

Transmission characteristics of solo songs and duets in a neotropical thicket habitat specialist bird

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The Acoustic Adaptation Hypothesis posits that habitat characteristics influence the structure of animal vocalizations and that animals will vocalize and display behaviours optimized for sound transmission. White-eared ground-sparrows *Melospiza leucotis* live in habitats with dense vegetation where vocal communication is an ideal mode of communication for territory defence and mate attraction. On the basis of the Acoustic Adaptation Hypothesis, if solos and duets of these ground-sparrows are used in long-distance communication, we should expect that these vocalizations will exhibit structures that enhance sound transmission. We conducted a sound transmission experiment where we broadcast and re-recorded solo songs and duets to study their transmission properties. We used two speaker heights and two microphone heights to simulate different perch heights of signallers and receivers and four distances between the speakers and microphones to simulate variable distances of separation. We found that solo and duet songs show similar patterns of degradation and attenuation with distance and proximity to the ground. These results suggest that solo and duet songs facilitate communication with receivers at similar distances. The highest perches, for both signallers and receivers, maximized acoustic transmission. This is the first study that evaluates the transmission properties of songs and duets in birds, despite the fact that many bird species in tropical forests produce both types of vocalizations. To our surprise, we found that solo and duet songs degraded to below-detectable levels in less than a typical territory's diameter, suggesting that this species has not experienced strong selection for long-distance communication.

Keywords: acoustic adaption; long-distance communication; *Melospiza leucotis*; sound transmission; thicket habitats; white-eared ground-sparrow

Introduction

The structure of vegetation and the ambient noise characteristics in wilderness habitats have a heavy influence on animal vocalizations (e.g. Dabelsteen et al. 1993; Forrest 1994; Balsby et al. 2003). Numerous investigations have demonstrated that animal signals are acoustically adapted to optimize transmission characteristics in their habitat (Boncoraglio and Saino 2007; Ey and Fisher 2009). If habitat characteristics change, the structure of the vocalizations may also change over time to enhance transmission distance (e.g. Perla and Slobodchikoff 2002; Derryberry 2009). By studying the transmission properties of animal vocalizations, we can explore the relationship between animal communication and animal habitats.

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Some habitats may present more significant challenges for the transmission of animal vocalizations than others. In particular, noisy environments and habitats with very dense vegetation may present substantial communication challenges to both signallers and receivers (Slabbekoorn et al. 2002; Slabbekoorn 2004; Redondo et al. 2013). In tropical environments, early successional habitats with dense vegetation – known as thickets – may present special barriers to signal transmission, because vegetation causes scattering, reflection and reverberation, thereby attenuating signals (Slabbekoorn et al. 2002; Dingle et al. 2008). Many thicket habitats are also located close to noisy places such as river edges, streets and towns (Sanchez-Azofeifa et al., 2001; Harvey et al. 2008; Biamonte et al. 2011), which may further impede acoustic communication between animals living therein (Ryan and Brenowitz 1985; Slabbekoorn and Peet 2003; Barker 2008).

Studies of sound transmission have focussed on the breeding vocalizations produced by animals, including a heavy focus on male songs (Boncoraglio and Saino 2007; Ey and Fisher 2009), likely because these vocalizations are amongst the most conspicuous long-distance vocalizations (Andersson 1994; Catchpole and Slater 2008). According to the Acoustic Adaptation Hypothesis (Morton 1975; Hansen 1979), the acoustic characteristics of animal vocalizations are adapted to optimize transmission in the habitat where they are typically transmitted (Boncoraglio and Saino 2007; Ey and Fisher 2009). Several investigations of the transmission properties of bird songs confirm that this is the case (Ryan et al. 1990; Brown et al. 1995). Yet, animals also produce a wide variety of other acoustic signals beyond male breeding songs: female songs, calls from both sexes, vocal duets and many types of soft songs (Langmore 1998; Matrosova et al. 2011; Geissmann 2002; Marler 2004). Some of these vocalizations may also be used in long-distance communication – such as vocal duets (Hall 2009) or contact calls (Marler 2004) – and, therefore, may be acoustically adapted to their environment. Consequently, it is worthwhile to explore acoustic adaptation in these other types of signals.

Our main objective in this investigation is to compare the transmission characteristics of the solo and duet songs of white-eared ground-sparrows *Melospiza leucotis*, a species that specializes in dense thicket habitats of the Neotropics (Sandoval and Mennill 2012). Males and females of this species live as territorial pairs throughout the year, as do many tropical birds (Stutchbury and Morton, 2008). White-eared ground-sparrows produce three main types of vocalizations: both sexes produce calls; males produce loud solo songs for female attraction and breeding partners combine their vocalizations to produce loud vocal duets for within-pair communication and territory defence (Sandoval et al. 2013, 2015). Whereas some birds use the same vocalization when they sing solos and duets, the duets of ground-sparrows are created with very different vocalizations than those used by males as solo songs (Sandoval et al. 2013, Sandoval and Mennill 2014). Whereas male solo songs are frequency-modulated tones between 3.5–11.2 kHz, the vocalizations that males and females contribute to duets are rapid, noisy sounds between 5.1–11.5 kHz (see Sandoval et al. 2015). On the basis of the Acoustic Adaptation Hypothesis, it is reasonable to predict that white-eared ground-sparrow solo songs should have evolved to maximize sound transmission through thicket habitats, especially because songs are used to attract females that may be located a substantial distance away. Duets, on the other hand, are used for within-pair communication and for territory defence against other pairs in this species (Sandoval et al. 2013, 2015), and, therefore, it is reasonable to predict that white-eared ground-sparrow duets should have evolved to optimize sound transmission within a territory and between adjacent territories. The sound spectrograms of white-eared ground-sparrow vocalizations, however, show unexpected patterns; they exhibit broad bandwidth, relatively short duration of elements and prominent trills (Sandoval et al. 2015). Under the

Acoustic Adaptation Hypothesis we expect that vocalizations with narrow bandwidth, long duration and a low minimum frequency should maximize transmission in dense vegetation, and trills should be favoured in open environments rather than in dense vegetation (Morton 1975; Hansen 1979; Boncoraglio and Saino 2007). A field study of the transmission properties offers the opportunity to understand if these patterns could be an adaptation to optimize long-distance communication in thicket habitats.

We conducted a sound transmission experiment to evaluate the transmission characteristics of white-eared ground-sparrow's solo and duet songs. Specifically, we addressed two questions: (1) Do the solo and duet songs of white-eared ground-sparrows have different transmission properties? (2) Do the transmission properties of solo and duet songs vary with the perch height of the signaller or receiver? If white-eared ground-sparrow solo and duet songs are used to communicate with receivers at similar distances, we predicted that both types of vocalizations would share the same pattern of degradation and attenuation through thicket habitats. If one vocalization is used mainly for short-range communication (e.g. between pair members) and the other for long-range communication (e.g. with animals in adjacent territories), we predicted that one vocalization would show more degradation and attenuation than the other. Finally, we predicted that higher perches would increase sound transmission range, as has been reported in other studies (Krams 2001; Mathevon et al. 2005; Barker et al. 2009); therefore, vocalizations should show higher levels of degradation and attenuation closer to the ground.

Materials and methods

Study sites and territory measurements

We conducted this study in the Getsemaní region of Heredia province, Costa Rica (10°01'N, 84°06'W; 1300 m elevation), where white-eared ground-sparrows are common inhabitants in young secondary forest edges, shade coffee plantations and naturally occurring thickets. The study was conducted from 30 July to 2 August 2012, during the last part of this species' breeding season (Sandoval and Mennill 2012). The weather was similar throughout the four-day experiment, with a clear sky and little wind. All the playback sessions took place inside three typical white-eared ground-sparrow territories (one in a thicket-like shade coffee plantation and the other two in natural thickets). All experiments took place in the morning between 6:00 and 9:00 am, a time when both male solo songs and vocal duets are produced by this species (Sandoval et al. 2015).

To describe vegetation density within occupied territories, we measured the number of trees (plants > 2 m tall and with a diameter at breast height \geq 10 cm), bushes (plants 1–2 m tall with the main trunk diameter of 2–10 cm), and the percentage of ground covered by grasses and small plants (15–100 cm tall) in 19 white-eared ground-sparrow territories, including the three territories where the transmission experiment was performed. We collected 8–12 measurements per territory using 2 × 2 m plots. We originally endeavoured to take 12 measurements in each territory, but some territories were too small for 12 plots; in other territories, the land structure included steep slopes or creeks, prohibiting 12 plots. We distributed the plots along the cardinal axes (north, south, east and west) at three distances from the territory centre: 5, 10 and 20 m.

Transmission playback stimuli

To create stimuli for playback, we used representative vocalizations (common solo types and duet types within our study populations, with species-typical frequency ranges), which

we recorded during previous investigations of this species. Recordings were collected with a Marantz PMD661 digital recorder (sampling rate: 44.1 kHz; accuracy: 16-bit and file format: WAVE) and a Sennheiser ME66/K6 directional microphone. We selected our highest quality recordings, focussing on sounds with little or no overlapping background sounds and with a high signal-to-noise ratio (Figure 1). Sounds used in the experiment were selected from five different individuals. For male solo song stimuli, we chose a solo song from two different males. For duet stimuli, we chose three duet contributions, one from a male and two from individuals of unknown sex (owing to the dense vegetation at our study site and the fact that pair members often forage in very close proximity, we could not assign the sex of the singer with confidence). We used non-overlapping duet contributions (i.e. incomplete duets, see Sandoval et al. 2015), rather than the overlapping male–female duets (i.e. a vocalization produced by both members of the pair singing simultaneously), because male and females overlap in frequency and time (Sandoval et al. 2015), making it impossible to separate the sexes' contributions for the analysis. These recordings were obtained from individuals recorded at less than 5 m.

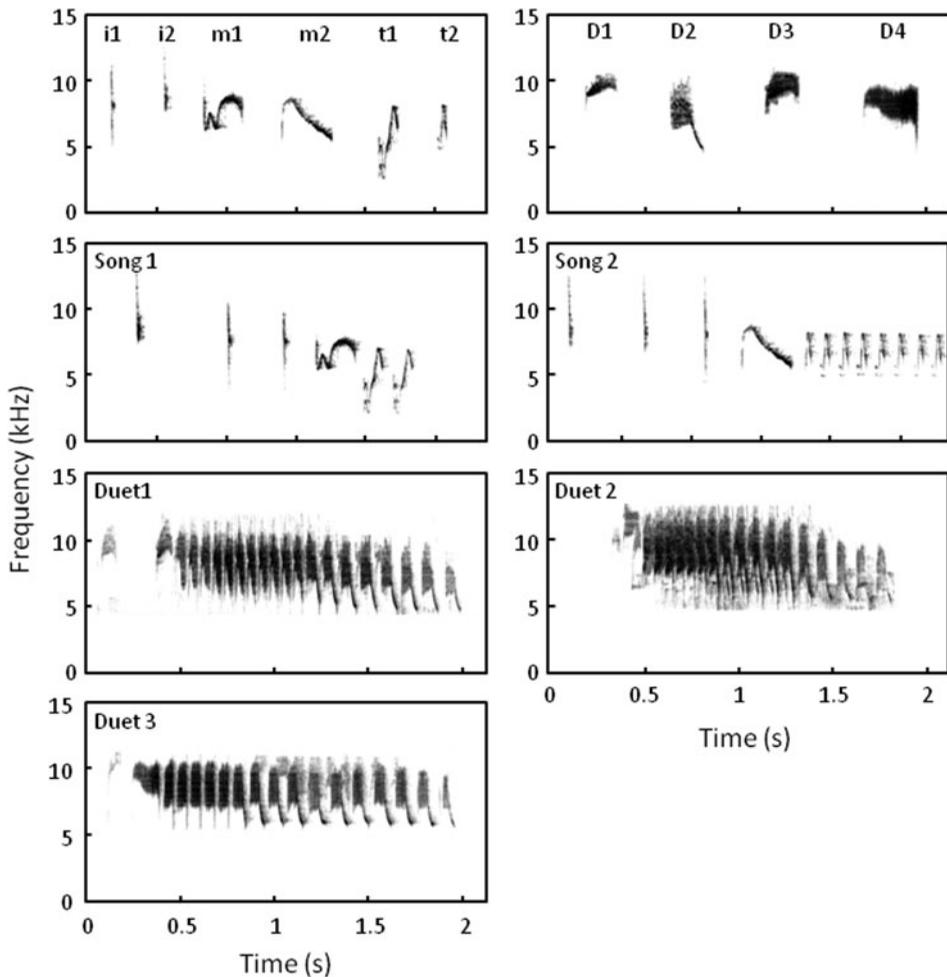


Figure 1. Spectrograms of the solo songs and duets of white-eared ground-sparrows used in the transmission experiments.

We also analysed degradation and attenuation in isolated elements of solo songs ($N = 6$ elements, 3 from each of 2 males' songs) and duets ($N = 4$ elements from three different birds; Figure 1), because the context in which sounds are broadcast can influence the assessment of their transmission characteristics; the tail of a preceding element within a song could influence the analysis of the subsequent measurement. However, our results revealed no differences between our analyses of complete solo and duet songs and the isolated elements of those sounds, and, so, we present only the analyses of complete solo and duet songs in the article.

The stimuli were composed of a sequence of five repetitions of two complete solo songs, and three duet songs (Figure 1). Each repetition was separated by 3 s of silence. Solo and duet songs were separated by 1.5 s of silence. Given the variable frequency range of solo and duet songs, we used different filters to isolate the sounds of interests, by excluding background sounds, for our playback stimuli. For solo songs, we used the following filters: solo song 1: 1.5–11 kHz; and solo song 2: 4–13.5 kHz (Figure 1). For duet songs, we used the following filters: duet 1: 4–11.5 kHz; duet 2: 4–12 kHz and duet 3: 4–10.5 kHz (Figure 1). We applied these filters using the passive option of the Fast Fourier Transformed filter in Audition 1.0 (Adobe Systems, San Jose, CA, USA). Stimuli were standardized to -1 dB using the normalize feature in Audition. The stimuli were transferred to a portable audio player (model: Ipod Touch Nano, Apple, Cupertino, CA) for playback in the field.

Transmission experiment

We broadcast the stimuli from an active loudspeaker (Anchor Audio; Minivox; frequency response: 0.1–12 kHz), re-recorded them using an omnidirectional microphone (Sennheiser ME62/K6) and a solid-state digital recorder (Marantz PMD661; sampling rate: 44.1 kHz; accuracy: 16-bit; file format: WAVE) and connected via a microphone preamplifier (Sound Device MP-1; frequency response: 0.02–22 kHz). We played back the stimuli at a constant volume of 80 dB SPL, measured at 1 m from the speaker using a digital sound level meter (Radio Shack model 33–2055 using C weighting, slow response). This broadcast amplitude matched how loud the ground-sparrow solo songs and duets are in the field, according to the perception of two investigators with 3 years of experience in recording this species. As the distance between the loudspeaker and the microphone increased, we adjusted the level of our preamplifier so that we could still record the playback sounds (we applied no gain at distances of 4 and 8 m between the loudspeaker and microphone and a gain of 18 dB at 16 m and 32 m distances; we compensated for this difference in our analysis, by adding 18 dB to the appropriate measurements).

For each of the three transmission tests, we played sounds across four horizontal distances (4, 8, 16 and 32 m between the loudspeaker and microphone) and at two microphones and speaker heights (0.4 and 2.2 m). We used these heights for the microphone and speaker to represent the two common heights where we have observed white-eared ground-sparrows producing duets and solo songs, respectively. Solo songs are produced from perches that vary between 1 and 3 m in height, with an average of 2.30 ± 0.13 m (\pm SE, $N = 18$); meanwhile, duets are produced mainly from perches close to or directly on the ground, with an average of 0.35 ± 0.09 m ($N = 17$). The horizontal distances were selected to represent the distances we often observed between the pair members (i.e. the two shorter distances) and between neighbouring pairs (i.e. the two longer distances). Rather than repeating the playback at the four horizontal distances along

a linear transect, as has been done in previous studies (e.g. Barker et al. 2009, Sabatini et al. 2011), we distributed the four horizontal distances at different axes within each territory. In doing so, we hoped to include more of the birds' territories in our transmission test, providing a more representative sampling of the effect of habitat on sound transmission. We chose these playback axes according to the cardinal points (north, south, east and west) in two of the territories; for the third, the shape of the territory prevented us from conducting the transmission test in the cardinal directions, and, therefore, the four transects in this territory started at the same point but were distributed at different distances to the south. We measured the temperature (mean \pm SE: $24.6 \pm 0.6^\circ\text{C}$) and relative humidity (mean \pm SE: $94.8 \pm 0.2\%$) every 5 min during the experiment using the internal humidity and temperature device of the SM2 + Wildlife Acoustic Song Meters (Wildlife Acoustics, Inc., Concord, MA, USA) placed at a height of 1 m inside each territory.

Sound analysis

We used SigPro 3.25 software (Pedersen 1998) to analyse the rerecorded sounds. Rather than comparing the re-recorded sounds to the playback stimuli, we compared them to re-recorded sounds collected at a distance of 1.0 m. This allowed us to control for changes in the sound that may have arisen because of the playback equipment. For the 1.0-m recording, the speaker was oriented upwards, and the microphone was hung 1.0 m directly overhead in the centre of an open field of 20×20 m. We did this to avoid recording the re-recorded sound with reverberations produced by the ground and vegetation in the recording. The first three repetitions of each sound for each unique transmission test that were not overlapped by any other sound were selected for use in the analysis.

We measured the variation in background noise using the same filter settings that we used to isolate each of the stimulus sounds; we measured noise levels immediately before the start of the stimulus for each sound that we analysed (as described in Dabelsteen et al. 1993). As in other transmission studies (e.g. Dabelsteen et al. 1993, Sabatini et al. 2011), we assumed that the background noise before each stimulus was the same as the noise that overlapped the experimental sounds.

For each experimental sound, after we applied a bandpass filter to remove background noise outside the range of the signal of interest, we measured the following four variables: the signal-to-noise ratio (the comparison between the amount of energy in the observed sound versus energy in the background noise immediately before the sound of interest), the tail-to-signal ratio (the amount of energy in the reverberant tail compared with the energy in the observed sound), the blur ratio (the distortion of the signal's frequency and amplitude pattern over time) and the excess attenuation (attenuation beyond the spherical spreading of 6 dB per doubling of the distance). Details about the formulas used to collect these measurements in SigPro are presented in the studies done by Dabelsteen et al. (1993), Holland et al. (1998) and Lampe et al. (2007). For several of the 32-m playback sessions, the re-recorded sound was too faint for analysis even with the use of the preamplifier, and these sounds were excluded from our analysis.

Statistical analysis

We performed two-sample *t*-tests to compare the territorial characteristics between the territories where transmission experiments were conducted against territories without transmission experiments. For trees and bushes, we conducted this analysis on raw data;

for the percentage of ground covered by grasses and small plants, we transformed the data using a square root arcsine function to meet the requirements of the test (McCune and Grace 2002). We performed linear mixed-effects models (LMM) to analyse the effect of the sound transmission experiments on signal degradation. The LMM were used to compare the transmission properties of solo songs versus duets. There were four fixed factors in the LMM: the distance between the speaker and microphone (four levels: 4, 8, 16 and 32 m), the speaker height (two levels: 0.4 m and 2.2 m), the microphone height (two levels: 0.4 m and 2.2 m) and sound type (two levels in our analysis of whole songs: solos and duets). The response variables were the four sound degradation measurements (signal-to-noise ratio, tail-to-signal ratio, blur ratio and excess attenuation), which we ran separately in four independent models. We included as a random effect, the territory where each experiment was conducted and the playback stimuli. We estimated only the main effects and the two-factor interactions in our analysis. Finally, we performed post-hoc tests on all pairwise comparisons between the main effects and the two-factor interactions using Bonferroni corrections, adjusting the alpha for all tests. The residuals of our response variables were normally distributed (Kolmogorov–Smirnov normality test: $p > 0.05$) and showed equality of variances.

We analysed variation in background noise by following the technique used in several previous transmission studies (Nemeth et al. 2001; Barker et al. 2009; Sabatini et al. 2011); specifically, we conducted another LMM on measurements collected from the period immediately before each bout of broadcast sounds, measuring the region of the sound spectrum that remained after the aforementioned filters were applied to each sound. This analysis allowed us to understand how background noise may vary between the different frequency ranges of the test sounds and contribute to the signal-to-noise ratio. There were four independent factors in this analysis: the distance between the speaker and microphone (four levels), sound type (two levels), speaker height (two levels) and microphone height (two levels). The response variable was the background noise level measurement. We included as a random effect the territory where each experiment was conducted and the playback stimuli. Throughout, we report all values as mean \pm SE. Statistical analyses were conducted in JMP (version 10.0; SAS Institute, Cary, NC, USA).

Results

Vegetation characteristics

We sampled the vegetation in 19 white-eared ground-sparrow territories and found 0.10 trees/m² (range: 0–0.23 trees/m²) and 0.45 bushes/m² (range: 0.06–1.20 bushes/m²). The percentage cover of grass and small plants was 52% (range: 11–100%). The three territories used for the experiment showed vegetation characteristics that were very close to the population average (trees/m² = 0.08 \pm 0.12: $t = 0.25$, $df = 17$, $p = 0.80$; bushes/m² = 0.48 \pm 0.05: $t = 0.24$, $df = 17$, $p = 0.81$; percentage of cover = 60.1 \pm 11.4: $t = 1.74$, $df = 17$, $p = 0.10$), supporting the idea that our transmission locations were representative of white-eared ground sparrow territory characteristics generally.

Degradation of solo and duet songs

For comparisons between solo and duet songs, we observed a significant variation in signal-to-noise ratio (LMM whole model: $p < 0.001$), tail-to-signal ratio ($p < 0.001$), blur ratio ($p < 0.001$) and excess attenuation ($p < 0.001$) for both the main effects and the two-factor interaction terms (Table 1). As expected, with the increasing distance between the

Table 1. Main effects and two-factor interactions in linear mixed-effects models comparing the complete solo songs versus complete duets for each attenuation and degradation measurement.

	Signal-to-noise Ratio			Tail-to-Signal Ratio			Blur Ratio			Excess Attenuation		
	df	F	p	df	F	p	df	F	p	df	F	p
Distance	3,678	580.76	>0.001	3,491	117.53	>0.001	3,695	14.41	>0.001	3,696	210.15	>0.001
Speaker height	1,678	4.80	0.03	1,490	0.25	0.62	1,695	1.41	0.24	1,696	0.03	0.87
Microphone height	1,678	57.74	>0.001	1,490	0.49	0.48	1,695	8.79	>0.001	1,696	17.91	>0.001
Sound type	1,4	1.42	0.31	1,119	22.70	>0.001	1,112	0.25	0.62	1,31	0	0.97
Distance X speaker height	3,678	17.63	>0.001	3,491	2.48	0.06	3,695	2.97	0.03	3,696	23.98	>0.001
Distance X microphone height	3,678	14.35	>0.001	3,492	6.06	>0.001	3,695	8.11	>0.001	3,696	32.22	>0.001
Distance X sound type	3,678	0.69	0.56	3,491	8.6	>0.001	3,695	1.91	0.13	3,696	0.62	0.60
Speaker height X microphone height	1,678	13.18	>0.001	1,491	19.02	>0.001	1,695	1.34	0.25	1,696	59.99	>0.001
Speaker height X sound type	1,678	0.81	0.37	1,491	5.19	0.02	1,695	6.52	0.01	1,696	0.22	0.64
Microphone height X sound type	1,678	2.52	0.11	1,490	7.51	0.01	1,695	5.70	0.02	1,696	0.11	0.74

loudspeaker and the microphone, sounds showed lower signal-to-noise ratios, higher tail-to-signal ratios, a higher blur ratio and an increased excess attenuation (Figure 2). When speakers were closer to the ground (0.4 m vs. 2.2 m), sounds showed lower signal-to-noise ratios (Figure 2), but the other three variables did not show any statistical variation with height. When microphones were closer to the ground (0.4 m vs. 2.2 m), sounds showed lower signal-to-noise ratios and a higher blur ratio (Figure 2), but tail-to-signal ratios and excess attenuation were not statistically different. Solo songs showed higher tail-to-signal ratios than duets (Figure 2), but the other three variables were not statistically different.

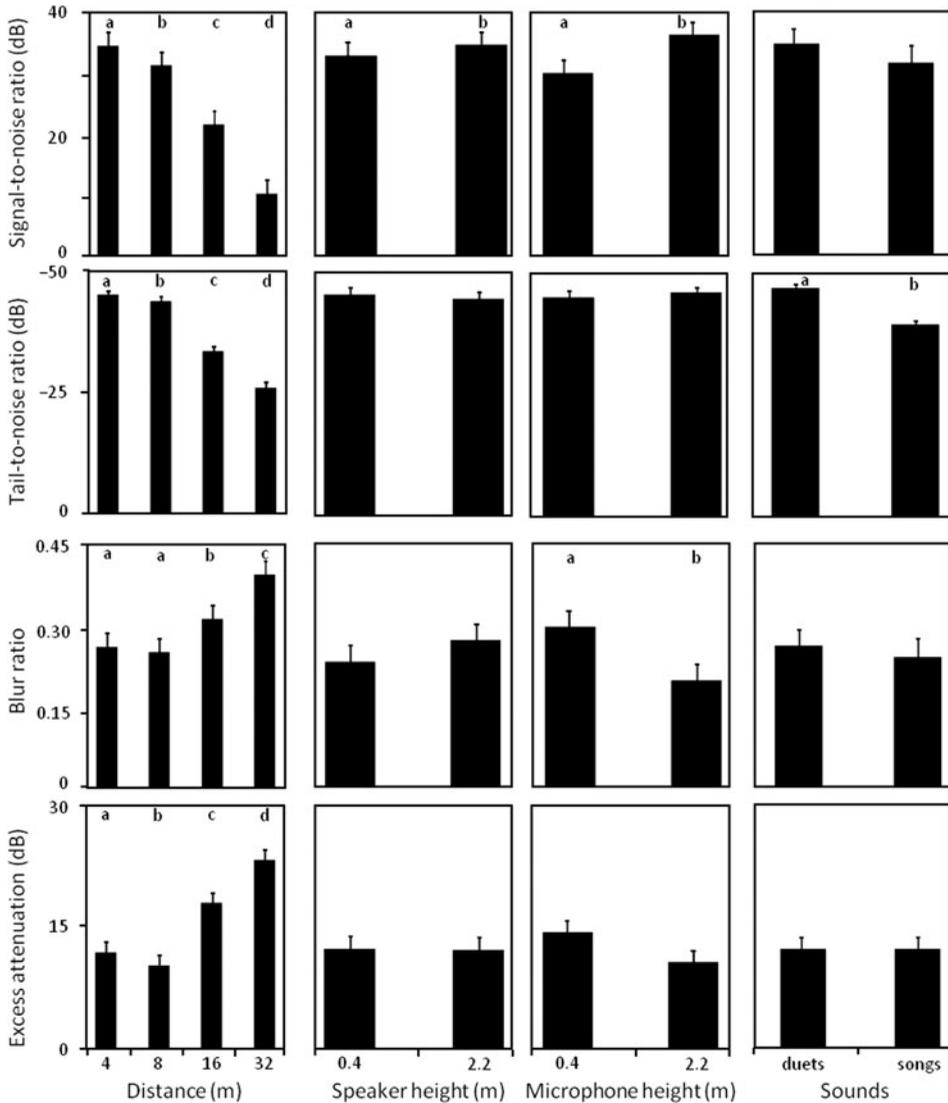


Figure 2. Variation in four measurements of sound degradation according to distance, speaker and microphone heights and sound type used in the transmission experiments. Error bars are standard errors around the mean. Lowercase letters above the bars show the results of post-hoc tests for comparisons that showed statistically significant differences; bars with the same letters are not statistically different.

The distance \times speaker height interaction showed higher signal-to-noise ratios for higher perches at shorter distances; lower blur ratios for lower perches at shorter distances and for higher perches at larger distances and similar excess attenuation at both perch heights at shorter distances and decreased excess attenuation for higher perches at larger distances (Table 1; Figure 3). The distance \times microphone height interaction showed higher signal-to-noise ratios at shorter distances and higher perches; similar tail-to-signal ratios for both perch heights at shorter distances and lower tail-to-signal ratios for higher perches at larger distances; lower blur ratio for higher perches at shorter distances and decreased excess attenuation for higher perches at larger distances (Table 1; Figure 3).

The distance \times sound interaction showed higher tail-to-song ratios with increased distance, but at 32 m, the tail-to-signal ratio was similar for both perch heights (Table 1; Figure 3). The speaker height \times microphone height interaction showed similarly low signal-to-noise ratios when stimuli were produced close to the ground and recorded at both heights, but higher signal-to-noise ratios when stimuli were produced and recorded at higher perches and higher tail-to-signal ratios at diagonal propagation (i.e. from a high song post to a low receiver post or vice versa; Table 1; Figure 4). Speaker height \times sounds and microphone height \times sounds interactions showed songs with higher tail-to-signal ratios and blur ratios at both heights in comparison with duets (Table 1; Figure 4).

Background noise variation

In our analysis of the background noise that preceded each bout of recording, we found that background noise levels varied with distance (Table 2), where there was slightly more background noise at 32 m than at 16 m, and a similar noise level at both 8 m and 4 m. In addition, we found a slightly more background noise in our analysis of solo songs versus duets (Table 2). The only interactions that affected the background noise levels were distance \times sound type and speaker height \times microphone height (Table 2). The distance \times sound type interaction showed more background noise at 32-m solo songs than at 32-m duet songs and 16-m solo and duet songs, and a similar noise level at both 8 m and 4 m solo and duet songs. The speaker height \times microphone height interaction showed more background noise when both the apparatuses were at 2.2 m in height, the lowest noise levels when the speaker was at 2.2 m and the microphone at 0.4 m in height and similar medium noise levels when both apparatus were at 0.4 m and speaker at 0.4 and microphone at 2.2 m in height.

Discussion

Using a sound transmission experiment, where we played the solo and duet songs of white-eared ground-sparrows across several different distances and at two different speaker and microphone heights in this species' native thicket habitat, we showed that the degradation and attenuation of solo and duet songs increased with distance and proximity to the ground. We found that solo and duet songs experienced similar patterns of attenuation and degradation, indicating that both types of vocalizations transmit similar distances when they are emitted at the same source level and suggesting that both solos and duets are designed to communicate with receivers located at similar distances from signallers. Speaker and microphone height positively influenced the transmission of vocalizations, demonstrating that ground-sparrow solos and duets experience less degradation and attenuation from higher perches. Patterns of attenuation were influenced by the interaction

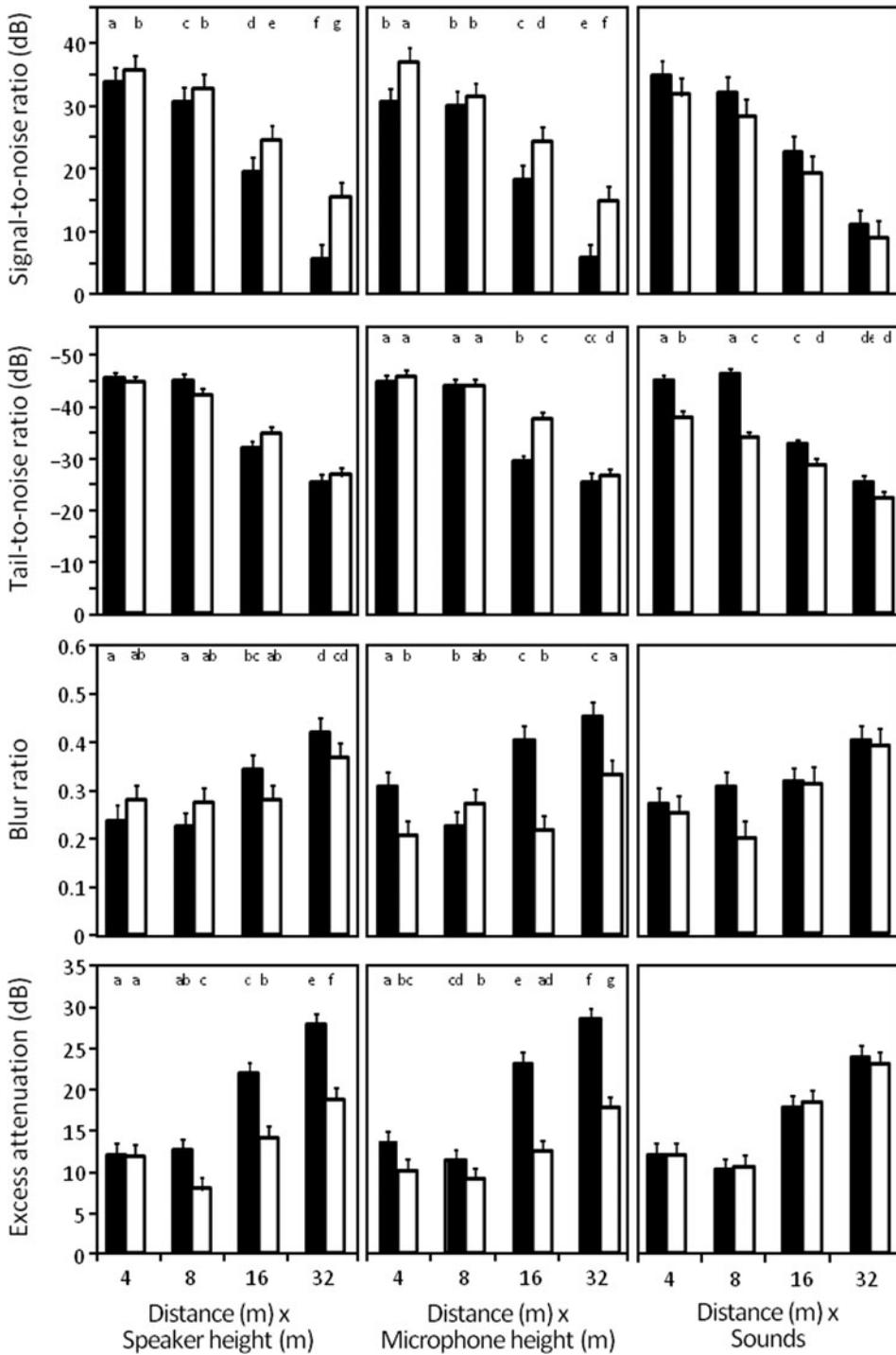


Figure 3. Second-order interactions between distance and speaker and microphone heights (black, 0.4 m; white, 2.2 m) and between distance and sound type (black, duets; white, songs) for solo songs and duets. Error bars are standard errors of the mean. Lowercase letters above the bars show the results of post-hoc tests for comparisons that showed statistically significant differences; bars with the same letters are not statistically different.

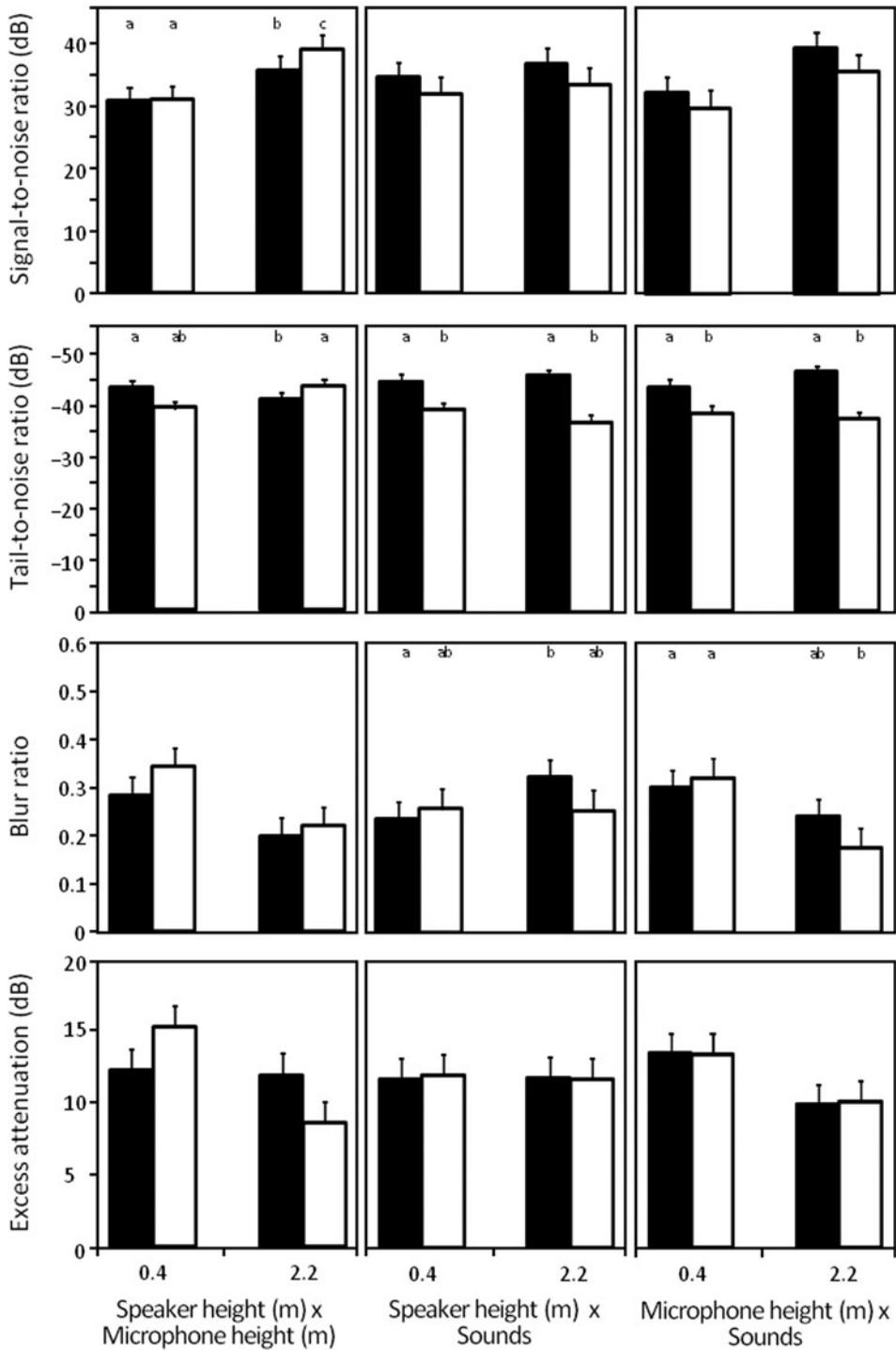


Figure 4. Second-order interactions between speaker and microphone heights (black, 0.4 m; white, 2.2 m) and between speaker and microphone heights and sound type (black, duets; white, songs) for solo songs and duets. Error bars are standard errors of the mean. Lowercase letters above the bars show the results of post-hoc tests for comparisons that showed statistically significant differences; bars with the same letters are not statistically different.

Table 2. Main effects and two-factor interactions in the linear mixed-effects model comparing the background noise detected during the sound transmission experiment.

	df	F	p
Distance	3,219	83.38	<0.001
Speaker height	1,219	0.16	0.69
Microphone height	1,219	1.59	0.21
Sound type	1,219	18.96	<0.001
Distance × speaker height	3,219	0.22	0.88
Distance × microphone height	3,219	0.62	0.60
Distance × sound type	3,219	8.75	<0.001
Speaker height × microphone height	1,219	5.00	0.02
Speaker height × sound type	1,219	0.06	0.81
Microphone height × sound type	1,219	0.23	0.63

between the distance and other factors such as speaker and microphone height, and – rarely – with the type of sound analysed.

Our vegetation measurements corroborate the idea that white-eared ground-sparrows inhabit areas with very dense vegetation. Such high vegetation density imposes a limitation on visual communication, and, therefore, acoustic communication may be an, especially, important modality for long-range signalling for animals in this environment. High vegetation density, however, affects sound transmission by increasing degradation (Nemeth et al. 2001; Slabbekoorn and Smith 2002; Slabbekoorn 2004), especially if the vocalizations are not adapted to transmit well in this type of habitat. Song elements with narrow bandwidth and long duration tend to transmit well in dense vegetation, but broadband, short elements do not (Wiley 1991). Our results reveal that the solo and duet songs of white-eared ground-sparrows are not particularly well-adapted to transmit through dense habitat. The measurements we collected of signal attenuation and degradation (signal-to-noise ratio, excess attenuation and blur ratio) were higher than reported in other transmission studies. For example, in temperate forests, common blackbirds *Turdus merula* (Dabelsteen et al. 1993) and blackcaps *Sylvia atricapilla* (Mathevon et al. 2005) showed signal-to-noise ratios that were more than double the values we reported here, excess attenuation values were less than one-third of our reported values, and blur ratio values were less than half of those reported here at the longest distances. In one of the few studies of degradation conducted in a tropical forest, rufous-and-white wrens *Thryophilus rufalbus* (Barker et al. 2009) showed signal-to-noise ratios that were 1.5 times higher than those reported here, excess attenuation values were less than one-seventh of those reported here, and blur ratio values were less than half of those reported here. These comparisons unambiguously show that thicket habitats impose a significant barrier to effective sound communication and demonstrate that white-eared ground-sparrow songs and duets – vocalizations with broad bandwidth, short duration and repeated trill elements – are poorly adapted to transmit long distances inside thicket habitats.

Prior field observations suggest that white-eared ground-sparrow territories have a diameter of approximately 50 to 70 m (estimated territory sizes based on tracking 42 banded pairs between 2011 and 2013) and that birds often occupy territories that abut multiple neighbours (Sandoval et al. 2014, 2015). Given these observations of territoriality, combined with the rapid attenuation and degradation we quantified in the current study, solo and duet songs of white-eared ground-sparrows are not expected to propagate more than one territory diameter, limiting the vocal interactions with other pairs

or potential mates further than one territory apart. We found very similar patterns of degradation between solo and duet songs. Solo and duet songs appear to serve different functions in this ground-sparrow, where solo songs appear to be important in mate attraction, whereas duets appear to be important in partner and territory defence (Sandoval et al. 2013, 2015). The similarity we found for patterns of degradation may be the result of constraints that drive both types of vocalization to communicate with receivers that are found at similar distances, within adjacent territories. Some acoustic signals evolved with acoustic characteristics that favour high levels of degradation and attenuation, because the context of production may require privacy (e.g. mating signals) or minimize the opportunity for eavesdropping (Mennill et al. 2002; Dabelsteen 2005). Acoustic characteristics that favour high levels of degradation and attenuation observed in the solo and duet songs of white-eared ground-sparrows may be maintained because they minimize the potential for eavesdropping.

White-eared ground-sparrows may use behavioural strategies to enhance sound transmission, as has been reported for other bird species (e.g. Krams 2001; Mathevon et al. 2005; Barker and Mennill 2009). For example, we have observed birds singing on the edge of their territories and pairs approaching the shared boundary of a neighbouring territory where a neighbouring pair was vocalizing. These behaviours may make vocal interactions between neighbouring animals more efficient, considering the limitations of sound transmission we found, here, by reducing the distance between signallers and receivers. Another behaviour that may help to increase the transmission of the sounds is the use of higher perches for vocalizing, and the advantage of this behaviour was corroborated by our results. We found that male solo and duet songs were transmitted with less degradation (higher signal-to-noise ratio and lower excess attenuation) at higher perches, although we observed more background noise at these perches, as has been observed in other species in a variety of different types of habitat (Dabelsteen et al. 1993; Krams 2001; Mathevon et al. 2005; Barker et al. 2009).

In white-eared ground-sparrows, duets are vocalizations used for communication within pairs and between neighbouring pairs during interactions (Sandoval et al. 2013; 2015). If the primary receiver for ground-sparrow duets is the bird's partner, located on the same territory, there may be little necessity for this vocalization to transmit long distances. This stands in contrast to the function of male solo songs, where vocalizations are used mainly for mate attraction and possibly territory defence (Sandoval et al. 2013, 2015). If potential receivers are more than one territory width away, we would expect animals to produce vocalizations that transmit over such distances. Our data reveal that this is not the case for white-eared ground-sparrows; attenuation and degradation increase rapidly with distance such that their sounds should rarely transmit even one territory width. However, field observations of two males that lost their partner during the breeding season suggest that males may change their vocal behaviour to enhance signal transmission. In the case of these two bachelor males, we observed birds singing from perches that varied from 8 to 15 m height; this is three to five times higher than average singing perches observed during the mornings in males with pairs (2.30 ± 0.13 m, $N = 18$). A future transmission experiment using solo songs at these heights is encouraged to evaluate the possibility that males may further enhance the transmission range of their mate-attraction solos or improve the conditions for hearing a vocal response by using higher perches than we studied here.

Thick vegetation is expected to increase the tail-to-signal ratio of an animal vocalization through reverberation (Slabbekoorn et al. 2002; Bradbury and Vehrencamp 2011). This may cause little distortion or amplification on unmodulated tonal sound (Nemeth et al. 2006; Slabbekoorn et al. 2002; Barker et al. 2009), but for the dramatic

frequency-modulated sounds of ground-sparrows, the tail serves to distort the signal (Ryan and Brenowitz 1985; Brumm and Naguib 2009), although may contain information about the distance to the sender (e.g. Holland et al. 2001). Ground-sparrow solo and duet songs showed higher tails when the sounds were produced from higher perches and received closer to the ground. This effect that might be driven by stronger wind levels at these heights, as suggested in other studies (Barker et al. 2009), but likely arises owing to the thick ground vegetation that characterized thicket habitats.

Degradation of solo and duet song characteristics may provide cues of the distance and position of signallers (Morton 1986; Naguib 1995; Sabatini et al. 2011), given that sound degradation varied with both factors in white-eared ground-sparrows. The evolution of vocalizations that provide information on the exact position of the signaller may enhance the efficiency of communication in closed habitats, such as thickets where visual signals are limited even at close distances. This idea needs further investigation.

Although many bird species in tropical habitats produce solo and duets songs (Langmore 1998; Gil and Gahr 2002; Hall 2009), this is the first study to directly compare the transmission properties of solo and duet songs in the same species. We found that both vocalizations showed the same pattern of degradation relative to the distance, suggesting that both vocalizations are designed to communicate with receivers at similar distances when both sounds are emitted at the same level and the receivers are located at the same height above ground level. More comparative transmission studies are necessary to understand the role of both vocalizations in the communication between signallers and receivers, especially for species where duets are composed of different types of vocalizations than solo songs, as is the case for the ground-sparrows we studied here. For example, if solo songs travel larger distances than duets with less degradation, it suggests the main function of this vocalization is likely to attract female birds that are far away; in contrast, duets are likely used for close-range communication. It is important to analyse the transmission properties of calls, because some of them may be used in close-range and long-range communications; there are very few transmission studies of calls to date.

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No potential conflict of interest was reported by the authors.

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