

A QUANTITATIVE DESCRIPTION OF VOCALIZATIONS AND VOCAL BEHAVIOUR OF THE RUSTY-CROWNED GROUND-SPARROW (*MELOZONE KIENERI*)

Luis Sandoval^{1,2} & Daniel J. Mennill¹

¹Department of Biological Sciences, University of Windsor, Windsor, Ontario, N9B3P4, Canada. *E-mail*: biosandoval@hotmail.com

²*Current address*: Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica, CP 2090.

Resumen. – Descripción cuantitativa de las vocalizaciones y el comportamiento vocal del Cuatro-ojos Gorra Naranja (*Melozone kieneri*). – Muchas especies de emberízidos (Emberizidae) han servido como modelo para entender el canto y el comportamiento vocal en aves. En contraste, el comportamiento vocal y los repertorios vocales para la mayoría de especies tropicales de emberízidos son poco conocidos, aunque la diversidad de especies sea mayor. Nosotros presentamos la primera descripción cuantitativa del repertorio y el comportamiento vocal del Cuatro-ojos de Gorra Naranja (*Melozone kieneri*), endémico de México. También proveemos información sobre el efecto de la distribución espacial en la similitud de los repertorios, así como la variación diaria de las vocalizaciones, todo esto basado en grabaciones focales, autónomas, y oportunísticas en una población de El Tuito, Jalisco, México. Nuestros resultados demuestran que el Cuatro-ojos de Gorra Naranja produce tres categorías de vocalizaciones - llamadas, cantos solos y duetos - como ocurre en otras especies de *Melozone*. Encontramos que los cantos solo y los duetos en esta especie presentaron características intermedias a especies de *Melozone* que se distribuyen más al norte o sur. La similitud de los repertorios entre machos cercanos fue mayor, sugiriendo que el aprendizaje del canto puede ocurrir después del establecimiento territorial. Las llamadas y los cantos presentaron un pico marcado temprano en la mañana indicando que esta especie participa de los coros del amanecer. Este estudio es la primera descripción cuantitativa de las vocalizaciones del Cuatro-ojos de Gorra Naranja, el cual generó importante información descriptiva en esta especie poca estudiada de *Melozone* Neotropical.

Abstract. – Many species of sparrows (Emberizidae) in the temperate zone provide model systems for understanding bird song and singing behaviour. In contrast, the vocal repertoire and vocal behaviour for most tropical sparrows is poorly understood, in spite of their impressive biodiversity. We present here the first detailed quantitative description of vocal repertoires and vocal behaviour of the Rusty-crowned Ground-sparrow (*Melozone kieneri*), an endemic Mexican sparrow. We provide information on the effect of territory spacing on song repertoire-use and details of the diel pattern of variation in vocal output, using focal, autonomous, and opportunistic recordings of birds in El Tuito, Jalisco, Mexico. Our results demonstrate that Rusty-crowned Ground-sparrows produce three distinct categories of vocalizations – calls, solo songs, and duets – as in other *Melozone* ground-sparrows. We found that solo songs and duets in this species showed an acoustic structure intermediate to other northern and southern *Melozone* ground-sparrows. Patterns of repertoire-use in male solo songs were highly similar between males holding nearby territories, suggesting that song learning may occur after territory establishment. The diel pattern for output of calls and solo songs showed a pronounced peak early in the morning, indicative of dawn-chorus singing behaviour. This study provides the first quantitative investigation of Rusty-crowned

Ground-sparrow vocalizations, providing important descriptive information on this little-studied Neotropical *Melospiza* species. Accepted on 13 August 2014.

Key words: Rusty-crowned Ground-sparrow, *Melospiza kieneri*, bird calls, diel variation, duets, Emberizidae, solo songs, sparrows.

INTRODUCTION

Decades of investigations of temperate sparrows (family: Emberizidae) have led to the development of many key principles of avian acoustic communication (e.g., vocalizations, vocal behaviour) (Marler 2004a, Catchpole & Slater 2008). For example, White-crowned Sparrows (*Zonotrichia leucophrys*) were the initial species used to examine geographic variation at both broad and local scales (Marler & Tamura 1962) which lead to the study of cultural transmission in animals that learn their vocalizations (Marler 1970, 2004b). Song syntax was first studied in Swamp Sparrows (*Melospiza georgiana*), providing evidence that animals arrange their vocalizations with species-specific syntactical structure, much like human language (Marler & Pickert 1984). Our understanding of the production of overtones (Nowicki 1987), the function of graded signals (Beecher & Campbell 2005, Searcy & Beecher 2009), and the dynamics of conventional signals during aggressive interactions (Vehrencamp 2001) arose from seminal studies of Song Sparrows (*Melospiza melodia*).

Information on the vocal repertoires and vocal behaviour for the majority of tropical sparrows, in contrast, is limited or absent. One exception is the Rufous-collared Sparrow (*Zonotrichia capensis*); this widely studied tropical sparrow has been instrumental in enhancing our understanding of geographic variation and the relationship between habitat and population divergence in vocalizations (e.g., King 1972, Handford 1988, Handford & Loughheed 1991, Kopuchian *et al.* 2004, Danner *et al.* 2011). Further investigations of the vocalizations and vocal behaviour of other tropical sparrow species is an important

research priority because such studies will allow us to conduct comparative studies between tropical and temperate species, to better understand the phylogenetic relationships between species (Cadena & Cuervo 2010), and may lead to additional important insights that will further expand our understanding of animal vocal behaviour generally.

In this investigation, we studied the Rusty-crowned Ground-sparrow (*Melospiza kieneri*). This endemic Mexican sparrow inhabits both deciduous and dry forest habitat from sea level to 2000 m a.s.l., with a range extending from the south of Sonora to western Oaxaca, and the interior of Jalisco (Miller *et al.* 1957, Howell & Webb 1995, Rising 2011). Pairs of Rusty-crowned Ground-sparrows appear to defend territories using vocalizations, as do the other tropical species in the genus *Melospiza* (Benedict & McEntee 2009; Sandoval *et al.* 2013, 2014), although their vocal repertoires and behaviour has never been described in detail (Howell & Webb 1995, Rising 2011). With this study our goal is to present the first quantitative description of the vocal repertoire and vocal behaviour of the Rusty-crowned Ground-sparrow. In addition, we investigate the relationship between territory spacing and song type sharing, and describe the diel pattern of variation in vocal output.

METHODS

Field recordings. We recorded Rusty-crowned Ground-sparrows at Rancho Primavera, El Tuito, Jalisco state, Mexico (20°21'N, 105°20'W, 585 m a.s.l.). We collected recordings from 27 June to 3 July 2012, during the species' breeding season (Rowley 1962). Our

field observations confirmed that some of the study birds were actively breeding during the recording period: we observed adults carrying nesting material in two of the recorded pairs, and for two other pairs we observed behaviour consistent with incubation (i.e., one member of the pair disappeared after a period of foraging early during the day).

Recorded individuals were not colour-banded; we distinguished between territorial pairs based on their location (we collected GPS coordinates of the centre of each identified territory). Based on previous field observations of this species, and observations of colour-banded study populations of a closely related species (White-eared Ground-sparrow, *Melospiza leucotis*; Sandoval *et al.* 2013, 2014; Sandoval 2014), we considered birds to belong to a distinct pair when they were > 50 m away from the centre of the neighbouring pair's territory. Daily, we monitored and confirmed the presence of previously recorded pairs at the same locations. These observations made us confident that pairs recorded on different days were distinct and that pairs occupied the same territories throughout our recording period. The sexes are monomorphic in Rusty-crowned Ground-sparrows, so we were unable to assign sex to the unbanded study individuals. In a sister species, however, our field observations of colour-banded pairs reveals that vocalizations are sex-specific (Sandoval 2014). We make the assumption that the same pattern is true in this species, and our field observations support this assumption (i.e., during specific observation periods, only one member of the pair produced some vocalizations, whereas others were produced by both members of the pair).

We used three recording techniques to describe the vocal and repertoire behaviour for this species. First, we collected focal recordings by following a territorial pair for 1 h period between 07:00 and 08:00 h (at the

sun rises at approximately 07:05 h during the studied period); each pair was recorded on one day using this technique (N = 13 pairs). Second, we used autonomous digital recorders (Wildlife Acoustics Song Meters model SM1) set up inside birds' territories to record birds for a period that varied from 6 to 15 hours (mean \pm SE: 10.33 \pm 2.18 h; N = 5 pairs). All of these recordings included a continuous period from 07:00 to 09:00 h, when this species is most vocally active (see Results). Third, we collected opportunistic recordings between 08:00 and 19:00 h while we were walking nearby or inside birds' territories, when we detected birds vocalizing; we collected 03:35 h of recordings using this approach. Focal and opportunistic recordings were collected with a shotgun microphone (Sennheiser ME66/K6) connected to a digital recorder (Marantz PMD660 and Marantz PMD661), and with a parabola-mounted omnidirectional microphone (23 in Telinga parabola with a Sennheiser ME62/K6 microphone) and digital recorder (Zoom H4n). All recordings were collected in WAV format, with 16 bit accuracy and a 44.1 kHz sampling rate. Focal and opportunistic recordings were used for collecting fine structural acoustic measurements of the vocalizations (see below), and to describe the contexts of use for each vocalization. All recordings – including focal, opportunistic, and automated recordings – were used to describe the species' vocal repertoire. Only autonomous recordings were used to describe the species' pattern of diel variation.

Vocal analysis. We classified vocalizations based on their appearance on sound spectrograms, following similar approaches used in other studies (e.g., Franco & Slabbekoorn 2009, Sandoval *et al.* 2014). We measured fine-structural details in Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, NY, USA), using a combination of the

waveform, spectrogram, and power spectrum to obtain the most accurate measurements (Charif *et al.* 2004, Redondo *et al.* 2013). We generated spectrograms with a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz using the following settings: Hann window with 50 % overlap and 256 Hz transform size.

For each vocalization obtained in the focal and opportunistic recordings, we measured the following measurements: duration (s), the minimum frequency (Hz), the maximum frequency (Hz), and the frequency of maximum amplitude (Hz). From both the focal and autonomous recordings, we calculated the number of unique solo song types produced per individual. We defined solo song types based on the number of different elements (smaller discrete unit of continuous sound) and the element shape. Each solo song type was then compared among others included in a library of sounds that we developed.

We annotated manually the number of calls, solo songs, and duets produced by each pair from 05:00 to 20:00 h to analyze diel variation in the vocal output, based on data from the autonomous recorders.

Statistical analysis. We evaluated whether the fine structural details of two distinct call types (see Results) differed significantly from each other using a two sample *t*-test. We first calculated an average for each fine acoustic measurement per call type per pair, and then used these values as the dependent variable in the analysis, and the call type as the independent variable. We report exact *P*-values based on Bonferroni corrections for multiple comparisons; four separate tests were conducted for each of the four measured acoustic characters. We conducted Bonferroni corrections for multiple comparisons, where we divided the alpha by the number of comparisons, and then corrected the revised alpha value relative to 0.05 using the built-in function in PAST

(version 2.17; Øyvind Hammer, Natural History Museum, University of Oslo, Norway).

We estimated male solo song repertoire size for all individuals where we recorded ≥ 80 songs, using the Wildenthal equation for curve-fitting (1965). We used a Markov chain analysis to estimate if the ground-sparrows delivered song types with a predictable order using the technique described in Lemon and Chatfield (1971). This approach analyzes the probability of a bird singing a song type within their repertoire as a function of the previous song type (Leonardo & Konishi 1999).

We conducted a Mantel test to evaluate repertoire-use similarity, measured using a Morisita index of similarity as described in Sandoval *et al.* (2014), as a function of the physical distance between individuals' territories. We defined repertoire-use similarity as the production of shared vocalization types in similar proportion between males (see Sandoval *et al.* 2014 for details). We predicted that closer individuals would have higher repertoire-use similarity than would individuals further away from each other.

To examine patterns of diel variation in vocal output within this species, we calculated the number of vocalizations per hour (mean \pm SE) from 05:00 to 20:00 h. We grouping both types of calls for this analysis, because the two calls appear to share a similar function (see results); furthermore, one of the calls was produced in a very low proportion. We then used Kolmogorov-Smirnov one-sample tests to compare if the average proportion of calls, solo songs, and combined vocalizations (both calls and solo songs) showed a peak output during the day. The values of *P* for Mantel test and Kolmogorov-Smirnov test are reported based on 10,000 permutations.

For duets, we only reported descriptive statistics because our sample size for this vocalization type was too small for statistical

analysis. All duets were recorded using focal recording approach. We conducted statistical analyses in PAST (and report means \pm SE throughout the paper).

RESULTS

The vocal repertoire of Rusty-crowned Ground-sparrows at Rancho Primavera, El Tuito, Jalisco state, Mexico includes three main types of vocalizations: calls, solo songs, and duets. Calls ($N = 956$ calls recorded from 12 pairs, one pair was never recorded producing calls) and solo songs ($N = 1906$ songs recorded from 12 males, one male was never recorded producing songs) were common vocalizations. Duets, in contrast, were rare; we recorded only eight duets from three pairs over 71 h of recordings collected over seven days.

We observed two types of calls which we distinguish as “*chip*” and “*tseet*” (Fig. 1). These two calls were significantly different in their fine-structural characteristics (two sample *t*-test: $P < 0.04$, $df = 18$, for all comparisons after Bonferroni correction). On average, the duration of the *chip* call was 0.07 ± 0.004 s (range = 0.06–0.10 s, CV = 18.3%), with a minimum frequency of 7850 ± 104 Hz (range = 6968–8284 Hz, CV = 4.6%), a maximum frequency of $12,654 \pm 169$ Hz (range = 10,867–12,551 Hz, CV = 5.0%), and a frequency of maximum amplitude of 8574 ± 79 Hz (range = 7977–8964 Hz, CV = 3.2%). We recorded *chip* calls from both members of the pair when they were foraging ($N = 11$ pairs). For two pairs, we also noted *chip* calls when we approached nests that were under construction.

On average, the duration of the *tseet* call was 0.36 ± 0.026 s (range = 0.26–0.41 s, CV = 19.4%), with a minimum frequency of 7204 ± 232 Hz (range = 6596–8356 Hz, CV = 8.5%), a maximum frequency of 9478 ± 245 Hz (range = 8241–10,351 Hz, CV = 6.9%),

and a frequency of maximum amplitude of 8050 ± 193 Hz (range = 7373–8958 Hz, CV = 6.3%). We recorded the ground-sparrows using this vocalization when pair members were far apart from each other ($N = 7$ pairs).

We observed only one individual per pair producing solo songs, and we assumed that this was the male (an observation which matches our knowledge of other ground-sparrow species). As in other ground-sparrow species, the male sang from exposed perches that varied from approximately 1.5 to 3.5 m. Songs recorded using the focal recording approach were performed in bouts separated by long silent intervals, with a bout length of 16.43 ± 3.16 min (based on recordings of $N = 12$ individuals). Male solo songs were variable and readily classifiable into distinct song types (Fig. 1). We detected 29 unique song types in our sample of 1482 analyzed songs.

Solo songs had three sections: (1) the introductory section began with high frequency elements similar to *chip* calls; (2) the middle section contained broadband frequency-modulated elements; and (3) the concluding section contained a trill (Fig. 1). Solo songs showed an average duration of 2.2 ± 0.1 s (range = 1.6–4.1 s, CV = 22.7%), a minimum frequency of 3470 ± 121 Hz (range = 2607–4916 Hz, coefficient of variation: CV = 18.8%), a maximum frequency of $11,111 \pm 130$ Hz (range = 8949–11918 Hz, CV = 6.3%), and a frequency of maximum amplitude of 5635 ± 111 Hz (range = 3728–6388 Hz, CV = 10.7%).

Among 10 males for which we recorded ≥ 80 songs, the repertoire size varied from four to ten song types (average: 6.3 ± 0.7 songs, e.g., Fig. 2). All of the individuals we studied delivered their song types in a predictable order that deviated significantly from random (Markov chain: $P < 0.007$ for all individuals, $N = 10$). Individuals with nearby territories showed more similar patterns of repertoire

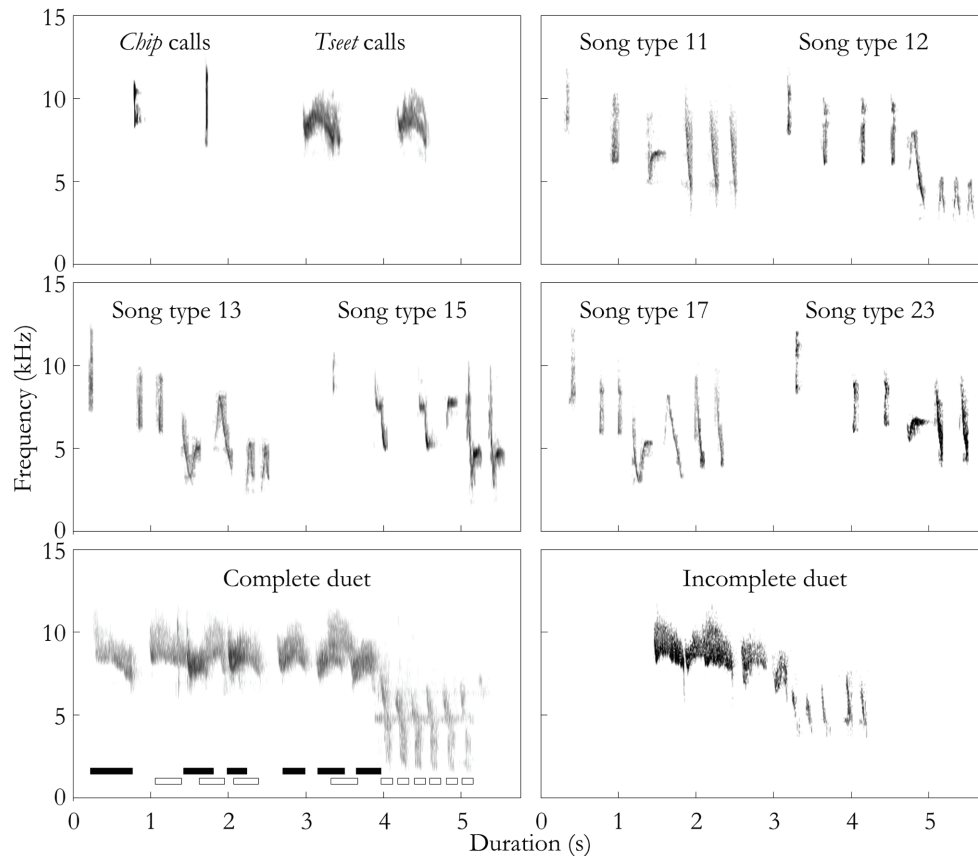


FIG. 1. Sound spectrograms of the three main categories of vocalizations produced by Rusty-crowned Ground-sparrows, at Rancho Primavera, El Tuito, Jalisco state, Mexico recorded from 27 June to 3 July 2012 with two examples of the two call types; six common male solo song types produced in the study site; a complete duet (black and grey blocks show the contribution of each individual of the pair); and an incomplete duet featuring a contribution by one individual.

use than they did with far-away individuals (Mantel test: $r = 0.49$, $P = 0.002$, $N = 10$).

Duets were produced by both members of the pair when they were near one another or when one individual arrived next to the other. Duets included elements overlapping in both time and frequency (Fig. 1). Vocalizations used to construct duets were different from vocalizations used as solo songs (Fig. 1). Complete duets showed an average duration of 4.3 ± 0.4 s (range = 3.7–5.0 s, CV = 15.8%), minimum frequency of 1314 ± 35 Hz

(range = 1244–1349 Hz, CV = 4.6%), maximum frequency of $11,240 \pm 539$ Hz (range = 10,188–11,971 Hz, CV = 8.3%), and frequency of maximum amplitude of 7763 ± 397 Hz (range = 6977–8250 Hz, CV = 8.8%). On three occasions, we observed just one individual of the pair producing an unanswered duet contribution, which was shorter in duration than a complete duet (Fig. 1). We classified these solo vocalizations as “incomplete duets” (Fig. 1). Incomplete duets showed an average duration of 3.0 ± 0.4 s (range =

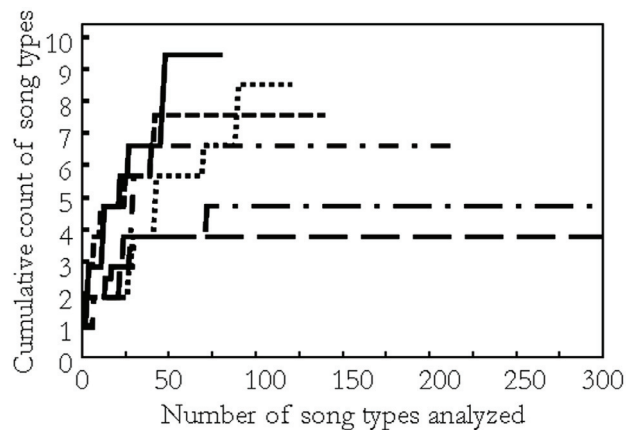


FIG. 2. Repertoire asymptote curves for Rusty-crowned Ground-sparrows, at Rancho Primavera, El Tuito, Jalisco state, Mexico recorded from 27 June to 3 July 2012 showing six males chosen to show the full range of variation in our dataset; the remaining four males had repertoire asymptote curves overlapped by the curves shown.

1.9–3.8 s, CV = 26.0%), minimum frequency of 4747 ± 686 Hz (range = 3277–6600 Hz, CV = 32.3%), maximum frequency of $10,215 \pm 367$ Hz (range = 9327–11,557 Hz, CV = 8.0%), and frequency of maximum amplitude of 8219 ± 155 Hz (range = 7666–8625 Hz, CV = 4.2%).

Rusty-crowned Ground-sparrow vocal output varied throughout the day, with the highest peak occurring between 07:00 and 10:00 h (KS: $D_{\max} = 0.80$, $P < 0.001$; Fig. 3); 59% of all vocalizations occurred during this period of heightened vocal output (Fig. 3). The same diel patterns for combined vocalizations was observed for both calls ($D_{\max} = 0.72$, $P < 0.001$; Fig. 3), and solo songs ($D_{\max} = 0.73$, $P < 0.001$; Fig. 3). Birds produced too few duets to conduct a meaningful analysis of diel variation ($N = 8$ duets from 3 pairs) although all duets were recorded in the first part of the day (range: 07:05–12:16 h).

DISCUSSION

The vocal repertoire of Rusty-crowned Ground-sparrows includes three main categories

of vocalizations: calls, solo songs, and duets. Prior anecdotal descriptions of this species' vocalizations mention only solo songs (Howell & Webb 1995, Rising 2011). Calls and duets were produced by both individuals of the pair, whereas solo songs were produced only by one individual in the pair; we assumed that the solo singers were males based on knowledge of vocal behaviour in related ground-sparrows. Pair members created duets using vocalizations different from male solo songs, although duets were quite rare during our study period. Rusty-crowned Ground-sparrows exhibited a diel pattern of variation with one peak of vocal output, coincident with dawn. This is the first quantitative description of the vocalizations of this little-studied endemic Mexican sparrow.

Rusty-crowned Ground-sparrows produced two types of calls, which we distinguish as *chip* and *tseet* calls. Two similar call types have been reported in other ground-sparrow species (Sandoval 2014), sharing similarity in both acoustic structure and context of use. Our observations revealed that the *chip* call

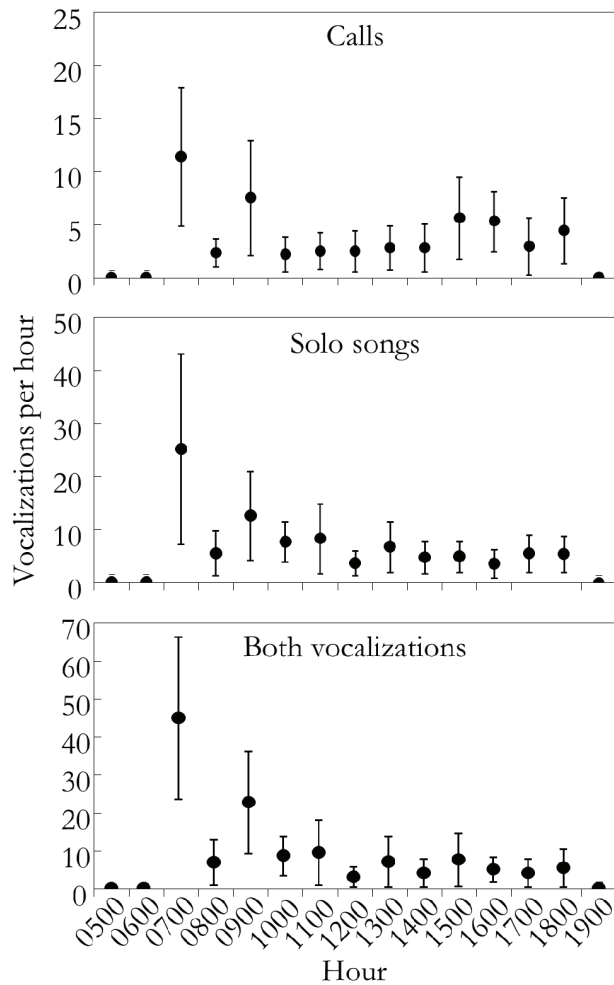


FIG. 3. Diel variation in vocal output in Rusty-crowned Ground-sparrows at Rancho Primavera, El Tuito, Jalisco state, Mexico recorded from 27 June to 3 July 2012 according to calls, solo songs, and both vocalizations together, recording exclusively in autonomous digital recorders (Wildlife Acoustics Song Meters model SM1). Dots show means and the whiskers show standard error for $N = 5$ pairs recorded for a 52 hour period.

was used mainly in the context of contact between the pair members while foraging. We also observed birds producing this call at highest rate when we approached to the nest site during the nest construction stage, which suggests this vocalization may also be used as an alarm signal, as has been suggested for White-eared Ground-sparrow *chip* calls (San-

doval *et al.* 2013). The *tseet* calls also appear to be used to initiate or maintain contact, but less frequently than *chip* calls. The *chip* call occurs at a higher frequency, with a broad bandwidth, and short duration, making it easy to localize the position of the sender (Marler 2004b), but these properties may reduce the distance that the call can travel through the

birds' habitat (Wiley 1991, Bradbury & Vehrencamp 2011). In comparison, the *tseet* call showed narrow bandwidth, with a longer duration, suggesting that this vocalization can transmit over longer distances, but may be harder for potential receivers to localize as a result (Wiley 1991, Bradbury & Vehrencamp 2011). The acoustic properties of *chip* calls may help other individuals to localize potential predators, initiating a mobbing response, thereby better deterring potential predators (Marler 2004b, Sandoval & Wilson 2012).

Solo song was the most variable vocalization in terms of structure, because it included several types of elements in different combinations and frequency of occurrence, a pattern found widely among sparrows (Searcy 1992, Beecher *et al.* 2000). These high levels of variability are believed to be the result of sexual selection on this vocalization, by female selection or male-male competition (Searcy 1992, Gil & Gahr 2002). In the Rusty-crowned Ground-sparrow, only a single individual within a pair produced this vocalization; this was likely the male, based on studies in other species within this genus (Sandoval *et al.* 2013, 2014). In some sparrows, females prefer males with larger vocal repertoires (Searcy 1984, Reid *et al.* 2004). If this is true in Rusty-crowned Ground-sparrows, this may be a force driving the elaboration of male vocal repertoires. In other sparrows, males use solo song repertoires as a signal during male-male interactions (Beecher *et al.* 1994, Vehrencamp 2001). If this holds true in Rusty-crowned Ground-sparrows, then shared song types between neighbouring males may be an important social force that selects for vocal repertoires in solo song types.

We observed a relationship between repertoire-use similarity and distance between territories, where nearby males share and use their repertoires more similarly than with males located at further distances; this pattern has also been observed in a sister taxon, the

White-eared Ground-sparrow (Sandoval *et al.* 2014). This pattern may indicate that males tend to learn their songs during the territory establishment period, or that they preferentially use shared components of their repertoires learned earlier in life (McGregor & Krebs 1989). One advantage to repertoire sharing between immediate neighbours is the use of similar song types during male-male interactions, especially if matched song types are important signals of escalation during interactions (Krebs *et al.* 1981, Beecher *et al.* 2000, Todt & Naguib 2000). To further evaluate these possible hypotheses for solo song function, future playback studies and recordings of color marked birds will be helpful.

In general, song structure in Rusty-crowned Ground-sparrows (i.e., male solo songs with several trill elements) showed an intermediate pattern between the song structures observed among northern and southern species in the genus *Melospiza* (Tweit & Finch 1994, Johnson & Haight 1996, Benedict *et al.* 2011; Sandoval *et al.* 2013, 2014). In northern *Melospiza* species, solo songs contain longer trills (Tweit & Finch 1994, Johnson & Haight 1996, Benedict *et al.* 2011), while in southern *Melospiza* species songs are a combination of several elements including frequency-modulated elements and trills (Sandoval *et al.* 2013, 2014). Duets of Rusty-crowned Ground-sparrows included introductory elements similar to elements observed in the duets of Prevost's (*M. biarcuata*) and White-eared Ground-sparrows (Sandoval *et al.* 2013, Sandoval 2014). The elements of the middle part of the duet were similar to the elements observed in the duets of the California Towhee (*M. crissalis*, Benedict & McEntee 2009).

The habitat structure that birds inhabit may influence the characteristics of vocalizations (Boncoraglio & Saino 2007). Rusty-crowned Ground-sparrows inhabit both deciduous and dry forests (Howell & Webb 1995, Rising 2011), which are more open hab-

itats than of the southern *Melospiza* species (e.g., thickets and young successional forest), but closely resemble the habitats of northern species (e.g., desert vegetation and grasslands). Alternatively, the presence of the observed intermediate properties of solo songs in the Rusty-crowned Ground-sparrow may be the result of phylogenetic relationships, given that this species shows similar relatedness with both ground-sparrow phylogenetic groups (DaCosta *et al.* 2009). A close evaluation of habitat structure and phylogeny effect is necessary to understand better the influence of habitat on vocalizations in these animals.

Duets were produced with a different vocalization than those used for solo songs, a pattern that appears to be widespread in *Melospiza* species (Benedict & McEntee 2009, Sandoval *et al.* 2013, 2014), but rare in many other duetting species where birds use the same vocalizations for solos and duets (e.g., Mann *et al.* 2003, Mennill & Vehrencamp 2005, Logue 2006). Although we recorded very few duets during our field study, our observations suggest that duets in this species are used in a similar way that has been observed for the White-eared Ground-sparrow: territory defence and maintaining acoustic contact (Sandoval *et al.* 2013). For example, when we played back duets to previous recorded pairs to corroborate their presence on their territory, both individuals approached quickly to the playback loudspeaker. Future playback studies of color-marked birds will allow for careful tests of these hypotheses.

Rusty-crowned Ground-sparrows showed significant variation in vocal output over the course of the day. The primary peak in vocal output occurred from 07:00 to 10:00 h, just after sunrise, coinciding with the dawn chorus in the study area. Calls and solo songs showed the same pattern throughout the day, similar to patterns observed in the White-eared Ground-sparrow (Sandoval 2014), the only

other species in this genus where diel patterns have been studied.

In conclusion, Rusty-crowned Ground-sparrows showed a vocal repertoire similar to that observed in other ground-sparrow species and the vocalizations (solo songs and duets) shared acoustic structural characteristics with both northern and southern species in this genus. The function of each vocalization is also similar to those reported previously for closely related species. Solo song repertoire-use similarity was higher in nearby individuals, suggesting that song vocal learning may occur after territory establishment. The description of bird vocal repertoire and diel pattern is highly recommended because it is the basic information required to conduct comparative studies and address experimental questions.

ACKNOWLEDGMENTS

We thank the Rancho Primavera and Bonnie Jáuregui for logistical support and access to study area. We also thank Melania Fernández and Sandra Gallo by all the help during the field work. 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.

REFERENCES

- Beecher, M. D., & S. E. Campbell. 2005. The role of unshared songs in singing interactions between neighbouring Song Sparrows. *Anim. Behav.* 70: 1297–1304.

- Beecher, M. D., S. E. Campbell, & J. C. Nordby. 2000. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Anim. Behav.* 59: 29–37.
- Beecher, M. D., S. E. Campbell, & P. K. Stoddard. 1994. Correlation of song learning and territory establishment strategies in the Song Sparrow. *Proc. Nat. Acad. Sci.* 91: 1450–1454.
- Benedict, L., & J. P. McEntee. 2009. Context, structural variability and distinctiveness of California Towhee (*Pipilo crissalis*) vocal duets. *Ethology* 115: 77–86.
- Benedict, L., M. R. Kunzmann, K. Ellison, K. L. Purcell, R. R. Johnson, & L. T. Haight. 2011. California Towhee (*Melospiza crissalis*). In Poole, A. (ed.). *The birds of North America*, no. 632. Cornell Lab of Ornithology, Ithaca, New York, USA. Downloaded on 20 November 2013 from <http://bna.birds.cornell.edu/bna/species/632>.
- Boncoraglio, G., & N. Saino. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Funct. Ecol.* 21: 134–142.
- Bradbury, J. W., & S. L. Vehrencamp. 2011. *Principles of animal communication*. 2nd ed. Sinauer Assoc., Sunderland, Massachusetts, USA.
- Cadena, C. D., & A. M. Cuervo. 2010. Molecules, ecology, morphology, and songs in concert: how many species is *Arremon torquatus* (Aves: Emberizidae)? *Biol. J. Linn. Soc.* 99: 152–176.
- Catchpole, C. K., & P. J. B. Slater. 2008. *Bird song biological themes and variation*. Cambridge Univ. Press, Cambridge, UK.
- Charif, R., C. Clark, & K. Fristrup. 2004. *Raven 1.2 User's Manual*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- DaCosta, J. M., G. M. Spellman, P. Escalante, & J. Klicka. 2009. A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. *J. Avian Biol.* 40: 206–216.
- Danner, J. E., R. M. Danner, F. Bonier, P. R. Martin, T. W. Small, & I. T. Moore. 2011. Female, but not male, tropical sparrows respond more strongly to the local song dialect: implications for population divergence. *Am. Nat.* 178: 53–63.
- Fisher, J. B. 1954. Evolution and bird sociality. Pp. 71–83 in Huxley, J., A. C. Hardy, & E. B. Ford (eds). *Evolution as a process*. Allen & Unwin, London, UK.
- Franco, R., & H. Slabbekoorn. 2009. Repertoire size and composition in great tits: a flexibility test using playbacks. *Anim. Behav.* 77: 261–269.
- Gil, D., & M. Gahr. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* 17: 133–141.
- Handford, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Can. J. Zool.* 66: 2658–2670.
- Handford, P., & S. C. Loughheed. 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.
- Howell, S. N. G., & S. Webb. 1995. *A guide to the birds of Mexico and northern Central America*. Oxford Univ. Press, New York, New York, USA.
- Johnson, R. R., & L. T. Haight. 1996. Canyon Towhee (*Melospiza fuscus*). In Poole, A. (ed.). *The birds of North America*, no. 264. Cornell Lab of Ornithology, Ithaca, New York, USA. Downloaded on 20 November 2013 from <http://bna.birds.cornell.edu/bna/species/264>.
- King, J. R. 1972. Variation in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, in Northwestern Argentina. *Z. Tierpsychol.* 30: 344–373.
- Kopuchian, C., D. A. Lijtmaer, P. L. Tubaro, & P. Handford. 2004. Temporal stability and change in a microgeographical pattern of song variation in the Rufous-collared Sparrow. *Anim. Behav.* 68: 551–559.
- Krebs, J. R., R. Ashcroft, & K. van Orsdol. 1981. Song matching in the Great Tit, *Parus major* L. *Anim. Behav.* 29: 918–923.
- Lemon, R. E., & C. Chatfield. 1971. Organization of song in Cardinals. *Anim. Behav.* 19: 1–17.
- Leonardo, A., & M. Konishi. 1999. Decrystallization of adult birdsong by perturbation of auditory feedback. *Nature* 399: 466–470.
- Logue, D. M. 2006. The duet code of the female Black-bellied Wren. *Condor* 108: 326–335.

- Mann, N. I., L. Marshall-Ball, & P. J. B. Slater. 2003. The complex song duet of the Plain Wren. *Condor* 105: 672–682.
- Marler, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Phys. Psych.* 71: 1–25.
- Marler, P. 2004a. Science and birdsong: the good old days. Pp. 1–38. *in* Marler, P., & H. Slabbekoorn (eds). *Nature's music, the science of bird song*. Elsevier Academic Press, San Diego, California, USA.
- Marler, P. 2004b. Bird calls: a cornucopia from communication. Pp. 132–177 *in* Marler, P., & H. Slabbekoorn (eds). *Nature's music, the science of bird song*. Elsevier Academic Press, San Diego, California, USA.
- Marler, P., & R. Pickert. 1984. Species-universal microstructure in the learned song of the Swamp Sparrow, *Melospiza georgiana*. *Anim. Behav.* 32: 673–689.
- Marler, P., & M. Tamura. 1962. Song “dialects” in three populations of White-crowned Sparrows. *Condor* 64: 368–377.
- McGregor, P. K., & J. R. Krebs. 1989. Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour* 108: 139–159.
- Mennill, D. J., & S. L. Vehrencamp. 2005. Sex differences in the singing and duetting behavior of Neotropical Rufous-and-white Wrens (*Troglodytes rufalbus*). *Auk* 122: 175–186.
- Miller, A. H., H. Friedmann, L. Griscom, & R. T. Moore. 1957. Distributional check-list of the birds of Mexico, part II. *Pac. Coast Avifauna* 33: 1–436.
- Nowicki, S. 1987. Vocal-tract resonances in oscine bird sound production: evidence from bird-songs in a helium atmosphere. *Nature* 325: 53–55.
- Redondo, P., G. Barrantes, & L. Sandoval. 2013. Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*. *Ibis* 155: 621–625.
- Rising, J. D. 2011. Family Emberizidae (buntings and New World sparrows). Pp. 428–683 *in* del Hoyo J, A. Elliott, & D. Christie (eds). *Handbook of the birds of the world. Volume 16: Tanagers to New World blackbirds*. Lynx Edicions, Barcelona, Spain.
- Rowley, J. S. 1962. Nesting of the birds of Morelos, Mexico. *Condor* 64: 253–272.
- Sandoval, L. 2014. Acoustic communication in thicket habitats: vocal behaviour and vocal divergence in Mesoamerican *Melospiza* ground-sparrows. Ph.D. diss., Univ. of Windsor, Windsor, Canada.
- Sandoval, L., & D. R. Wilson. 2012. Local predation pressure predicts the strength of mobbing responses in tropical birds. *Curr. Zool.* 58: 781–790.
- Sandoval, L., C. Méndez & D. J. Mennill. 2013. Different vocal signals, but not prior experience, influence heterospecific from conspecific discrimination. *Anim. Behav.* 85: 907–915.
- Sandoval, L., C. Méndez, & D. J. Mennill. 2014. Individual distinctiveness in the fine structural features and repertoire characteristics of the songs of white-eared ground-sparrows. *Ethology* 120: 275–286.
- Searcy, W. A. 1984. Song repertoire size and female preferences in Song Sparrows. *Behav. Ecol. Sociobiol.* 14: 281–286.
- Searcy, W. A. 1992. Song repertoire and mate choice in birds. *Am. Zool.* 32: 71–80.
- Searcy, W. A., & M. D. Beecher. 2009. Song as an aggressive signal in songbirds. *Anim. Behav.* 78: 1281–1292.
- Todt, D., & M. Naguib. 2000. Vocal interactions in birds: the use of song as a model in communication. *Adv. Stud. Behav.* 29: 247–295.
- Tweit, R. C., & D. M. Finch. 1994. Abert's Towhee (*Melospiza aberti*). *In* Poole, A. (ed.). *The birds of North America*, no. 111. Cornell Lab of Ornithology, Ithaca, New York, USA. Downloaded on 20 November 2013 from <http://bna.birds.cornell.edu/bna/species/111>.
- Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proc. R. Soc. Lond. B*: 268: 1637–1642.
- Wildenthal, J. L. 1965. Structure in primary song of the Mockingbird (*Mimus polyglottos*). *Auk* 82: 161–189.
- Wiley, R. H. 1991. Association of song properties with habitats for territorial oscine birds of eastern North America. *Am. Nat.* 138: 973–993.