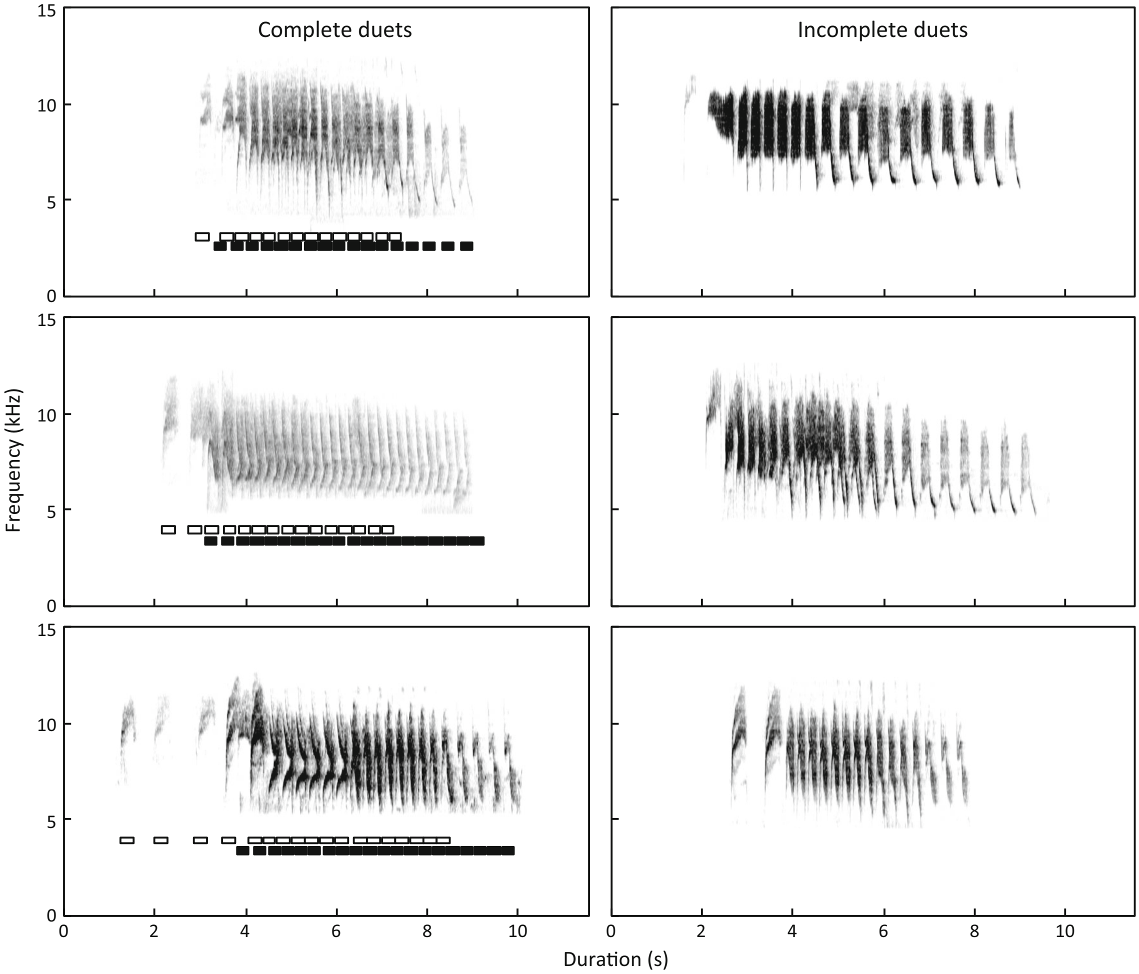

Fig. 3 Sound spectrograms showing three examples of complete duets (produced jointly by the male and female of the pair) and three incomplete duets (duet contributions produced by a single individual with no response from the partner) of White-eared Ground-sparrows. *Black* and *grey lines* under complete duets represent the contribution of each individual to the duet. Spectrograms were generated with a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz

each other using a paired *t* test, using $n = 38$ pairs where we recorded both duet types.

Since the number of elements inside each solo song type showed subtle variation, we conducted a Levene's test to compare the consistency in the number of elements in each male solo song type. For this analysis, we divided male solo songs into three components (see "Results"). Given that the number of elements in each solo song component varied according to the song type, using the raw data in this analysis would artificially increase the variation between song types. To control for this variation, we first estimated the average variance of each song component per song type; we then used the average value per song component as our response variable in the test, and song type as the independent variable.

We assessed whether males delivered song types in a predictable or random order using a Markov chain analysis as in Lemon and Chatfield (1971). This method allowed us to analyse the probability that each song type was sung in a random order (no preferred transition between songs types; Leonardo and Konishi 1999). This test reports a single value for each male; however, since we were interested in patterns across the population, we conducted two extra tests. First, we conducted multiple regression analysis to demonstrate that the results of our Markov chain analysis were not influenced by differences in the total number of songs recorded and the repertoire size of each male. In this analysis, we included the number of song types recorded and the total number of recorded songs as independent variables, and the probability of singing in a random order (as calculated for each male with the Markov chain approach) as the response variable. Given that some males produce their song types in a predictable order and others in random order (see "Results"), we conducted a binomial test to evaluate which type of singing behaviour occurred more often in the population.

To analyse diel variation in vocal behaviour, we count the total number of vocalisations per hour per individual from 0500 to 1800 hours. Then, we tested for variation in the hourly occurrence of each category of vocalisation throughout the day using linear mixed-models. In this analysis, the fixed factor was the hour of the day. The response variables were the total number of each vocalisation category produced per hour per individual. Finally, we used subject identity as a random factor to control for multiple values for the same subject.

All descriptive statistics are reported as mean ± SE. We conducted linear mixed-models in JMP (v.7.0; SAS Institute, Cary, NC, USA), the Markov chain test in PAST (v.2.14; Øyvind Hammer, Natural History Museum, University of Oslo, Norway), and the rest of the tests in Systat.

Results

Calls

White-eared Ground-sparrows produced two types of call. The first type of call, which we refer to as the "*chip*" call, is a single, short-duration, high-frequency, broadband note (Fig. 1). The second type of call, which we refer to as the "*tseet*" call, is a single narrow-bandwidth note that gradually ascends or descends (Fig. 1). Both types of calls were produced by males and females, and varied in the frequency of production (114.10 ± 15.03 *chip* calls per hour per pair; 8.72 ± 1.44 *tseet* calls per hour per pair based on 1.84 ± 0.15 h focal recordings of 49 pairs).

On average, the duration of the *chip* call was 0.08 ± 0.003 s (range = 0.06–0.09 s, CV = 25.4 %), with a minimum frequency of 7326 ± 62 Hz (range = 6833–8184 Hz, CV = 5.9 %), a maximum frequency of 12,345 ± 109 Hz (range = 10,189–13,314 Hz, CV = 6.1 %), and a frequency of maximum amplitude of 8315 ± 77 Hz (range = 7475–8892 Hz, CV = 6.5 %). We observed the Ground-sparrows using this vocalisation in two main contexts: as a contact call when foraging, and when they were excited after a potential predator was close to the nest or chicks.

On average, the duration of the *tseet* call was 0.28 ± 0.013 s (range = 0.16–0.40 s, CV = 27.6 %), with a minimum frequency of 8356 ± 107 Hz (range = 6833–9111 Hz, CV = 7.9 %), a maximum frequency of 10,520 ± 109 Hz (range = 9273–11,537 Hz, CV = 6.4 %), and a frequency of maximum amplitude of 9305 ± 91 Hz (range = 7755–10,565 Hz, CV = 6.0 %). We observed the Ground-sparrows using this vocalisation in two main contexts: before starting a duet, and when both individuals where far away from each other.

Both call types showed a low level of pair distinctiveness based on the pair that produced the vocalisation. In a discriminant analysis with cross-validation, *chip* calls (Wilks' $\lambda = 0.35$, $F_{192,36697} = 57.0$, $P < 0.001$) were correctly classified to the pair that produced the call 18 % of the time, significantly higher than the 2.08 % expected by chance (binomial test: $P < 0.001$; in comparison to chance expectation of 1 divided by 48 pairs included in the analysis). Similarly, *tseet* calls (Wilks' $\lambda = 0.24$, $F_{148,2611} = 7.5$, $P < 0.001$) were correctly classified to the pair that produced the call 32 % of the time, significantly higher than the 2.63 % expected by chance (binomial test: $P < 0.001$; in comparison to chance expectation of 1 divided by 38 pairs included in the analysis).

Solo Songs

Male solo songs were variable and readily classifiable into distinct song types (Fig. 2). We detected 33 unique song types in our sample of 3133 analysed songs (Fig. 2). Most male solo songs had three sections: (1) songs began with high frequency elements similar to *chip* calls; (2) the middle section of songs contained frequency-modulated elements; and (3) songs concluded with a short trill. Of the 33 song types we detected, there were two song types that lacked a frequency-modulated middle section (Fig. 2). Among song types, we found substantial variation in the number of song elements in the terminal trill section ($\sigma^2 = 11.90$), with less variation in the number of elements in the middle section ($\sigma^2 = 0.26$), and finally the least variable number of elements in the introductory section ($\sigma^2 = 0.01$; Levene's test: $F = 6.5$, $P = 0.003$). Solo songs showed an average duration of 1.9 ± 0.1 s (range = 0.6–3.1 s, CV = 16.4 %), a minimum frequency of 3535 ± 124 Hz (range = 1595–5769 Hz, coefficient of variation: CV = 20.2 %), a maximum frequency of 11,209 ± 161 Hz (range = 6220–13,801 Hz, CV = 8.3 %), a frequency of maximum amplitude of 5956 ± 106 Hz (range = 2498–9216 Hz, CV = 10.2 %).

The solo song repertoire size of White-eared Ground-sparrows, calculated on the basis of 19 males where we recorded 80 or more songs, varied from two to eight song types (3.5 ± 0.3 songs; e.g. Fig. 4). For most males, the repertoire asymptote was reach before the 40th song recorded, with the exception of two individuals, one male that reached an asymptote after 154 songs (not illustrated), and one male that failed to reach an asymptote even after recording 160 songs (Fig. 4). A significant majority of White-eared Ground sparrow males delivered their songs with immediate variety (binomial test: $P = 0.02$), with 24 males delivering their songs in a random order and 14 males in a predictable order (test of random order based on Markov chain approach). These results were not influenced

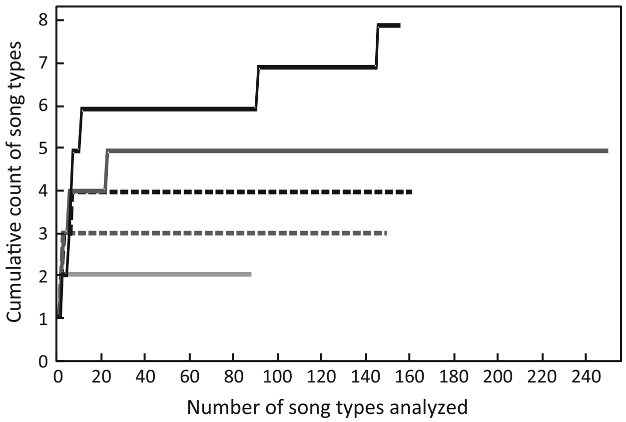

Fig. 4 Repertoire asymptote curves for White-eared Ground-sparrows, showing four males that reached an asymptote and one that did not. These five males were chosen to show the full range of variation in our dataset; the remaining 14 males had repertoire asymptote curves that were largely overlapped by the curves shown

by the repertoire size or the total number of songs recorded for each male (multiple regression: $F_{2,35} = 3.0$, $P = 0.064$, $r^2 = 0.15$).

Over 2 years of field study, we never detected a female producing solo songs. We cannot, however, rule out the possibility of female song entirely, because the secretive birds were often very difficult to observe through the thick vegetation.

Duets

Pairs of White-eared Ground-sparrows produced a third type of vocalisation that was given chiefly as coordinated vocal duets (Fig. 3). Unlike some other tropical birds (e.g. Mann et al. 2003; Mennill and Vehrencamp 2005; Logue 2006), the vocalisations that birds contributed to duets were acoustically and structurally distinct from the vocalisations used by males as solo songs (Figs. 2, 3). Based on our observations of colour-banded pairs, both sexes were able to create duets (i.e. respond to their partner's song, turning it from an incomplete duet into a duet). From a total of 812 recordings of this vocalisation obtained during the focal recording sessions, we found that this vocalisation was produced as a duet 71.68 % of the time, and the remaining as a vocalisation by just one individual of the pair, i.e. an "incomplete duet" (Fig. 3). We observed birds producing duets in two contexts: when one member of the pair approached the other inside their territory, and when the pair respond to the vocalisations produced by birds in a neighbouring territory.

Duets started with a series of one to six elements introductory elements (2.31 ± 0.13 elements) with longer inter-element intervals than the main duet elements (Fig. 3). Introductory duet elements varied from arc-shaped to a slight upward slope on the spectrogram (Fig. 3). The main elements in duets were the elements that overlapped between both individuals of the pair. They were broadband and noisy elements (Fig. 3). The vocalisations of the two individuals overlapped for 3.64 ± 0.22 s, on average. Duets were produced by the second individual overlapping the first one in both frequency and time (i.e. polyphonal duets; Fig. 3). The second bird concluded its song an average 1.57 ± 0.17 s after the first bird. Complete duets showed a low level of pair distinctiveness, with just 11 % of correct classification of duets based on the pair that produced the vocalisation (Wilks' $\lambda = 0.26$, $F_{188,2121} = 4.5$, $P < 0.001$), significantly higher than the 2 % expected by chance (binomial test: $P = 0.01$; in comparison to chance expectation of 1 divided by 48 pairs included in the analysis).

Complete duets were longer than incomplete duets (paired t test: $t = 6.44$, $df = 37$, $P < 0.001$; Table 1). Complete duets showed higher minimum frequencies than incomplete duets ($t = -3.77$, $df = 37$, $P = 0.001$; Table 1). Complete and incomplete duets showed similar values of maximum frequency ($t = 0.29$, $df = 37$, $P = 0.78$; Table 1), and frequency of maximum amplitude ($t = 0.25$, $df = 37$, $P = 0.81$; Table 1).

Diel variation

White-eared Ground-sparrow vocal output varied through the day, with the highest output between 0500 and

Table 1 Duration and frequency measurements for complete and incomplete duets of White-eared Ground-sparrow (*Melozone leucotis*) pairs

Measurement	Complete duets			Incomplete duets		
	Mean ± SE	Range	CV (%)	Mean ± SE	Range	CV (%)
Duration (s)	5.77 ± 0.20	3.79–8.42	24.0	4.33 ± 0.24	1.85–8.75	33.4
Minimum frequency (Hz)	5093 ± 14	3940–6046	14.4	5205 ± 142	3792–6409	16.8
Maximum frequency (Hz)	11,547 ± 80	10,405–12,605	4.8	11,385 ± 100	10,608–12,615	5.4
Frequency of maximum amplitude (Hz)	7444 ± 169	6202–8829	15.7	7609 ± 188	4565–8807	15.2

CV coefficient of variation

0600 hours (LMM: $F_{12,156} = 9.5$, $P < 0.001$; Fig. 5). We observed the same pattern of vocal output for calls ($F_{12,156} = 3.0$, $P < 0.001$; Fig. 5), solo songs ($F_{12,144} = 13.7$, $P < 0.001$; Fig. 5), and duets ($F_{12,156} = 30.8$, $P < 0.001$; Fig. 5). In the case of solo songs, we observed that males produced an overwhelming majority of their daily vocal output at the start of the day; males sang between the 82 and 93 % of all songs in the first hour of the day (Fig. 5). This effect was less pronounced in the other two types of vocalisation: only 18–31 % of calls and 33–39 % of duets were produced during the first hour of the day (Fig. 5). White-eared Ground-sparrows vocalised during all daylight hours, with lowest output around noon (Fig. 5). Songs were the first vocalisations produced in the day, with an average start time of 0505 hours ± 2.3 min, follow by calls at 0508 hours ± 0.9 min, and finally by duets at 0514 hours ± 3.4 min.

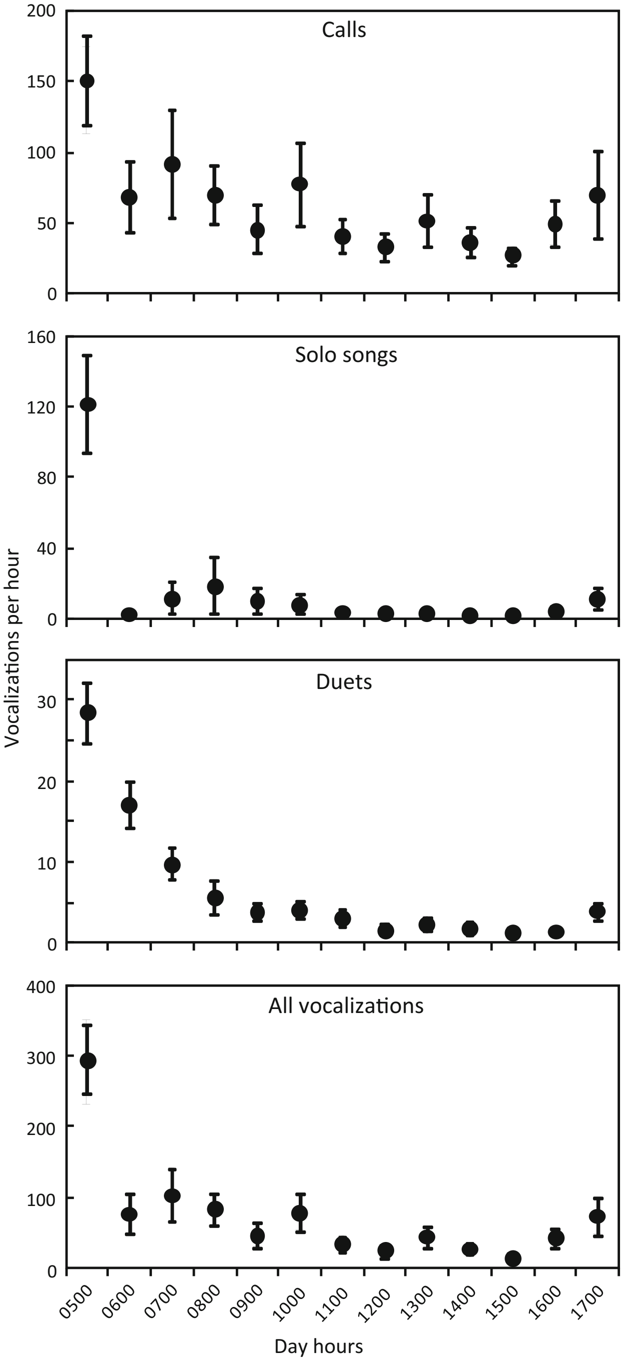

Fig. 5 Diel pattern of variation in vocal output for White-eared Ground-sparrows. *Dots* show means and the *whiskers* standard errors for $n = 15$ pairs recorded over a 507-h period. vocalisations between 0450 and 0500 hours were included in the 0500–0600 hours period

Discussion

White-eared Ground-sparrows produce three main categories of vocalisations: two types of calls, male solo songs, and duets. Our analyses, based on 2 years of focal and autonomous recordings from four populations in Costa Rica, substantiates previous anecdotal descriptions of vocalisations in this species, which report the occurrence of three main categories of vocalisations (Stiles and Skutch 1989; Howell and Webb 1995; Sandoval et al. 2014). Our analyses allowed us to observe similarities and differences between vocalisations and between pairs. Calls and duets were very similar in acoustic structure between pairs, whereas solo song types were highly variable in spite of their consistent structure (introductory section, frequency-modulated middle section, and terminal trill section). We quantified the pattern of diel variation of each vocalisation type during the breeding season, and found that all three vocalisation types were produced at higher levels at the start of the day (0450 to 0600 hours) compared to the rest of the day.

Our bioacoustics analyses reveal, for the first time, that White-eared Ground-sparrows produce two distinct types of calls. Both call types were highly different in acoustic and temporal structure but were used in similar contexts. The *chip* call and *tseet* call were used as a pair contact signal when the birds foraged or moved separately inside the territory. We also observed that *chip* calls were used as alarm signals when a potential predator was close (observed predators included pygmy owls, dogs, and snakes; birds behaved similarly when humans were close to the nest), or as a response to alarm calls by the bird's breeding partner. In the predation context, *chip* calls were produced at a higher rate than in a contact context. These two main contexts of White-eared Ground-sparrow calls have been reported as general functions of calls in several bird species (reviewed by Marler 2004). The dual function of *chip* call also occurs in other species, including Chaffinches (*Fringilla coelebs*; Marler 1956) and Steller's Jays (*Cyanocitta stelleri*; Hope 1980), in which they vary the production rate or the duty cycle. The function of the differences in call rate in this Ground-sparrow is still unknown, and, therefore, future research is needed.

The acoustic structure of *chip* call, with short duration and broad bandwidth, should make this vocalisation easy to localise (Marler 2004), which supports the idea that this call serves as a contact or alarm call function. In the case of a contact signal, considering that visual communication is highly limited—even at close distances—within the dense vegetation of the territories of these Ground-sparrows (Hale 2006; Sandoval and Barrantes 2012), the production of this call type will allow both individuals of the pair to know the location of the other. In the case of an alarm signal, considering that the main predators inside thickets are stationary predators (e.g. small mammals, lizards, snakes, and avian ambush predators), this type of vocalisation will be advantageous because it may communicate the position of the threat. The acoustic structure of the *tseet* call may transmit better inside dense vegetation of thicket habitats due to the longer call duration and the narrower bandwidth than the *chip* call, characteristics that are known to favour sound transmission in dense vegetation (Morton 1975; Wiley 1991; Bradbury and Vehrencamp 2011). Therefore, White-eared Ground-sparrows may benefit from using the *tseet* call to communicate at larger distances between pair individuals than using the *chip* call. Due to the acoustic characteristics of the *tseet* call, it may be more difficult to localise the position of the signaller.

Solo songs were the most variable vocalisation we recorded from White-eared Ground-sparrows, with spectrotemporal details that varied between songs from the same male. Songs were easily classified into distinct types, which males produced with eventual variety. A total of 94 % (31 of 33 song types) of all recorded songs showed the same structure of three types of elements (introductory notes, frequency-modulated middle part, and terminal trill). The song structure of White-eared Ground-sparrows shares much similarity with that of Prevost's Ground-sparrows (Sandoval et al. 2013), but substantial differences from that of congeneric Abert's, California, and Canyon Towhees; the latter three species produce solo songs composed of a single element repeated several times (Tweit and Finch 1994; Johnson and Haight 1996; Benedict et al. 2011). The song structure reported for three other closely related species—Rusty-crowned Ground-sparrow, Rusty Sparrow (*Aimophila rufescens*), and the non-trilled songs of Rufous-crowned Sparrow (*A. ruficeps*)—show intermediate characteristics between the two species groups, which all have solo songs composed of repetition of different trill elements (Wolf 1977; Collins 1999, Sandoval and Mennill 2012). These differences may reflect genetic divergence (DaCosta et al. 2009; Klicka et al. 2014), given that more closely related species exhibit more similar song structure. Alternatively, the differences in songs may reflect acoustic adaptation to different habitats, because the northern towhee species within *Melozone* and the two *Aimophila* species occupy more open habitats where fast repetition of trill elements may provide an acoustic advantage (Morton 1975; Handford and Lougheed 1991; Wiley 1991; Naguib 2003). Based on the number of solo song types sung by each White-eared Ground-sparrow male, this species has a small repertoire, according to the classification proposed by Garamszegi et al. (2005). However, one individual of the Canyon Towhee showed a repertoire of five song types (Marler and Isaac 1960), and ten individuals of the Rusty-crowned Ground-sparrow showed repertoires that varied from four to ten song types (Sandoval 2014; Sandoval and Mennill 2014), indicating that small solo song repertoires may be the rule for the genus *Melozone*.

We found that White-eared Ground-sparrows have a unique vocalisation, completely distinct in acoustic structure from male solo songs, used chiefly for duetting. This pattern has also been documented in all other *Melozone* species (Tweit and Finch 1994; Johnson and Haight 1996; Benedict et al. 2011; Sandoval et al. 2013; Sandoval and Mennill 2014), and also in two *Aimophila* species (Wolf 1977; Collins 1999), the Zapata Sparrow (*Torreornis inexpectata*, Morton and Gonzales Alonso 1982), and the Large-footed Finch (*Pezopetes capitalis*, Sandoval et al. 2013; Trejos-Araya and Barrantes 2014). The acoustic structure of duets bears a similarity to the duets of other species in the genus, especially with the duets of Prevost's Ground-sparrows (Sandoval et al. 2013), and to a lesser degree, the duets of California Towhees (Benedict and McEntee 2009; Benedict 2010). As in these congeners, White-eared Ground-sparrow duets start with introductory elements with a narrower bandwidth and are followed by noisier elements with broad bandwidths. In the case of California Towhees, duets have a single and clear frequency-modulated element between the introductory and noisy elements that is not found in White-eared or Prevost's Ground-sparrow duets (Benedict and McEntee 2009; Sandoval et al. 2013).

White-eared Ground-sparrow duets were created by both sexes responding to their partner's duet vocalisation. But, in some cases, one individual failed to respond to the other, producing incomplete duets, which seemed to occur more often when both pair individuals were far apart from each other, based on our field observations. The frequency and time overlap within duets is similar to the duets of the California Towhee (Benedict and McEntee 2009) and the Rusty-crowned Ground-sparrow (Sandoval and Mennill 2014), the only other species with a detailed description of this vocal behaviour. We observed duets being produced in two contexts. The first observed context was when a bird approached its breeding partner. This behaviour is consistent with the maintaining contact hypothesis which states that pair individuals create a duet to indicate their location, and the signalling commitment hypothesis which states that pair individuals create a duet to indicate the commitment between them (Hall 2004). This pattern has been quantified in two other duetting species, the Rufous-and-white Wren (*Thryophilus rufalbus*; Mennill and Vehrencamp 2008) and the Black-bellied Wren (*Pheugopedius fasciatoventris*; Logue 2007). The second context was when pairs responded to the duets of neighbouring pairs. This behaviour is consistent with the joint territorial defence hypothesis, which states that territorial pairs respond aggressively to vocalisations of neighbours or individual conspecific strangers (Hall 2004, 2009). Playback studies in White-eared Ground-sparrows reinforce this function for duets, because it was the most common vocalisation produced by territorial pairs as a response to simulated territory intrusions (Sandoval et al. 2013).

Our analyses showed that calls and duets were very similar between pairs of White-eared Ground-sparrows. This result may indicate that these vocalisations do not serve to communicate pair identity (or individual identity). However, in the case of calls, it is possible that our methods inflated the variation, reducing the probabilities of finding differences between pairs, since we grouped the calls produced by both sexes of the pair as the same unit of comparison. A more detailed study that distinguishes the individuals that produce each call would be necessary to discard the possibility that sex-differences in calls or duet contributions might obscure individually-distinctive differences in these vocalisations. Our results on low levels of individual distinctiveness in calls and duet contributions stand in contrast to the reported results for male solo songs in this Ground-sparrow, which show that males have high individual distinctiveness based on both acoustic and structural characteristics (Sandoval et al. 2014).

White-eared Ground-sparrows show a dramatic dawn chorus performance, where the overwhelming majority of vocalisations occur at the start of the day (i.e. 0450–0600 hours). High output of solo songs and duets early in the morning may contribute to territory defence against possible territorial intrusions, as has been suggested previously for other bird species (Staicer et al. 1996; Amrhein and Erne 2006; Koloff and Mennill 2013). The three types of vocalisation showed differences in their pattern of diel variation, and this is probably related to the functions of each vocalisation. Calls and duets were produced at similar levels after the first hour, which reinforces the proposed function for both vocalisations. Behaviours associated with pair contact during foraging, displacement inside the territory, and individual approaches are not expected to have a peak during the day; therefore, we expected a parallel output for calls and duets throughout the day.

Males produced more than 88 % of the song output at the start of the day, before males and females started to conduct their usual pair behaviours (e.g. foraging and joint territory defence). Based on preliminary observations we have collected outside the breeding season, males apparently only sing during the breeding season, and song is routinely produced across all breeding stages (Sandoval et al. 2014). This singing behaviour in White-eared Ground-sparrows is similar to the behaviour displayed by seasonal breeding bird species in the temperate forest, where the main function of the song is mate attraction during the reproductive season (Collins 2004; Catchpole and Slater 2008). Males of this Ground-sparrow species, however, live in pairs year round (Sandoval and Mennill 2012), and may mate with the same female during several consecutive years (personal observation), reducing the probability that male solo song is used to attract a pair each year. Our observations suggest that males may sing to attract neighbouring females for extra-pair copulations, as occurs in other bird species that continue producing a dawn chorus performance after pair formation (Gibbs et al. 1990; Richardson and Burke 2001; Mennill et al. 2004). A detailed study that evaluates the occurrence of extra pair copulations would be necessary to evaluate this assumption about the solo song output function in this species.

Quantitative descriptions of the vocalisations and vocal behaviours of birds are necessary to perform comparative studies to understand the evolution of vocalisation types in closely related species. For example, this study on White-eared Ground-sparrows allowed us to conduct comparisons in term of vocalisations with the North American species in the genus *Melozone*, and revealed similarities and differences between this species and its congeners. All described vocalisations showed multiple functions in this species, revealing that even with a small vocal repertoire it is possible to conduct several communication functions. Our study also showed that vocalisations that appear to be related to within-pair communication and territory defence (calls and duets) were more similar between pairs (i.e. had lower pair distinctiveness) than those reported between males singing solo songs (a vocalisation more related with female attraction; Sandoval et al. 2014). This study will facilitate future experimental analyses of the function of each vocalisation, and will help to have a broader understanding of the vocal diversity among Neotropical birds and its functions.

Acknowledgments We thank the Estación Biológica Monteverde, Lankester Botanical Garden, and Bosquesito Leonel Oviedo from Universidad de Costa Rica for logistical support and access to reserves. LS was supported by scholarships and grants from the Ministerio de Ciencia y Tecnología (MICIT) and the Consejo Nacional para Investigaciones Científicas y Tecnológicas (CONICIT) of Costa Rica, the Government of Ontario, and the University of

Windsor. Additional funding was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation (CFI), the Government of Ontario, and the University of Windsor to DJM. This investigation was conducted under the permit 071-2011-SINAC of Ministerio de Ambiente Energía y Telecomunicaciones and the Sistema Nacional de Áreas de Conservación of Costa Rica. None of the authors have a conflict of interest to declare.

References

Amrhein V, Erne N (2006) Dawn singing reflects past territorial challenges in the Winter Wren. Anim Behav 71:1075–1080

Baker MC (2004) The chorus song of cooperatively breeding laughing Kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): characterization and comparison among groups. Ethology 110:21–35

Baker MC (2009) Information content in chorus songs of the group-living Australian Magpie (Cracticus tibicen dorsalis) in Western Australia. Ethology 115:227–238

Beecher MD, Brenowitz EA (2005) Functional aspects of song learning in songbirds. Trends Ecol Evol 20:143–149

Benedict L (2010) California Towhee vocal duets are multi-functional signals for multiple receivers. Behaviour 147:953–978

Benedict L, McEntee JP (2009) Context, structural variability and distinctiveness of California towhee (*Pipilo crissalis*) vocal duets. Ethology 115:77–86

Benedict L, Kunzmann MR, Ellison K, Purcell KL, Johnson RR, Haight LT (2011) California Towhee (*Melozone crissalis*), In: Poole A (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca. Accessed 20 Oct 2013

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer, Sunderland

Cadena CD, Cuervo AM (2010) Molecules, ecology, morphology, and songs in concert: how many species is *Arremon torquatus* (Aves: Emberizidae)? Biol J Linn Soc 99:152–176

Catchpole CK, Slater PJR (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge

Chesser RT, Banks RC, Barker FK, Cicero C, Dunn JL, Kratter AW, Lovette IJ, Rasmussen PC, Remsen JV Jr, Rising JD, Stotz DF, Winker K (2010) Fifty-first supplement to the American Ornithologists' Union check-list of North American birds. Auk 127:726–744

Collins PW (1999) Rufous-crowned sparrow (*Aimophila ruficeps*). In: Poole A, Gill F (eds) The birds of North America. Birds of North America, Philadelphia, p 472

Collins S (2004) Vocal fighting and flirting: the functions of birdsongs. In: Marler P, Slabbekoorn H (eds) Naturés music, the science of bird song. Elsevier, San Diego, pp 39–79

DaCosta JM, Spellman GM, Escalante P, Klicka J (2009) A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. J Avian Biol 40:206–216

Franco P, Slabbekoorn H (2009) Repertoire size and composition in great tits: a flexibility test using playbacks. Anim Behav 77:261–269

Garamszegi LZ, Balsby TJ, Bell BD, Borowiec M, Byers BE, Draganoiu T, Eens M, Forstemeier W, Galeotti P, Gil D, Gorissen L, Hansen P, Lampe HM, Leitner S, Lontkowski J, Nagle L, Nemeth E, Pinxten R, Rossi JM, Saino N, Tanvez A, Titus R, Török J, Van Duyse E, Møller AP (2005) Estimating the complexity of bird song by using capture-recapture approaches from community ecology. Behav Ecol Sociobiol 57:305–317

Gibbs HL, Weatherhead PJ, Boag PT, White BN, Tabak LM, Hoysak DJ (1990) Realized reproductive success of polygynous Red-winged Blackbirds revealed by DNA markers. Science 250:1394–1397

Hale A (2006) Group living in the black-breasted wood-quail and the use of playbacks as a survey technique. Condor 108:107–119

Hall ML (2004) A review of the hypotheses for the functions of avian duetting. Behav Ecol Sociobiol 55:415–430

Hall ML (2009) A review of vocal duetting in birds. Adv Study Behav 40:67–121

Handford P, Lougheed SC (1991) Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. Condor 93:644–658

Hope S (1980) Call form in relation to function in the Steller's jay. Am Nat 116:788–820

Howell SNG, Webb S (1995) A guide to the birds of Mexico and northern Central America. Oxford University Press, New York

Johnson RR, Haight LT (1996) Canyon Towhee (*Melozone fuscus*). In: Poole A (ed) The birds of north America online. Cornell Lab of Ornithology, Ithaca. Accessed 20 Oct 2013

Klicka J, Barker FK, Burns KJ, Lanyon SM, Lovette IJ, Chaves JA, Bryson RW Jr (2014) A comprehensive multilocus assessment of sparrow (Aves: Passerellidae) relationships. Mol Phylogenet Evol 77:177–182

Koloff J, Mennill DJ (2013) Vocal behaviour of Barred Antshrikes, a Neotropical duetting suboscine bird. J Ornithol 154:51–61

Langmore NE (1998) Functions of duet and solo songs of female birds. Trends Ecol Evol 13:136–140

Lemon RE, Chatfield C (1971) Organization of song in cardinals. Anim Behav 19:1–17

Leonardo A, Konishi M (1999) Decrystallization of adult birdsong by perturbation of auditory feedback. Nature 399:466–470

Logue DM (2006) The duet code of the female black-bellied wren. Condor 108:326–335

Logue DM (2007) Duetting in space: a radio-telemetry study of the black-bellied wren. Proc R Soc Lond B 274:3005–3010

Mann NI, Marshall-Ball L, Slater PJB (2003) The complex song duet of the plain wren. Condor 105:672–682

Marler P (1956) The voice of the chaffinch and its function as a language. Ibis 98:231–261

Marler P, Isaac D (1960) Song variation in a population of brown towhees. Condor 62:272–283

Marler P (2004) Bird calls: a cornucopia from communication. In: Marler P, Slabbekoorn H (eds) Naturés music, the science of bird song. Elsevier, San Diego, pp 132–177

Mennill DJ, Vehrencamp SL (2005) Sex differences in the singing and duetting behavior of neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). Auk 122:175–186

Mennill DJ, Vehrencamp SL (2008) Context-dependent functions of avian duets revealed through microphone array recordings and multi-speaker playback. Curr Biol 18:1314–1319

Mennill DJ, Ramsay SM, Boag PT, Ratcliffe LM (2004) Patterns of extrapair mating in relation to male dominance status and female nest placement in Black-capped Chickadees. Behav Ecol 15:757–765

Millsap BA, Seipke SH, Clark WS (2011) The Gray Hawk (*Buteo nitidus*) is two species. Condor 113:326–339

Morton ES (1975) Ecological sources of selection on avian sound. Am Nat 109:17–34

Morton ES, Gonzales Alonso HJ (1982) The biology of *Torreornis inexpectata* I. A comparison of vocalizations in *T. i. inexpectata* and *T. i. sigmani*. Condor 94:433–446

Naguib M (2003) Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication. J Acoust Soc Am 113:1749–1756

Price JJ, Lanyon SM (2002) Reconstructing the evolution of complex bird song in the oropendolas. Evolution 56:1514–1529

Price JJ, Clapp MK, Omland KE (2011) Where have all the trees gone? The declining use of phylogenies in animal behaviour journals. Anim Behav 81:667–670

Richardson DS, Burke T (2001) Extra-pair paternity and variance in reproductive success related to breeding density in Bullock's Orioles. Anim Behav 62:519–525

Rising JD (2011) Familiy Emberizidae (buntings and New World sparrows). In: del Hoyo J, Elliot A, Christie D (eds) Handbook of the birds of the world, vol 16. Lynx, Barcelona, pp 428–683

Sandoval L (2014) Acoustic communication in thicket habitats: vocal behaviour and vocal divergence in Mesoamerican *Melozone* ground-sparrows. Disertation, University of Windsor

Sandoval L, Barrantes G (2012) Characteristics of male spot-bellied bobwhite (*Colinus leucopogon*) song during territory establishment. J Ornitol 153:547–554

Sandoval L, Mennill DJ (2012) Breeding biology of White-eared Ground-sparrow (*Melozone leucotis*), with a description of a new nest type. Ornitol Neotrop 23:225–234

Sandoval L, Mennill DJ (2014) A quantitative description of vocalizations and vocal behaviour of Rusty-crowned Ground-sparrow (*Melozone kieneri*). Ornitol Neotrop 25:219–230

Sandoval L, Méndez C, Mennill DJ (2013) Different vocal signals, but not prior experience, influence heterospecific from conspecific discrimination. Anim Behav 85:907–915

Sandoval L, Méndez C, Mennill DJ (2014) Individual distinctiveness in the fine structural features and repertoire characteristics of the songs of White-eared Ground-sparrows. Ethology 120:275–286

Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, pp 426–453

Stiles FG (2009) A review of the genus *Momotus* (Coraciiformes: Momotidae) in northern South America and adjacent areas. Ornitol Colomb 8:29–75

Stiles FG, Skutch AF (1989) A guide to the birds of Costa Rica. Cornell University Press, Ithaca

Trejos-Araya C, Barrantes G (2014) Natural history and acoustic repertoire of the Large-footed Finch (*Pezopetes capitalis*), an endemic, highland bird of Costa Rica and western Panama. Ornitol Neotrop 25:261–271

Tweit RC, Finch DM (1994) Abert's Towhee (*Melozone aberti*). In: Poole A (ed) The birds of north America online. Cornell Lab of Ornithology, Ithaca. Accessed 20 Oct 2013

Wildenthal JL (1965) Structure of the primary song of the mockingbird (*Mimus ployglottos*). Auk 82:161–189

Wiley RH (1991) Association of song properties with habitats for territorial oscine birds of eastern North America. Am Nat 138:973–993

Wolf LL (1977) Species relationships in the avian genus *Aimophila*. Ornithol Monogr 23:1–220