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**The effect of noise variation over time and between populations on the fine spectrotemporal characteristics of different vocalization types**

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**Highlights**

- Anthropogenic noise effect in bird calls, songs, and duets.
- Frequencies of calls varied with noise changes across populations and years.
- Frequencies of duets change among populations and years when noise increased.
- The function of each vocalization could explain the variation in response to noise effect.
- Noise had not a main effect on the acoustic characteristics of the vocalizations.

Abstract

Noise affects the recognition of acoustic signals by masking information. To compensate for increased noise, individuals often increase the minimum frequency of their vocalization to reduce noise interference. Our goal was to analyze the effect of noise on the characteristics of different bird vocalizations, through a comparative study of vocalizations on the same bird species. We analyzed the effects of noise variation on the fine spectrotemporal characteristics of calls, songs, and duets of White-eared Ground-sparrows (*Melospiza leucotis*) across three populations over a three-year period. We recorded vocalizations and noise levels simultaneously from 41 territories between 2012 and 2014. We measured the duration, minimum, maximum, and maximum amplitude frequency, and counted the number of songs elements for each vocalization recorded. As we predicted, noise influences the minimum frequency of song, but did not have an effect on the fine spectrotemporal characteristics for calls and duets. We did, however, find that low and high frequency of calls and duets increased with noise-population-year interaction. Our results suggest that differences in noise values at each population were inadequate to observe changes in vocalization characteristics. In conclusion, evaluating responses to different noise levels on different vocalization types for the same species expands our understanding of the flexibility of birds to adjust vocalizations in response to anthropogenic noise.

*Keywords:* anthropogenic noise; calls; duets; plasticity; signal to-noise ratio

## **1. Introduction**

Environmental factors such as background noise and vegetation structure affect the propagation of sound produced by animals for communication (Ryan and Brenowitz, 1985; Cynx et al., 1998; Brumm, 2004; Wood and Yezerinac, 2006). For example, high frequency signals attenuate faster in

forests than in open habitats, because high frequencies experience greater scattering as they propagate through dense vegetation than low frequencies (Wiley and Richards, 1982; Wiley, 1991). Signals with broad bandwidth also attenuate and degrade faster inside forests than in open habitats, because they are often subjected to greater reverberation (Richards and Wiley, 1980; Wiley and Richards, 1982; but see Slabbekoorn et al., 2002).

Background noise is another factor that affects acoustic communication as it decreases the threshold of audibility for a specific range of frequencies (Shannon et al., 2012). High levels of background noise affect the detection and recognition of vocalizations because communication depends substantially on the signal-to-noise ratio (Brumm, 2004). For a given species, background noise comprises natural occurring sounds, which may be either abiotic (e.g., wind, vegetation movement, rain, flowing water, and surf; Brumm, 2004; Wood and Yezerinac, 2006; Halfwerk and Slabbekoorn, 2009), biotic (e.g., sounds produced by other animals; Brumm, 2004; Dowling et al., 2012); or those produced by human activity (e.g., road traffic, construction, or industrial motors; Patricelli and Blickley, 2006; Hanna et al., 2011; Dowling et al., 2012).

Anthropogenic noise consists mainly of low frequencies (<3kHz), which could mask and limit the perception of vocalizations within the same frequency range (Brumm, 2004; Brumm and Slabbekoorn, 2005; Wood and Yezerinac, 2006). This type of noise presumably induces birds, amphibians, and mammals that inhabit noisy areas, to adjust the frequency range of their vocalizations to reduce overlap with background noise (Brumm et al., 2004; Slabbekoorn and den Boer-Visser, 2006; Bermúdez-Cuamatzin et al., 2009; Cunnington and Fahrig, 2010; Dowling et al., 2012). For example, some bird species such as Dark-eyed Juncos (*Junco hyemalis*; Slabbekoorn et al., 2007) and Song Sparrows (*Melospiza melodia*; Wood and Yezerinac, 2006), and some mammals such as Common Marmosets (*Callithrix jacchus*; Brumm et al., 2004) increase minimum frequency

of their vocalizations in response to increasing background noise. However, other mammals such as macaques (e.g., Pig-tailed Macaque *Macaca nemestrina* and Long-tailed Macaque *Macaca fascicularis*; Sinnott et al., 1975) also produce vocalizations with higher amplitude, a phenomenon known as Lombard effect (Cynx et al., 1998; Brumm, 2004; Zollinger and Brumm, 2011). Another strategy to communicate, used by some birds and amphibians in response to increasing background noise, is to change the timing when they vocalize. For example, European Robins (*Erithacus rubecula*) often sing during the night (Fuller et al., 2007), and this improves detection and recognition of their vocalizations (Lohr et al., 2003).

Although the effect of background noise has been extensively studied in birds (Brumm, 2004; Fuller et al., 2007; Bermúdez-Cuamatzin et al., 2009; Dowling et al., 2012; Redondo et al., 2013; Halfwerk et al., 2018), most studies have focused on male solo songs of birds that inhabit temperate zones. Male solo songs are long distance signals used in male-male or male-female interactions during the breeding season (Catchpole and Slater, 2008) and may be easily masked in habitats with high levels of noise (Richards and Wiley, 1980; Wiley, 1991). However, many birds in the Neotropics produce calls and duets to communicate at short and long distances year-round (Marler, 2004; Mennill and Vehrencamp, 2005; Martin et al., 2011). Calls are important as contact signals or to indicate the occurrence of food resources and danger (Manser, 2001; Templeton and Greene, 2007; Fallow et al., 2011). Duets are used in territory defense and within-pair communication (Hall, 2000; Sandoval et al., 2013; Dahlin and Benedict, 2013). Unlike songs, calls and duets are produced by both, males and females, year-round regardless of the birds' breeding status (Potvin et al., 2011).

To understand in a broader context the effect of background noise on acoustic communication is important to conduct experimental-comparative studies of noise effect on

different types of vocalizations rather than focus on solo songs. There are very few studies that have evaluated the effect of noise on several vocalization types (i.e., calls, songs, and duets) in a single species simultaneously. The research on Silvereye (*Zosterops lateralis*) compares the effect of noise on songs and calls (Potvin et al., 2011) and a study on Mountain Chickadees (*Poecile gambeli*) compares the effect of noise in calls, songs, and chorus (LaZerte et al., 2017). Bird species inhabiting urban areas will either avoid the noise by vocalizing during quieter time periods (Fuller et al., 2007), become habituated to it because noise does not largely affect the vocalization characteristics (e.g., species that vocalize at frequencies over noise levels; Slabbekoorn and Ripmeester, 2007), or may evolve higher frequency signals (Juárez et al. 2020a). Hence, bird species that inhabit noisy environments may have negative consequences for reproduction and survival (Bayne et al., 2008; Barber et al., 2009). However, how background noise level changes over time in the same territories and how the resident individuals respond to these changes, is still poorly understood.

We conducted this study on the White-eared Ground-sparrow (*Melospiza leucotis*), a year-round territorial bird that inhabits areas with high level of anthropogenic noise (urban areas and road edges) or ambient noise (rivers and creeks; Stiles and Skutch, 1989; Sandoval and Mennill, 2012). This ground-sparrow produces three types of vocalizations for social interactions: calls used for within-pair communication and alarm signals, songs used for mating attraction, and duets used for territory defense and within-pair communication (Sandoval et al., 2013, 2014, 2016; Méndez and Sandoval, 2017). Our main objective was to test the effect of noise over time and between territories on the fine spectrotemporal characteristics (hereafter traits) of the three vocalizations of the White-eared Ground-sparrow (i.e., calls, solo songs, and duets). If noise affects each vocalization differently, we expect more variation in the frequency and duration of songs and duets

in response to noise level than in calls. Because songs and duets are used as a long-distance signal and may be more easily masked in habitats with a high level of noise (Richards and Wiley, 1980; Wiley, 1991; Patricelli and Blickley, 2006; Wood and Yezerinac, 2006). We additionally predict that pairs living in populations with high noise level produce songs and duets with (1) higher minimum and maximum frequencies, and (2) with longer duration than pairs living in populations with lower noise level to avoid masking by noise (Slabbekoorn and Peet, 2003; Slabbekoorn and den Boer-Visser, 2006; Hanna et al., 2011), and improve communication in noisy habitats (Brumm et al., 2004; Redondo et al., 2013). Finally, if noise change between years within populations we predict that pairs living in those populations will change the frequency and duration values of each vocalization in response to the noise change.

## **2. Methods**

### *2.1. Study sites*

We sampled birds in three populations of color-banded White-eared Ground-sparrows that vary in urban development, traffic density, and levels of noise in the Costa Rican Central Valley. (1) the Universidad de Costa Rica main campus (UCR), San José province (09°56'N, 84°03'W, 1200 m) is the site with the largest urban development (a larger proportion of urban area compared with green or natural cover) and is bordered by two main roads; (2) the Jardín Botánico Lankester (JBL), Cartago province (9°50'N, 83°53'W, 1370 m) is the second most urbanized site (50-50 urban area and green area) and is bordered by secondary roads; and (3) Getsemaní (HDIA), Heredia province (10°01'N, 84°05'W, 1350 m) is the site with less urban development (more natural – river forest, coffee plantations, and thicket habitats – than urban area) and is crossed by a unique dirty road. All four sites have rivers that cross or border White-eared Ground-sparrow territories, but HDIA

includes the largest river, with large variation in water flow. In HDIA the river border four territories. The two rivers at UCR pass through five territories and they have as much water flow variation as that in HDIA, but the normal flow of both of them is only about half of that in HDIA. In JBL, a small stream with little water flow fluctuation crosses three territories.

## *2.2. Vocalization recordings and noise measurements*

We recorded White-eared Ground-sparrows and registered background noise simultaneously from April to June 2012 and 2013, and from March to June 2014, during the species' breeding season (Sandoval and Mennill, 2012). We recorded 41 different pairs of White-eared Ground-sparrows, which were color banded with a unique color-combination for identification (41 males and 23 females). Recordings were conducted continuously between 0455 and 0600 h, starting just before sunrise, when this species is more vocally active (Sandoval et al., 2015). We used the focal recording method to obtain all our recordings using a Marantz PMD661 digital recorder and a Sennheiser ME66/K6 shotgun microphone (recording format: WAVE; sampling rate: 44.1 kHz; accuracy: 24 bits). Each pair was recorded one or two days during one to three years (five pairs 2 days and eight 1 day during 2012, 32 pairs one day during 2013, and 13 pairs 2 days and 36 pairs 1 day during 2014). We recorded four pairs for 3 years, 16 pairs for 2 years, and 21 pairs for 1 year. By checking the color-bands, we confirmed that those pairs recorded more than a year were the same recorded in previous years.

During each recording session, we measured the lowest and highest noise level every 10 minutes using a Sper Scientific 840014 mini sound meter (measuring range 30–130 dB) with the fast response and A weighting setting, as in other investigations (Redondo et al. 2013, Juarez et al. 2020). The A weighting setting was used because sparrows have the best hearing range between 1



and 8 kHz (Okanaya and Dooling, 1988), and so we assured that measurements were within the range of the study species hearing. We then calculated the mean environmental noise per recording session/territory using two steps. First, we estimated the logarithmic mean for every 10 min to obtain seven measurements per recording session, and used this mean value, instead of lowest and maximum values because inside cities both the lowest and highest noise level change rapidly due to car traffic and persons passing by, and this may over or underestimate the noise level in the territories. Second, we used the seven mean values to calculate a general mean of noise per recording session/territory.

### 2.3. Vocalizations measurements

To analyze the noise effect on vocalization traits, we classified visually calls into two types *chip* and *tseet* independently, solo songs, and duets (Fig. 1). We selected those vocalizations with no overlapping sounds, based on their appearance on sound spectrogram using Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). We defined calls as short-duration vocalizations (duration  $\leq$  1 s) produced by both members of the pair; solo songs as vocalizations produced solely by males (duration  $>$  1 s) and with 2 or more different elements; and duets as those vocalizations produced simultaneously by both members of the pair (duration  $>$  1 s), involving the production of several elements that overlapped in time and frequency (Fig. 1). White-eared Ground-sparrows as all other *Melospiza*, *Pezopetes*, and *Aimophila* species (Trejos-Araya and Barrantes, 2014; Sandoval et al., 2016) produce duets that are unique in the sense that they are distinct in acoustic structure when compared with male solo songs (Fig. 1). Because male and female contribution to duets overlaps in frequency and time is very difficult to analyze the contribution of each sex independently.

Using Raven Pro 1.4, we measured the following traits in each type of vocalization: (1) the minimum frequency in Hz, (2) the maximum frequency in Hz, (3) the frequency of maximum amplitude in Hz, and (4) the duration in s. Additionally, for solo songs, we counted the number of elements. We collected measurements using the threshold method (Podos 1997), which includes several visualizations windows for each vocalization: the spectrogram (to identify sounds), the power spectrum (to measure frequency features with a threshold of -30dB related to vocalization's peak amplitude), and the waveform (to measure temporal features). 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. For calls analyses, we focused on each pair within each territory rather than on individuals, because in most cases the dense vegetation in territories of the ground-sparrows precludes us to individually identify the bird that produced the calls. We are confident with this approach since previous studies in this species (Sandoval et al., 2016) showed that both calls had a very low coefficient of variation for the duration (*chip* = 25.5% and *tseet* = 27.6%) and frequency measurements (*chip* = 5.9–6.6 % and *tseet* = 6.0–7.9%), indicating that calls traits are similar in both sexes. For the analysis of solo songs, we grouped all songs in only one category because: (1) individuals in each population share a very reduced number of song types (Sandoval et al., 2014), making it difficult to have enough song types with different noise levels to conduct statistical comparisons; (2) although some song types seem different (Fig. 1), they have a very low coefficient of variation for frequency characteristics (8.3–20.2%; Sandoval et al., 2016), and if frequency traits are similar across song types, all will be similarly affected by noise level; and (3) males' repertoires change very little in consecutive years (Sandoval et al., 2014, 2016), therefore if changes in frequency traits are detected, they are likely caused by changes in noise level.

#### 2.4. Statistical analysis

We first conducted a general linear mixed-effect model with a Gaussian error structure (LMM, library nlme), to test the temporal effect (i.e., between years) among populations on the mean value of noise in each territory (i.e., response variable). We included year (2012, 2013, and 2014), population (UCR, HDIA, and JBL), and a second order interactions (year\*population) as fixed factors; and territory as a random factor to account for repeated measurements of the same territory during different times of the same year.

We also used LMMs to test if temporal changes of noise affected the traits of calls (*tseet* and *chip* separately), songs, and duets. Each vocalization type was used as a response variable. In each model, we included year, population, noise, and three second order interaction (population\*noise, population\*year, and year\*noise) as fixed factors. For solo songs, we also analyzed the number of elements using the same model structure but with a Poisson error structure. We accounted for repeated measurements of the same individual or pair by including territory as a random factor. We checked for homoscedasticity and normality of residuals in all cases, and results were considered statistically significant when  $P \leq 0.05$ . Means are reported with standard errors. We used the library nlme for statistical models and the library effects to analyze the interactions in the R statistical language, version 3.0.1 (R Development Core Team, 2016).

### 3. Results

From a total of 18330 vocalizations measured, we analyzed  $234 \pm 35$  *chip* calls per pair ( $n = 9574$ ),  $102 \pm 17$  *tseet* calls per pair ( $n = 4148$ ),  $93 \pm 16$  solo songs per male ( $n = 3826$ ), and  $18 \pm 2$  duets per pair ( $n = 749$ ).

### 3.1. Noise measurements between populations

Mean noise level ( $n = 86$ ) differed among populations ( $F = 7.15$ ,  $df = 2,39$ ,  $P = 0.002$ ). Noise was higher and similar in UCR and HDIA populations ( $53.94 \pm 0.75$  dB and  $53.54 \pm 0.81$  dB, respectively) than in JBL population ( $43.32 \pm 1.04$  dB). Mean noise level differed among years ( $F = 22.39$ ,  $df = 2,55$ ,  $P < 0.001$ ); 2013 had the lowest value ( $49.49 \pm 0.73$  dB), then 2012 ( $52.49 \pm 0.92$  dB), and 2014 year had the highest noise level ( $54.83 \pm 0.54$  dB). Mean noise changed significantly between populations and years ( $F = 12.07$ ,  $df = 4,54$ ,  $P < 0.001$ ); it was higher for HDIA in 2014, but lower and similar for HDIA 2013, JBL 2012, and JBL 2013 (Table 1). The noise had intermediate values for UCR 2012, 2013, and 2014, HDIA 2012, and JBL 2014 in relation to other years and populations (Table 1).

### 3.2. Effect of noise on vocalizations

#### *Calls*

The *chip* call traits (minimum frequency, maximum frequency, frequency of maximum amplitude, and duration) were not affected by differences in noise level between territories (Table S1). *Chip* calls showed a shorter duration in 2014 than in 2013, and longer in 2013 than 2012, but the other traits did not change significantly among years (Fig.2; Table S1). The second order interaction between noise, population, and year had no effect on *chip* call traits (Fig.2; Table S1).

The *tseet* call traits (minimum frequency, maximum frequency, frequency of maximum amplitude, and duration) were not affected by changes in noise level (Table S2), but they varied across years and populations. The minimum frequency and frequency of maximum amplitude varied between years, with the lower values for 2012 and higher for 2013 (Fig. 3, Table S2); but the duration was

longer in 2012 than in 2013 (Fig. 3, Table S2). The minimum frequency of *tseet* calls was significantly higher in UCR than in HDIA, but other traits did not vary significantly among populations (Fig. 3; Table S2). The interactions of population\*noise, and population\*years varied significantly between populations for *tseet* calls (Table S2). The minimum frequency was lower in HDIA and JBL during 2012 compared with other population\*year (Fig. 3). The frequency of maximum amplitude was higher for JBL 2013 compared with HDIA 2014, but the other population\*year comparisons were similar (Fig. 3). Finally, the maximum frequency of *tseet* calls increased with the noise level in HDIA but decreased in the other two populations as the noise level increased (Fig. 3; Table S2).

### 3.3. Solo songs

The minimum frequency of songs increased as noise increased (Fig. 4), but it did not affect other song traits (Table S3). Songs showed longer duration in 2014 than the two previous years (Fig. 4; Table S3) and the minimum frequency was higher in 2013 when compared with 2014 and 2012 (Fig. 4; Table S3). The other song traits did not vary significantly between years (Table S3). Songs showed a larger number of elements in UCR than in JBL and HDIA, higher minimum frequencies in UCR than in JBL and HDIA, and higher frequency of maximum amplitude in JBL than in HDIA and UCR (Fig. 4; Table S3). For songs, the minimum frequency showed a large variation among years and populations. HDIA had the lowest value for the minimum frequency in 2012, but it drastically increased for 2013. While JBL registered the highest values of minimum frequency in 2013, but it drastically decreased the next year (Fig. 4). The frequency of maximum amplitude was higher in JBL 2013 and lower in UCR 2013 and HDIA 2012 (Fig. 4). All other population\*year comparisons of minimum frequency and frequency of maximum amplitude fell in between (Fig. 4; Table S3).

Finally, the minimum frequency of songs increased when the noise level increased along the years (Fig. 4; Table S3).

### 3.4. Duets

The maximum frequency of duets decreased as the noise level increased (Fig. 5), but other duet traits were not affected by noise change (Table S4). The minimum frequency and frequency of maximum amplitude were higher in 2013 and 2014 compared with 2012 (Fig. 5; Table S4). The maximum frequency of duets was higher at the UCR than HDIA and JBL (Fig. 5; Table S4); and the minimum frequency of duets increased in all populations as the noise level increased (Fig. 5; Table S4).

## 4. Discussion

### 4.1. Noise measurements between populations

Noise level increased across years in the JBL population, but it was lower than the noise level recorded in HDIA and UCR populations (Fig. S1-S3). The higher level of noise in the UCR population correlates with the increase of anthropogenic activity in the Costa Rican Central Valley between 1995 to 2014 (e.g., urbanizations, commercial and industrial constructions, and the continuous increase of private vehicle fleet through years; Biamonte et al., 2011; Martinez, 2014). The increasing noise in HDIA population was likely related to variation in ambient noise (the presence of a river with very variable flow and wind fluctuation) and changes in vegetation density near the territories rather than with an increase of anthropogenic activity. In a recent study, HDIA population was classified as a rural environment, JBL as suburban, and UCR as an urban environment (HDIA showed 0.75 % of urban surface cover, JBL 21.62% and UCR 65.56%; Juárez,

2018), showing that these populations occur along a gradient of urbanization similar to a study of Mountain Chickadees (Lazerte et al., 2017). This suggests that vocalization traits in HDIA population were more affected by ambient noise than in the other two populations where the background noise was mainly anthropogenic. In the JBL population, the occurrence of gravel roads that limit the traffic and large areas of grassland resulted in low levels of anthropogenic noise; though, there is a slow, but steady increasing in urbanization likely responsible for the noise increase detected in this population during the study period (Fig.2).

#### 4.2. Effect of noise on vocalizations

We found that the minimum frequency increased in solo songs, and the maximum frequency decreased in duets of White-eared Ground-sparrows when noise level was high. The other traits of *tseet* calls, solo songs, and duets correlated with noise level interacting with population and years. For *chip* calls, the duration, minimum frequency, and maximum frequency varied between years. Such variation may result from differences in the area urbanized around each population; for example, in UCR population the urbanized area was larger compared with HDIA and JBL populations (Juárez, 2020b), and this could have intensified the level of anthropogenic noise (Lazerte et al., 2017), due to more people and cars activity. We cannot rule out that the differences observed in *tseet* call, song, and duet traits unrelated with noise variation, may result from cultural differences, because this is a vocal learning species and is known that each population has different song types (Sandoval et al. 2014). Therefore, it is intuitive to expect that calls and duets also have some cultural variation between populations. Moreover, the significant effect of noise on traits of different vocalizations between years, was likely caused by an increase in background noise as urbanization rapidly expands in the Costa Rican Central Valley (Warren et al., 2006;

Martinez, 2014; LaZerte et al., 2017). Thus, birds could change the vocalization traits along years to avoid or reduce the noise overlap effect (Aylor, 1972; Bormpoudakis et al., 2013; LaZerte et al., 2017).

The lack of correlation between some traits with background noise in White-eared Ground-sparrows may be attributed to the fact that these birds sing mainly at dawn; the majority of vocalizations are produced before 06:00 h (Sandoval et al., 2016). This coincides with the time of the day when noise level is low because the rush hour and most people activity occur after 06:30 h in Costa Rica, reducing the overlap of vocalizations with the peak of anthropogenic noise (Gil et al., 2015; Halfwerk et al., 2018).

Although some variation in calls structure has been identified in different bird species (Marler, 2004; Catchpole and Slater, 2008; Halfwerk et al., 2018), they are generally considered to be less variable than other vocalizations (e.g., songs). Characteristics of calls are also expected to show little changes along an individual life or between different contexts (Marler, 2004; Halfwerk et al., 2018). However, we found that noise affected differently each call type in this ground-sparrow. *Tseet* calls which have longer duration and narrower frequency range increased in duration as noise increased. On the contrary, duration in *chip* calls decreases and its frequency range remains unchanged when noise increased. These differences may be attributed to differences in the acoustic traits and the communication role of each call. *Tseet* calls have lower minimum frequencies than *chip* calls (Sandoval et al., 2016), therefore the increase in noise level in some populations could have a stronger effect in *tseet* than in *chip* calls. Contrary to *chip* calls, *tseet* calls are used as a long-distance signal to maintain contact between pair members (Piza and Sandoval, 2016). It is then expected that birds modify the characteristics of *tseet* calls to reduce the probability of being masked by noise (Dabelsteen, 2005; Piza and Sandoval, 2016). Our results



showed that even inside the same species, the noise effect on different calls vary, depending on the acoustic traits of each call, and their function.

As we expected, the minimum frequency of the solo song increased when the noise level increased. Given that White-eared Ground-sparrow solo songs are used for female attraction (Sandoval et al., 2016), reducing overlap with noise will increase the probability to reach more receivers (Wiley and Richards 1982; Slabbekoorn et al., 2002). This is a pattern that has been found in many other animals that inhabit sites with different noise level (Slabbekoorn and Peet, 2003; Hu and Cardoso, 2010; Redondo et al., 2013; Lazerte et al., 2017). However, the White-crowned Sparrows (*Zonotrichia leucophrys*) did not show variation in the minimum frequency of songs in response to noise level (Derryberry et al., 2017). The fluctuating changes in anthropogenic noise (increase and decrease) in the populations of White-eared Ground-sparrow studied, may be the main cause for the lack of correlation between noise variation and differences in song traits (Derryberry et al., 2017). It is also likely that this species uses alternative behavioral strategies such as vocalize near the territory edge, vocalize close to the receiver, or use exposed perches to maximize sound transmission and avoid a possible effect of noise (Patricelli and Blickley, 2006; Luther and Derryberry, 2012; Sandoval et al., 2015). However, White-crowned Sparrows inhabit dense vegetation (Sandoval and Mennill, 2012), and increasing the song minimum frequency to avoid overlap with background noise, could increase the attenuation of high frequencies in this habitat (Wiley and Richards, 1978; Marler, 2004). Therefore, species that inhabit dense vegetation with high anthropogenic noise as singing mice, frogs, or crickets (Van den Bergh and Kappelle, 1998; Savage, 2002; Bailey, 2005) may not increase the minimum frequencies of their vocalizations because this will affect the song transmission and communication with other individuals.

Most bird species that produce duets do not produce solo songs; they use the duet for different functions (Hall, 2009). However, in the White-eared Ground-sparrow duets were produced with a different type of vocalization (Sandoval and Mennill, 2014; Sandoval et al., 2016), and they were affected by noise in a different way than solo songs. The adjustment of duets to the different noise levels recorded for this species was likely the result of a coordinate response of both members of the pair, since changes in noise level correlated with changes in duet frequency, and duets are produced by overlapping vocalizations produced by both members in a pair (Sandoval et al., 2016). Pairs in JBL population produced duets with narrowed-frequency bandwidth due to lower maximum frequency in years with higher noise level. This may optimize the distance at which this vocalization is transmitted, as has been suggested for Northern Cardinal (*Cardinalis cardinalis*) and Gray Catbird (*Dumetella carolinensis*) (Dowling et al., 2012). Additionally, in habitats with dense vegetation, as those used by White-eared Ground-sparrows (Sandoval and Mennill, 2012), vocalizations with relatively low minimum frequencies and a narrow-frequency bandwidth are transmitted better (Richards and Wiley, 1980; Dowling et al., 2012). Hence, at least some of the changes found in duet traits were likely related with differences in the structure of the habitat in different population rather than with variation in noise level. To understand the effect of anthropogenic noise in a particular species' vocalizations without confounding effects, we need to consider the effect of habitat structure, morphology, physiology, or species' life history which may vary over time and across populations (Slabbekoorn and Smith, 2002; Luther and Derryberry, 2012; Naguib et al., 2013). Characteristics of each habitat may introduce different selection pressures and provoke changes in the structure of vocalizations similar to those changes produced by variation in noise levels (Hu and Cardoso, 2010; Ríos-Chelén et al., 2012).

All the authors agree in this submission of our paper and agree with all the corrections made it.

### ***Ethical approval***

This study was conducted in accordance with the current laws in Costa Rica. Permission for research was given by the Ministerio de Ambiente y Energía de Costa Rica under permit number 071-2011-SINAC, 007-2013-SINAC, and under the project number of Vicerrectoría de Investigación, Universidad de Costa Rica 111-B5-241.

### **Declaration of Competing Interest**

Authors CM, GB, and LS declare that they have no conflict of interest.

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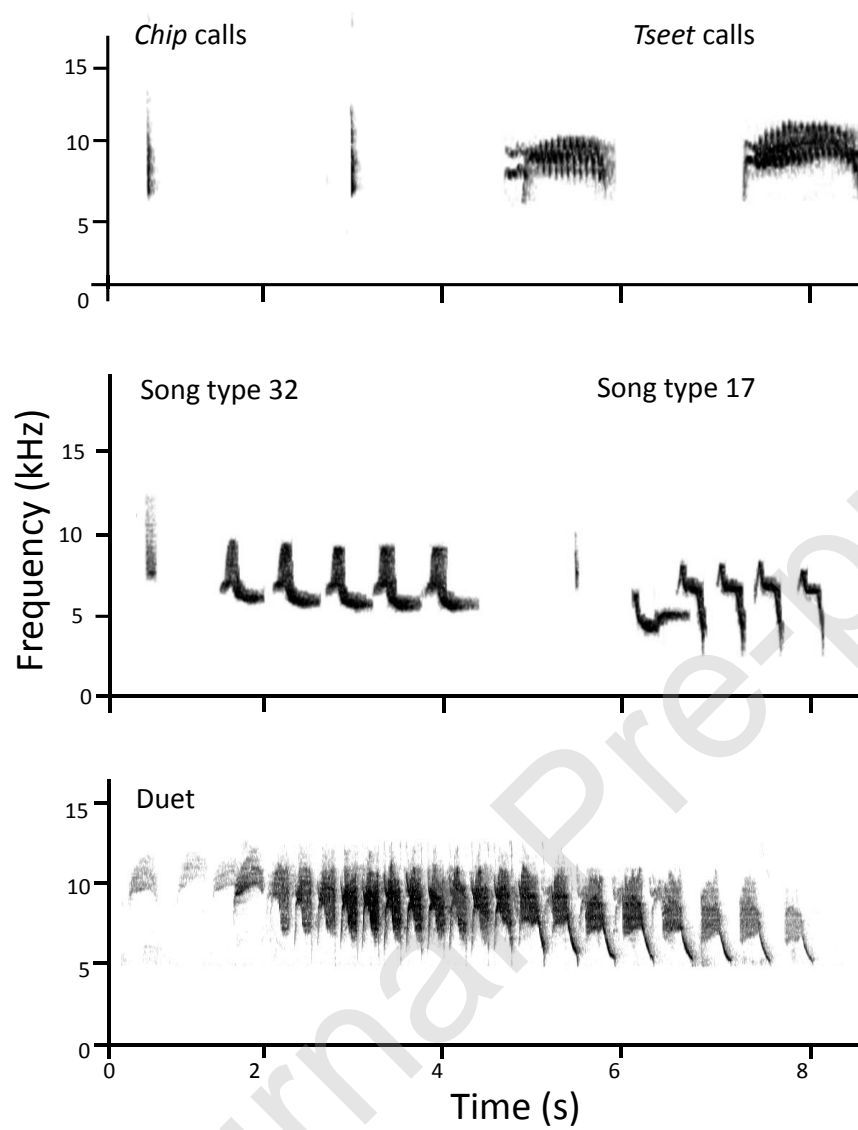
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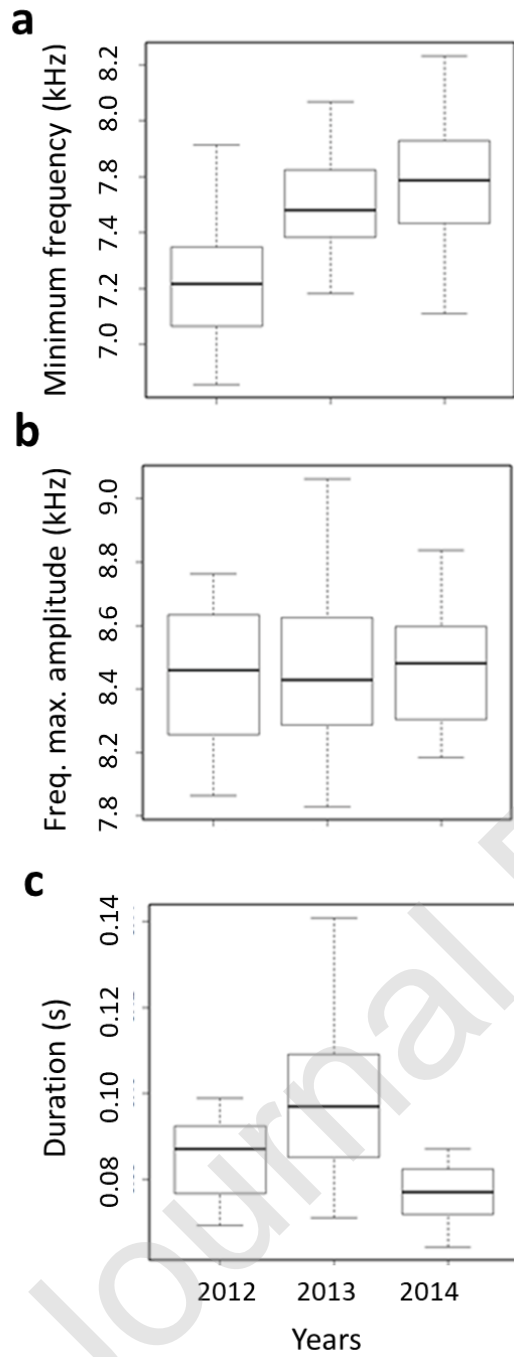
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## FIGURES

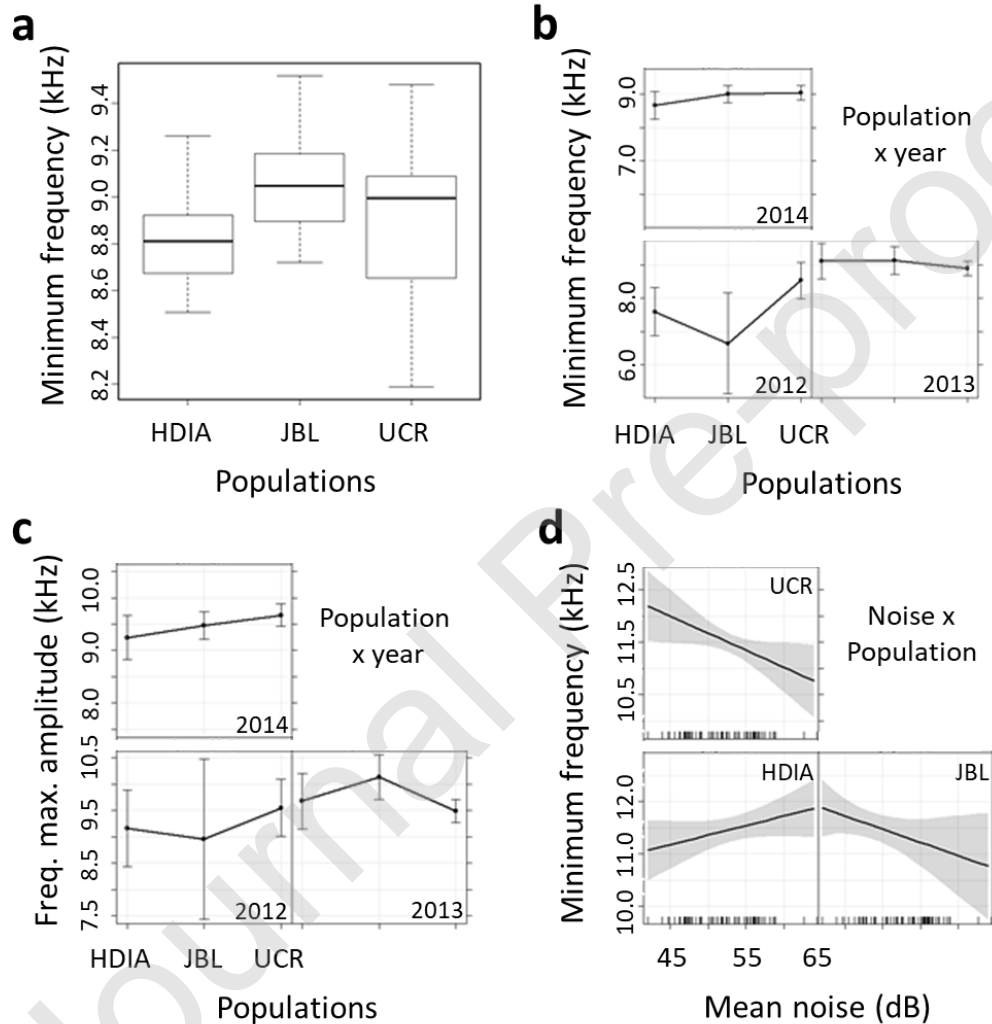


**Fig. 1.** Sound spectrograms representing the three types of vocalizations produced by the White-eared Ground-sparrow, with two examples of call types, two common male solo songs, and a complete duet.



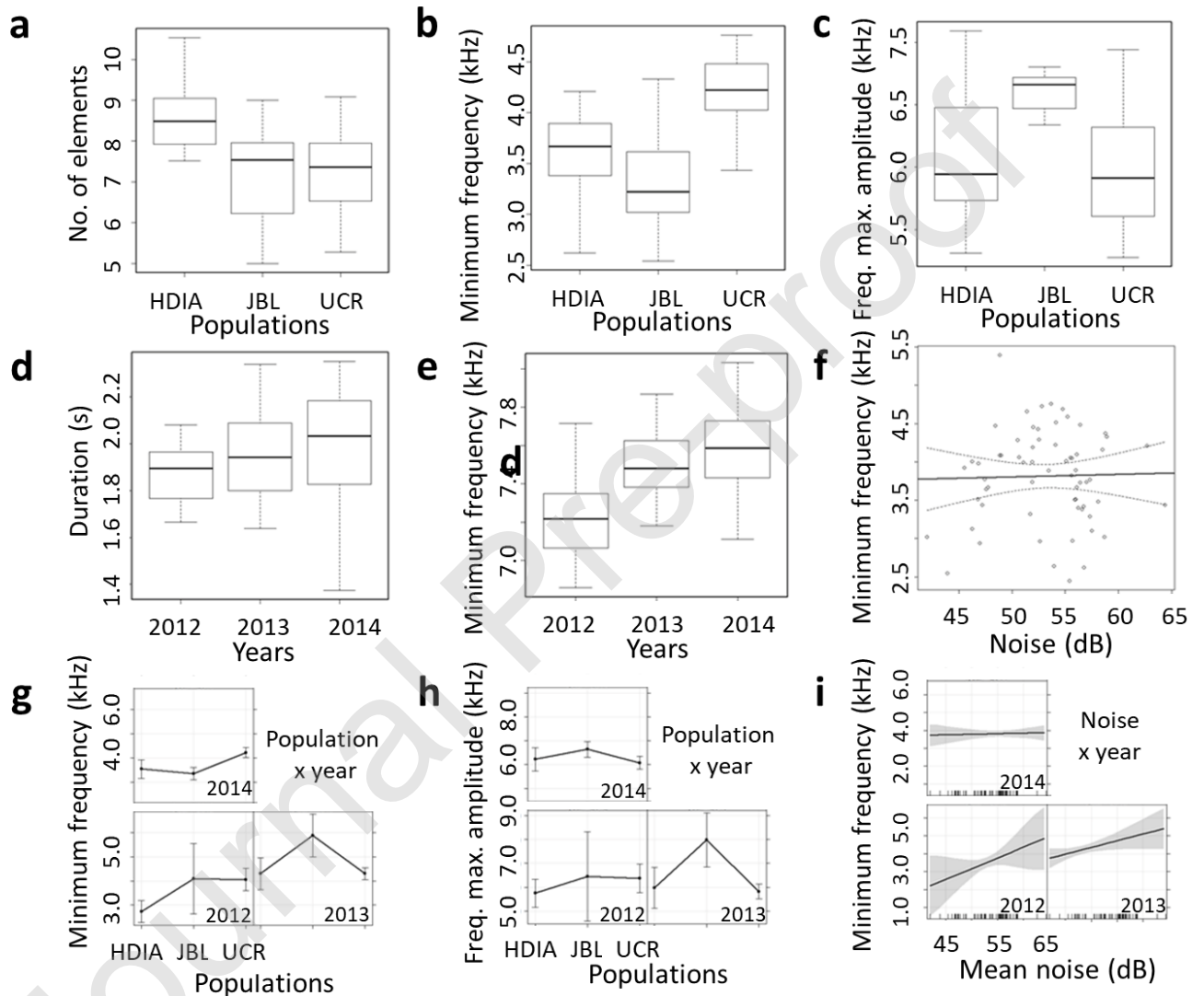
**Fig. 2.** Variation in the acoustic characteristics of White-eared Ground-sparrow *chip* calls over a three year period: (a) change in minimum frequency, (b) frequency of maximum amplitude, and (c)

duration of *chip* calls over a three year period. Whiskers represent the minimum and maximum for each variable, bold line represents the median, and bottom and top of the box represent the first and third quartile.



**Fig. 3.** Variation in the acoustic characteristics of White-eared Ground-sparrow *tseet* calls. (a) Differences in minimum frequency among the three populations (whisker represents the minimum and maximum, bold line represents the median, and bottom and top of the box represent the first

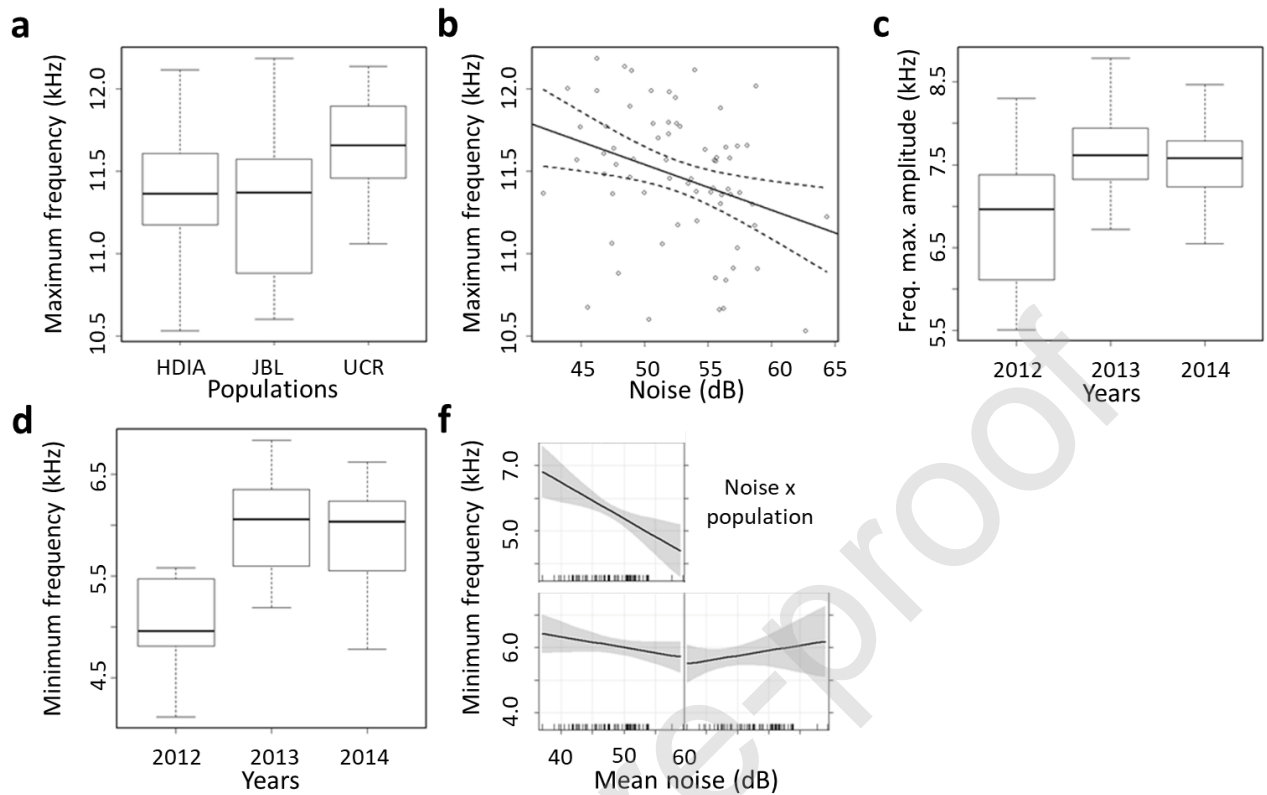
and third quartile). The other figures show the significant interactions population\*years for (b) the minimum frequency; and (c) frequency of maximum amplitude; (d) shows the significant interaction between population and noise level (grey area represents 95% confidence limits).



**Fig. 4.** Variation in the acoustic characteristics of the song of the White-eared Ground-sparrow. (a) Difference in number of elements, (b) minimum frequency, and (c) frequency of maximum amplitude across populations; and difference in (d) song duration, and (e) minimum frequency among years (whisker represents the minimum and maximum, bold line represents the median,

and bottom and top of the box represent the first and third quartile), and (f) with change in noise level (dotted line represent 95% confidence limits). The other figures show different significant interactions: (g) population\*years for minimum frequency, and (h) for frequency of maximum amplitude; and (i) the significant interaction between year and noise level (grey area represent 95% confidence limits).





**Fig. 5.** Variation in the acoustic characteristics in duets of the White-eared Ground-sparrow. (a) Difference of maximum frequency among populations (whisker represents the minimum and maximum, bold line represents the median, and bottom and top of the box represent the first and third quartile); (b) relationship between noise level and maximum frequency (dotted line represent 95% confidence intervals); (c) difference in frequency of maximum amplitude across years; (d) difference in minimum frequency across years; and (e) shows the significant interaction between populations and noise level for minimum frequency (grey area represents 95% confidence intervals).

## TABLES

**Table 1.** Variation of mean noise ( $\pm$  SE) between populations and years in White-eared Ground-sparrow territories. Cells with different letters are significantly different.

	Year		
Population	2012	2013	2014
HDIA	55.46 $\pm$ 1.44 ab	47.6 $\pm$ 1.10 c	57.56 $\pm$ 0.89 a
JBL	46.37 $\pm$ 1.89 c	47.96 $\pm$ 1.63 c	53.64 $\pm$ 1.11 b
UCR	55.6 $\pm$ 1.43 ab	52.91 $\pm$ 0.99 b	53.30 $\pm$ 0.76 b