

Degradation of male and female rufous-and-white wren songs in a tropical forest: effects of sex, perch height, and habitat

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Summary

We performed a song transmission experiment to investigate the effects of distance, song post height, receiver perch height, signaller sex, and microhabitat on song degradation in rufous-and-white wrens (*Thryothorus rufalbus*), a neotropical duetting songbird. We quantified the effects of these factors on excess attenuation, signal-to-noise ratio, tail-to-signal ratio, and blur ratio of male and female songs. As expected, song degradation increased with distance between signaller and receiver. Songs transmitted best when emitted from moderate heights (5–7 m), although this pattern varied with receiver distance, receiver height and microhabitat. The patterns regarding receiver height were subtle and inconsistent, but receivers may maximise their ability to hear male and female songs when perched at a height of 7 m and 5 m, respectively. Female songs were generally more degraded than male songs. Rufous-and-white wren songs appeared more attenuated in open field than forest habitats, but microhabitat conditions within the forests exerted a strong influence on song degradation. These findings match previous studies showing an effect of distance, song post height, and habitat, but contrast with other research by showing a minimal effect of receiver perch height. This study represents the first detailed investigation of differences in song transmission between males and females.

Keywords: duet, female song, rufous-and-white wren, sound transmission, tropical forest.

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Introduction

As animal signals propagate through the natural environment, they are distorted from their original structure by several processes, decreasing the ability of a receiver to detect and recognize those signals. Given that many important sexual signals, such as bird song, transmit over long distances, signal degradation can have implications for territorial defense, mate attraction, mate guarding, breeding synchrony and signalling pair commitment (Hall, 2004; Slater & Mann, 2004; Catchpole & Slater, 2008). Consequently, it is necessary to understand the complex influences that degradation has on animal signalling behaviour before we can fully appreciate the dynamics of animal communication.

Degradation is the sum of all changes that occur to sounds as they transmit through the environment (*sensu* Dabelsteen et al., 1993; Nemeth et al., 2001; Lampe et al., 2007). Amplitude, time, and frequency patterns are all affected by processes of attenuation, irregular amplitude fluctuations, reverberation, and scattering (Wiley & Richards, 1978, 1982; Bradbury & Vehrencamp, 1998; Slabbekoorn, 2004). The extent to which a species' vocalizations are able to resist degradation will influence the ability of conspecifics to detect, recognize, and localize each other (Naguib & Wiley, 2001). In some cases, however, reverberations can lengthen signals or increase their amplitude if the original signals have sufficiently narrow frequency bandwidths, or are long enough to accumulate superimposing reflections (Slabbekoorn et al., 2002, Nemeth et al., 2006).

Previous research has shown that sound degradation increases with distance (e.g., Waser & Brown, 1986; Ryan et al., 1990; Dabelsteen et al., 1993; Penna & Solis, 1998; Naguib, 2003; Lampe et al., 2007), is affected by the perch height of signallers as well as receivers (e.g., Arak & Eiriksson, 1992; Mathevon et al., 1996; Blumenrath & Dabelsteen, 2004; Mathevon et al., 2005), changes with the structure of the sound (e.g., Holland et al., 1998; Nemeth et al., 2001; Slabbekoorn et al., 2002; Nemeth et al., 2006), and tends to increase as foliage density increases (Blumenrath & Dabelsteen, 2004; Lampe et al., 2007). The majority of song transmission experiments have investigated degradation in temperate habitats; however, most birds live in tropical habitats, tropical habitats are different from temperate ones (Terborgh, 1985) and tropical bird songs appear to have different structures than temperate bird songs (Barker, 2008). Consequently, song transmission in tropical species is an important avenue for further study.

Tropical birds have substantially different life histories and behavioural ecologies than temperate ones (Morton, 1996; Stutchbury & Morton, 2001, 2008), which may lead to unique selection pressures on song structure and singing behaviour (reviewed in Barker, 2008). Larger territories may require birds' songs to reach greater distances through foliage that is more complex or dense than in temperate forests (Richards, 1952; Terborgh, 1985; Terborgh et al., 1990). Female song occurs more widely in tropical bird species than in temperate species, and in some species paired males and females sing together to produce coordinated duets (Langmore, 1998; Hall, 2004; Slater & Mann, 2004). Selection on song structure and singing behaviour can, therefore, act on males as well as females, in both intra-pair and extra-pair contexts. Despite this, female song has been neglected in all previous song transmission studies.

Rufous-and-white wrens (*Thryothorus rufalbus*) are resident neotropical songbirds. Males and females possess similarly-structured songs, which they sing as solos and in loosely coordinated duets (Mennill & Vehrencamp, 2005; Mann et al., 2009). Solos and duet songs in this species are multi-functional and context-dependent, and previous research has shown a connection with territorial defense, mate and paternity guarding, coordination of breeding activities, as well as maintaining acoustic contact within pairs (Mennill & Vehrencamp, 2005, 2008; Mennill, 2006; Topp & Mennill, 2008). Male and female songs are similar; nearly all songs in our population consist of a variable number of introductory syllables, a trill of repeated syllables, and a single loud terminal syllable (Mennill & Vehrencamp, 2005). However, males have larger song type repertoires and higher song outputs than females, male songs are lower pitched and have more trill syllables than female songs, and females appear to sing more quietly than males (Mennill & Vehrencamp, 2005; Topp & Mennill, 2008).

We used a song transmission experiment to study the propagation of male and female rufous-and-white wren songs in a neotropical forest in Costa Rica. We investigated the effects of distance between signaller and receiver, song post height, receiver perch height, sex of signaller, and microhabitat. Here, we address four primary questions. (1) Do male and female rufous-and-white wren songs have different transmission properties? (2) Can rufous-and-white wrens enhance transmission of their songs or the perception of conspecific songs by varying their perch height? (3) Does microhabitat influence degradation of rufous-and-white wren songs? (4) Do the dif-

ferent components of rufous-and-white wren songs demonstrate consistent patterns of degradation?

Methods

Experimental setup

We conducted the transmission experiment in Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W) from 8 July to 15 July 2007. This time of year corresponds to the middle of the rainy season as well as the breeding season for rufous-and-white wrens (Topp & Mennill, 2008). Tropical dry forests undergo dramatic foliation shortly after the rains start in May (Janzen, 1967), and this annual period of leaf-growth is complete by July. Five transects were chosen to represent three different habitats within the study site: two transects were in a mature humid forest; two were in a newer regenerating habitat; and one was in a treeless open field. The first two habitats represent typical rufous-and-white wren habitat, while the field was included as a dramatically different point of contrast. The humid forest has larger trees (both taller and with broader trunks) and a sparser understory than the regenerating forest. The field, maintained by annual burning as a demonstration plot adjacent to the other sites, consists of thin tufts of jaragua grass (*Hyparrhenia rufa*) up to 40 cm in height, as well as less common woodier grasses that extend up to 1 m.

The test sequence used in this transmission study was composed of recordings of rufous-and-white wren songs that had a high signal-to-noise ratio and no overlapping sounds, which were usually recorded at a distance of 5 m from the bird. For males, we selected 20 songs (contributed by 10 males) from Santa Rosa for inclusion in the test sequence, representing two examples of each of the 10 most common song types in our study population (see Mennill & Vehrencamp, 2005 for an explanation of song types). For females, who sing less often and have more variable songs than males, we chose the 10 best recorded songs (contributed by eight females) from our Santa Rosa site, regardless of song type. We bandpass filtered all songs (highpass frequency 0.5 kHz; lowpass frequency 4 kHz); some minor additional filtering was applied to individual songs, as necessary, to remove heterospecific background sounds that were not removed with the bandpass filter. The peak values of all songs were then normalised to -1 dB. Each song was repeated four times, with 5 s between different song types. We analysed a subset of 5 male and 5 female introductory syllables, 5 male and 5 female trills, and 2 male and

2 female terminal syllables (Figure 1; introductory, trill, and terminal syllables as defined in Mennill & Vehrencamp, 2005). Song types are shared between birds and each song type is consistent across the population (Mennill & Vehrencamp, 2005), so the contributor of each syllable or trill should have little influence on the results. Nevertheless, the syllables chosen to represent the full spectrum of variation in rufous-and-white wren songs within

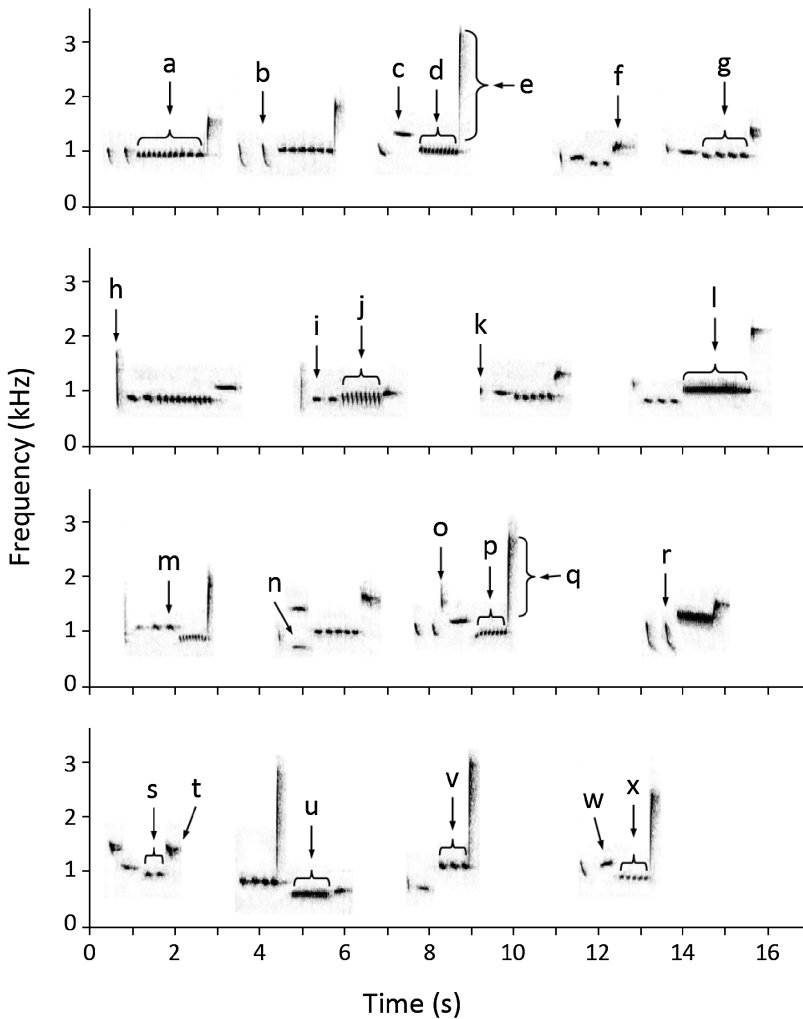


Figure 1. Spectrograms of seventeen rufous-and-white wren songs. Lowercase letters above each spectrogram refer to the individual song elements that were analyzed in this study, with elements a–l from males and elements m–x from females.

our test sequence came from six different males and seven different females in the population, with no more than two example introductory syllables, trills, or terminal syllables coming from the same individual.

For each trial, we played the entire test sequence through a loudspeaker and re-recorded it after transmission through the natural environment. The playback sound level was standardized at 75 dB (as measured at 1 m horizontal distance from the loudspeaker with a Realistic 33–4050 sound level meter on ‘slow’ setting), which is comparable to the amplitude of songs from free-living rufous-and-white wrens as assessed by authors NKB and DJM based on comparisons in the field. During each trial, we placed the speaker at one of three heights (7 m, 5 m, 1 m) to represent a variety of song post heights. Songs were recorded simultaneously by three microphones at different heights (7 m, 5 m, 1 m). We chose these heights because our preliminary observations suggest that rufous-and-white wrens spend most of their time between 0 m and 5 m, and seem to climb to heights of 5 m and above primarily when singing. Heights of 1–6 m within the forest at our study site correspond to the understory, consisting of grasses, vines, shrubs, and smaller trees all substantially below the forest canopy. We chose a transmission distance of 20 m between speaker and microphones to represent the average distance of separation between duetting rufous-and-white wrens (actual average distance: 19.2 ± 2.2 m across 525 duets recorded from 19 pairs; Mennill & Vehrencamp, 2008). The remaining distances were chosen by halving or doubling this distance, resulting in final (horizontal) distances of 5, 10, 20 and 40 m between the loudspeaker and the microphones. These horizontal distances were measured as the linear distance from the vertical pole on which the microphones were mounted to the point on the ground directly below the loudspeaker; actual distances were slightly greater than this for diagonal propagation, and these differences were more pronounced at closer horizontal recording distances. Sounds that were broadcast from the speaker and re-recorded after transmission through the natural environment represent the ‘observation sounds’. ‘Model sounds’ were obtained by re-recording at a distance of 2.5 m, which avoids near-field effects while still minimizing the effects of transmission. All possible combinations of distance, speaker height, and microphone height were used.

Sound analysis

We assessed the effects of transmission through the natural environment by comparing degraded (observation) sounds to un-degraded (model) sounds.

We used the program SIGPRO (Pedersen, 1998), and followed an established analytical protocol (e.g., Dabelsteen et al., 1993; Holland et al., 1998; Balsby et al., 2003; Lampe et al., 2007). Slightly different methods were used for terminal syllables than for trills and introductory syllables. The terminal syllable is the loudest component of both male and female songs (Mennill & Vehrencamp, 2005) and the higher volume of terminal syllables relative to introductory syllables and trills resulted in artificial distortion in recordings of terminal syllables when recorded at 2.5 m. Consequently, the 2.5 m recording distance was used as the model sound for introductory syllables and trill syllables, whereas the 5 m recording distance was used as the model for terminal syllables. We then conducted separate statistical analyses of the three sound types. For all song elements, we used one model for each transect, created by tightly cropping the sound in time and filtering it with an element-specific filter to eliminate background noise (Filters: a, 0.80–1.04 kHz; b, 0.55–1.25 kHz; c, 0.904–1.68 kHz; d, 0.646–1.335 kHz; e, 1.11–3.3 kHz; f, 0.894–1.189 kHz; g, 0.59–1.10 kHz; h, 0.66–1.87 kHz; i, 0.62–0.98 kHz; j, 0.61–1.16 kHz; k, 0.86–1.12 kHz; l, 0.90–1.09 kHz; m, 0.85–1.23 kHz; n, 0.61–0.82 kHz; o, 1.25–1.98 kHz; p, 0.69–1.20 kHz; q, 1.13–3.20 kHz; r, 0.72–1.23 kHz; s, 0.60–1.30 kHz; t, 1.18–1.706 kHz; u, 0.85–1.17 kHz; v, 1.00–1.46 kHz; w, 0.99–1.20 kHz; x, 0.81–0.91 kHz; letters correspond to the elements depicted in Figure 1). Observation sounds, along with the 5 s of silence preceding and following the sounds, were filtered with the same element-specific settings as the corresponding model. The background noise was estimated by measuring the root-mean-square value of the silence before or after the observation sounds, and was assumed to reflect the background noise occurring during the sounds. After the background noise level was set for a particular observation sound, the model and observation sounds were lined up to maximise cross-correlation; all cross-correlations were verified visually to ensure that the initiation of model and observation sounds matched.

Cross-correlation comparisons between model and observation sounds ultimately yielded four measures: excess attenuation; signal-to-noise ratio; tail-to-signal ratio; and blur ratio. Excess attenuation (EA) is the attenuation beyond that which is caused by spherical spreading (6 dB per doubling of distance). The signal-to-noise ratio (SNR) represents the amount of energy in the observation sound compared to the amount of energy contained in the background noise. The tail-to-signal ratio (TSR) is the amount of energy in the echoes following the observation sound compared to the amount of

energy in the signal. The blur ratio (BR) describes the temporal distortion and frequency-dependent attenuation of the signal. Formulae and details of these measures are provided in Dabelsteen et al. (1993), Holland et al. (1998) and Lampe et al. (2007).

For each element, we analyzed the first two instances that were not overlapped by transient noises. However, obtaining two instances was sometimes not possible due to singing birds, wind, or other spontaneous noises during the playback of the test sequence. Due to high winds, rain, and technical problems with our recording equipment, we were unable to complete the 40 m trials for transect 1 (field) and transect 3 (regenerating forest), respectively. For analyses of introductory syllables and trills, sample sizes were very large, despite missing values. For introductory syllables, we analyzed 5 elements from males and 5 from females, in 9 combinations of speaker and microphone height at each of 4 distances, repeated in 5 different transects, with 2 replicates, for a total of 2998 measurements. For trills, with this same combination of factors, we analyzed 2960 measurements. For the analysis of terminal syllables (which are higher pitched than introductory syllables and trills), continuous high frequency spontaneous noises (i.e., parakeets) prevented the inclusion of the field transect. We also analyzed four terminal syllables rather than 10 as for introductory syllables and trills. The sample size for the terminal syllable analysis was 759 measurements, based on 2 elements from males and 2 from females, in 9 combinations of speaker and microphone height at each of 3 distances, repeated in 4 different transects, with 2 replicates.

Statistical analyses

We analyzed introductory syllables, trills and terminal syllables separately, performing a mixed model ANOVA for each of the four measures of sound degradation for each sound type. Use of multi-factorial ANOVAs allows us to include all of our observations (previous paragraph) to understand how five variables (distance, speaker height, microphone height, sex, and transect), influence sound degradation without pseudoreplication. The model used for introductory syllables and trills was identical: 4 distances (5, 10, 20, 40 m) \times 3 speaker heights (1, 5, 7 m) \times 3 microphone heights (1, 5, 7 m) \times 2 sexes \times 5 transects (1 field, 2 mature, 2 regenerating). The model used for terminal syllables was slightly different: 3 distances (10, 20, 40 m) \times 3 speaker heights (1, 5, 7 m) \times 3 microphone heights (1, 5, 7 m) \times 2 sexes \times 4 transects

(2 mature, 2 regenerating). In both models, transect was a random factor, while all others were fixed. Only main effects and two-factor interactions were included in the model. To meet the requirements of ANOVA, TSR (absolute values) and BR were Box–Cox transformed $((x^{0.3} - 1)/0.3)$, while background noise was $\log_{10}(x)$ transformed. We limit our discussion to interactions that were significant across several degradation measures, but given that sex was a primary focus of our study we present all interactions that included sex even if they were only significant for few degradation measures.

Equipment and software

To record songs for the test sequence, we used Marantz PMD660 solid-state digital recorders with Sennheiser ME66/K6 directional microphones. For broadcasting we used a Sony Walkman portable CD player or an Apple iPod Nano (playing uncompressed WAV files) attached to an Anchor Audio Minivox PB-25 speaker (frequency response: 100–12 000 Hz). We controlled the speaker height by attaching it to a rope that hung over a branch, and stabilising the speaker with two additional ropes anchored close to the ground. A large isolated tree near the border between forest and field was used during the field trial. We re-recorded the broadcasted test sequence with two Marantz PMD660 recorders and three Sennheiser ME62/K6 omnidirectional microphones. Microphones were clamped onto telescopic poles that were anchored to a ladder. We filtered and normalized recordings in Audition (Adobe Systems, San Jose, CA, USA) and assembled the test sequence in SYRINX-PC (J. Burt, Seattle, WA, USA). Sound analyses were performed in SIGPRO (Pedersen, 1998).

Results

Rufous-and-white wren songs showed significant degradation; all three song components were negatively affected by transmission through the natural environment, although there was variation in the degradation of each song component and in the effect of distance, speaker height, receiver height, sex and microhabitat.

Degradation of introductory syllables

For introductory syllables, EA, SNR, TSR and BR, showed different patterns in which main factors and interactions were significant (Tables 1–4).

Table 1. Mixed-model ANOVA table for excess attenuation (EA) of introductory syllables, trills and terminal syllables, with main effects and two-factor interactions.

	Introductory (<i>N</i> = 2998)			Trill (<i>N</i> = 2960)			Terminal (<i>N</i> = 759)		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Distance	3	6.42	0.01	3	5.61	0.02	2	14.46	0.008
Speaker height	2	8.65	0.007	2	11.28	0.004	2	0.07	0.93
Microphone height	2	0.16	0.85	2	0.40	0.69	2	3.68	0.09
Sex	1	7.44	0.05	1	1.51	0.29	1	4.97	0.11
Transect	4	0.69	0.63	4	13.39	<0.001	3	4.92	0.06
Distance × speaker height	6	1.48	0.18	6	5.26	<0.001	4	2.20	0.07
Distance × microphone height	6	4.76	<0.001	6	12.47	<0.001	4	2.87	0.02
Distance × sex	3	0.26	0.86	3	1.56	0.20	2	0.72	0.49
Distance × transect	10	6.51	<0.001	10	6.60	<0.001	5	1.88	0.10
Speaker height × microphone height	4	10.74	<0.001	4	4.11	0.003	4	2.13	0.08
Speaker height × sex	2	3.19	0.04	2	0.10	0.91	2	0.13	0.88
Speaker height × transect	8	1.56	0.13	8	3.13	0.002	6	3.74	0.001
Microphone height × sex	2	3.36	0.04	2	0.16	0.85	2	5.54	0.004
Microphone height × transect	8	2.35	0.02	8	2.61	0.008	6	0.96	0.45
Sex × transect	4	43.15	<0.001	4	9.81	<0.001	3	12.14	<0.001

Distance had a significant effect on all four measures; degradation increased with distance (Figure 2). Speaker height had a significant effect on EA only, with 1 m and 7 m showing more EA than 5 m (Figure 3a). Microphone height, on its own, did not significantly influence any measures. Male introductory syllables experienced significantly higher EA and SNR than female introductory syllables, and showed significantly lower BR as well (Figures 2–4). Transect significantly affected BR, and approached significance for SNR. All other main effects were non-significant for introductory syllables.

Several interactions significantly affected degradation of introductory syllables. Most of the interactions involving speaker height and transect were significant. All four measures were affected by the distance × transect interaction, the speaker height × microphone height interaction and the sex × transect interaction. The first interaction shows that the pattern of degradation over distance depends on specific microhabitat conditions found in each transect.

Table 2. Mixed-model ANOVA table for signal-to-noise ratio (SNR) of introductory syllables, trills and terminal syllables, with main effects and two-factor interactions.

	Introductory (<i>N</i> = 2970)			Trill (<i>N</i> = 2938)			Terminal (<i>N</i> = 759)		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Distance	3	27.24	<0.001	3	23.04	<0.001	2	23.87	0.003
Speaker height	2	0.45	0.65	2	0.34	0.73	2	0.16	0.86
Microphone height	2	2.48	0.13	2	2.20	0.17	2	0.42	0.68
Sex	1	7.17	0.05	1	48.67	0.002	1	70.33	0.003
Transect	4	2.98	0.06	4	2.92	0.06	3	4.31	0.04
Distance × speaker height	6	3.53	0.002	6	4.84	<0.001	4	10.99	<0.001
Distance × microphone height	6	3.10	0.005	6	6.46	<0.001	4	1.08	0.37
Distance × sex	3	6.24	<0.001	3	4.24	0.005	2	7.20	0.001
Distance × transect	10	62.10	<0.001	10	88.85	<0.001	5	32.84	<0.001
Speaker height × microphone height	4	17.81	<0.001	4	16.23	<0.001	4	2.22	0.07
Speaker height × sex	2	2.92	0.054	2	3.92	0.02	2	5.97	0.003
Speaker height × transect	8	8.37	<0.001	8	12.72	<0.001	6	17.54	<0.001
Microphone height × sex	2	1.55	0.21	2	0.23	0.79	2	1.97	0.14
Microphone height × transect	8	1.05	0.40	8	1.16	0.32	6	0.85	0.53
Sex × transect	4	4.97	0.001	4	9.09	<0.001	3	1.60	0.19

The second interaction likely stems from the increased distance of diagonal propagations; the greatest degradation (i.e., highest EA, lowest SNR, highest TSR, and highest BR) occurred at a speaker height of 7 m and a microphone height of 1 m, for all four degradation measures. Introductory syllables were least degraded when speaker and microphone were at the same height, although the particular height depended on the measure (EA 5 m, SNR 1 m, TSR and BR 7 m). The third interaction demonstrates that microhabitat affects whether male and female introductory syllables experience differential degradation. The largest contrast was for BR where female syllables showed more degradation than male syllables in some transects, but less degradation in other transects. The distance × microphone height interaction was significant for EA, SNR and BR, where the most degradation occurred at a distance of 40 m and microphone height of 1 m, and the least occurred at a distance of 5 m and microphone height of 5 m (for SNR and BR), or a distance of

Table 3. Mixed-model ANOVA table for tail-to-signal ratio (TSR) of introductory syllables, trills and terminal syllables, with main effects and two-factor interactions.

	Introductory (<i>N</i> = 2940)			Trill (<i>N</i> = 1180)			Terminal (<i>N</i> = 757)		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Distance	3	18.18	<0.001	3	27.19	<0.001	2	30.72	0.002
Speaker height	2	1.09	0.37	2	1.43	0.28	2	0.79	0.49
Microphone height	2	1.21	0.34	2	0.57	0.59	2	0.96	0.43
Sex	1	1.64	0.26	1	1046.58	<0.001	1	98.45	0.002
Transect	4	3.23	0.07	4	4.94	0.02	3	2.14	0.22
Distance × speaker height	6	1.35	0.23	6	2.78	0.01	4	0.60	0.66
Distance × microphone height	6	1.40	0.21	6	3.61	0.002	4	0.89	0.47
Distance × sex	3	1.51	0.21	3	0.92	0.43	2	0.83	0.44
Distance × transect	10	4.62	<0.001	10	3.12	0.001	5	1.87	0.10
Speaker height × microphone height	4	2.89	0.02	4	2.85	0.02	4	1.32	0.26
Speaker height × sex	2	0.75	0.47	2	3.16	0.04	2	0.51	0.60
Speaker height × transect	8	0.66	0.73	8	0.79	0.61	6	1.32	0.24
Microphone height × sex	2	1.49	0.23	2	1.72	0.18	2	1.16	0.32
Microphone height × transect	8	0.97	0.46	8	2.30	0.02	6	1.20	0.30
Sex × transect	4	2.54	0.04	4	3.07	0.02	3	2.70	0.05

10 m and microphone height of 1 m (for EA). Male and female introductory syllables showed different patterns of EA with respect to speaker height (Figure 3a) and different patterns of EA and BR with respect to microphone height (Figure 4a and 4d). The remaining interactions were significant for two or fewer measures.

Degradation of trills

As with introductory syllables, the four degradation measures showed different patterns in which main factors and interactions had significant effects on the degradation of trills (Tables 1–4). Distance significantly affected all four measures, where degradation increased with distance (Figure 2). Speaker height significantly influenced EA only, with a height of 1 m causing more EA than 5 m or 7 m (Figure 3a). Sex significantly affected SNR and TSR, such that female trills experienced more degradation than male trills

Table 4. Mixed-model ANOVA table for blur ratio (BR) of introductory syllables, trills and terminal syllables, with main effects and two-factor interactions.

	Introductory (<i>N</i> = 2998)			Trill (<i>N</i> = 2960)			Terminal (<i>N</i> = 759)		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Distance	3	23.22	<0.001	3	19.19	<0.001	2	10.15	0.02
Speaker height	2	0.75	0.50	2	1.61	0.26	2	0.09	0.92
Microphone height	2	0.44	0.66	2	0.78	0.49	2	1.19	0.36
Sex	1	11.79	0.02	1	0.57	0.49	1	6.49	0.08
Transect	4	4.77	0.01	4	2.56	0.08	3	2.57	0.19
Distance × speaker height	6	2.91	0.008	6	5.41	<0.001	4	0.05	1.00
Distance × microphone height	6	4.19	<0.001	6	5.93	<0.001	4	1.72	0.14
Distance × sex	3	0.63	0.60	3	5.28	0.001	2	0.28	0.76
Distance × transect	10	6.13	<0.001	10	16.02	<0.001	5	1.24	0.29
Speaker height × microphone height	4	9.09	<0.001	4	4.97	0.001	4	0.60	0.66
Speaker height × sex	2	2.27	0.10	2	0.70	0.50	2	1.11	0.33
Speaker height × transect	8	1.06	0.39	8	2.48	0.01	6	2.12	0.05
Microphone height × sex	2	3.72	0.02	2	0.38	0.68	2	1.88	0.15
Microphone height × transect	8	2.32	0.02	8	2.54	0.009	6	0.69	0.66
Sex × transect	4	3.45	0.008	4	10.73	<0.001	3	2.86	0.04

(Figures 2–5). Microphone height did not have a significant effect on any measures of trill degradation. Transect had a significant impact on EA and TSR, as well as a nearly significant impact on SNR (Figure 5). All other main effects were non-significant.

More interactions significantly affected song degradation for trills than for introductory syllables. Most of the interactions involving distance, speaker height, and transect were significant. All four measures were affected by the interactions between distance and speaker height, distance and microphone height, distance and transect, speaker height and microphone height, and sex and transect. A speaker height of 5 m at a distance of 5 m resulted in the lowest degradation across all four measures, while degradation was usually highest at a distance of 40 m and a speaker height of 1 m, although SNR was lower at a height of 5 m than 1 m (Figure 3). The microphone height resulting in the lowest degradation depended on the distance, although degradation

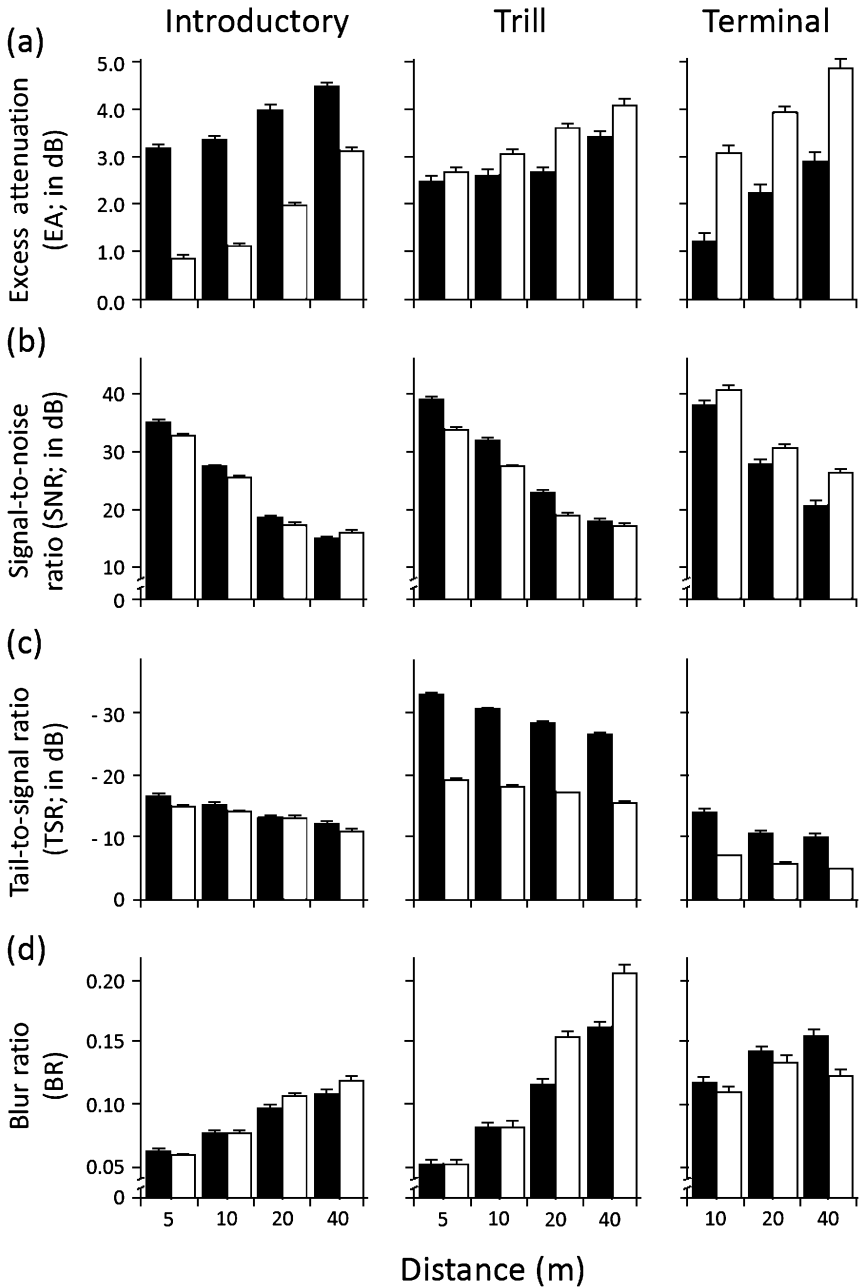


Figure 2. Interaction effect of distance and sex on four degradation measures (black, male; white, female). Error bars denote standard errors of the means.

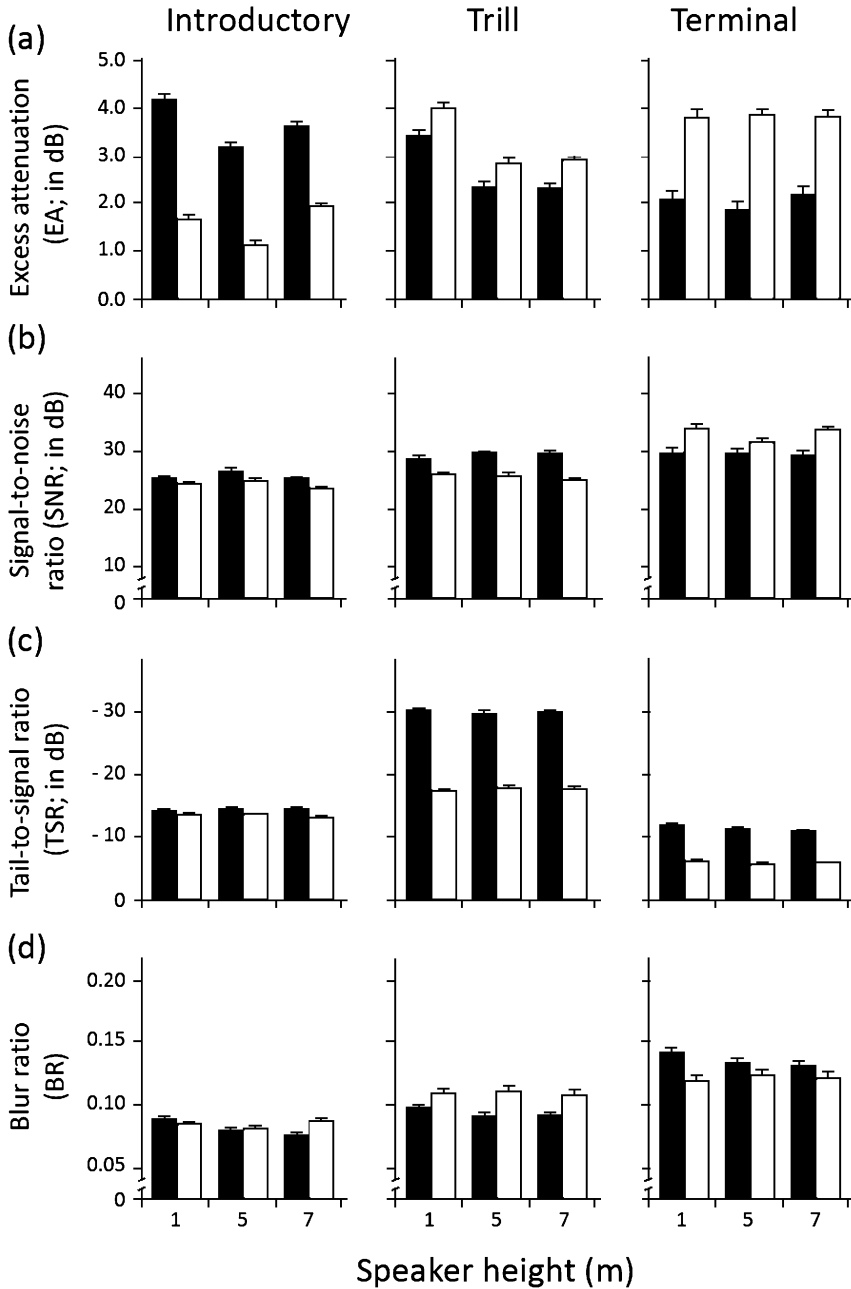


Figure 3. Interaction effect of speaker height and sex on four degradation measures (black, male; white, female). Error bars denote standard errors of the means.

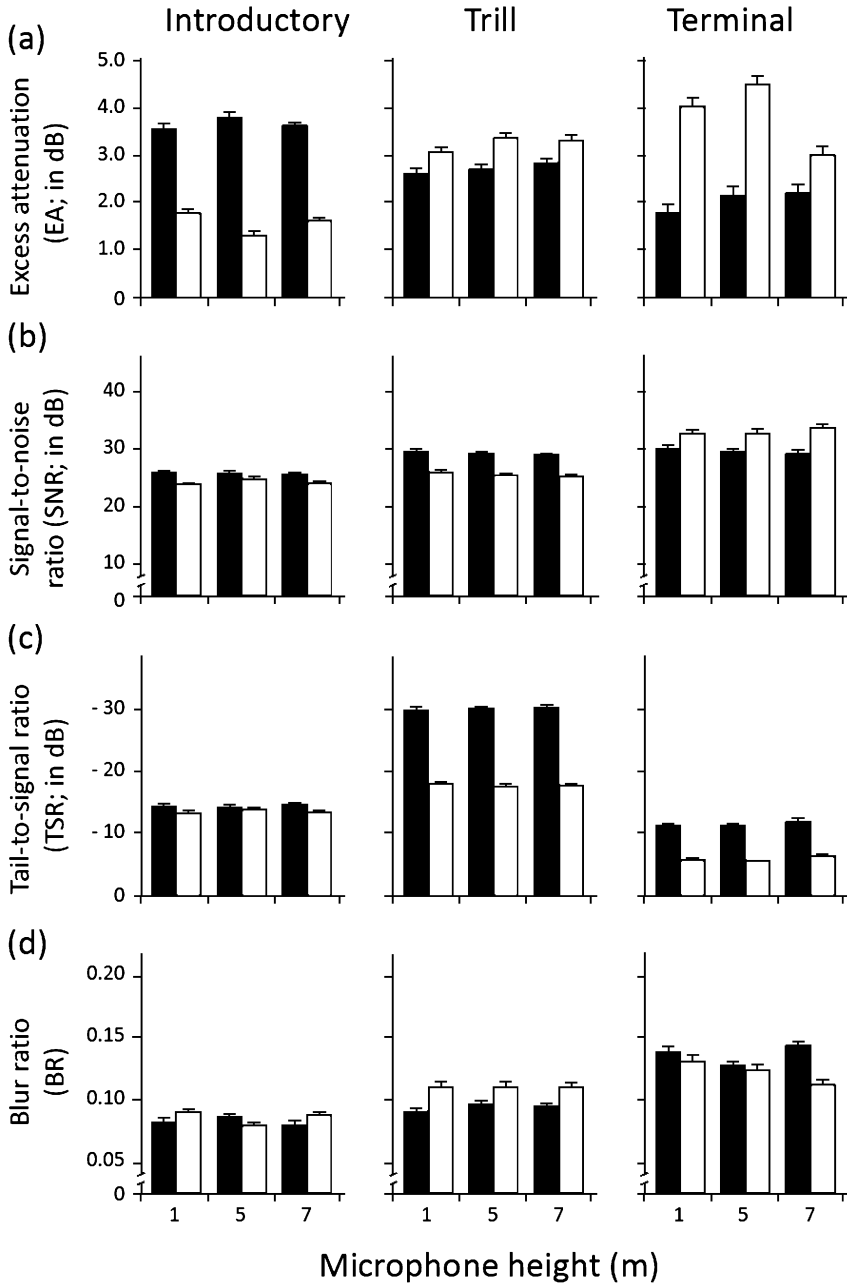


Figure 4. Interaction effect of microphone height and sex on four degradation measures (black, male; white, female). Error bars denote standard errors of the means.

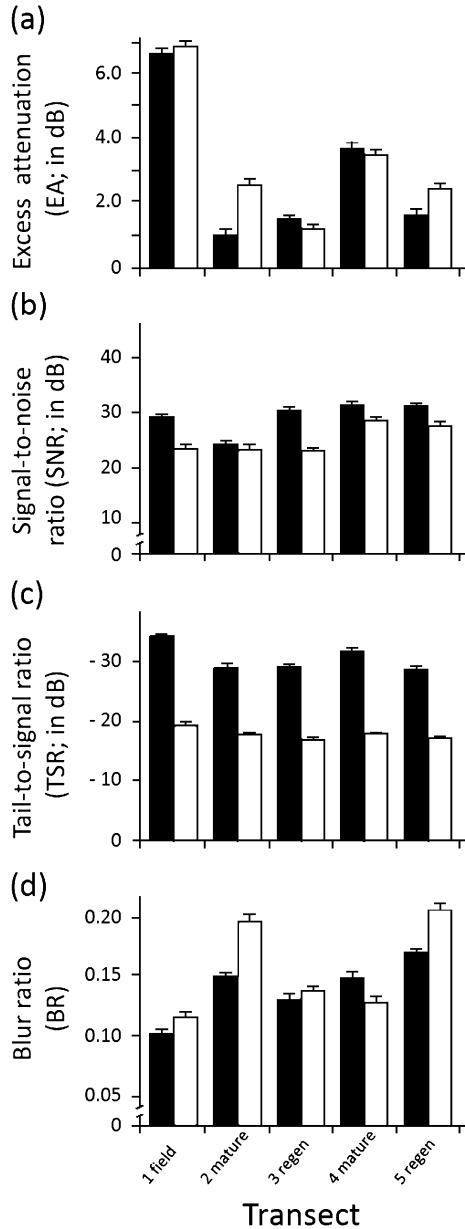


Figure 5. Interaction effect of transect and sex on four degradation measures for trills (black, male; white, female). Error bars denote standard errors of the means. Transect 1 was an open field, transects 2 and 4 were mature forest, and transects 3 and 5 were regenerating forest.

was generally lowest at a distance of 5 m and a microphone height of 5 m, and highest at a distance of 40 m and a microphone height of 1 m or 7 m, with the exception of EA which was lowest at a distance of 10 m and microphone height of 1 m. As previously mentioned, it is not surprising that the distance \times transect and speaker height \times microphone height interactions were significant; the relationship between degradation and distance is affected by microhabitat conditions, and the diagonal propagation leads to more degradation due to greater distance between speaker and microphone. The greatest degradation usually occurred when songs propagated from a speaker height of 1 m to a microphone height of 7 m, while the least degradation usually occurred when speaker and microphone were at the same height. As for introductory syllables, microhabitat affected whether female trills experience more or less degradation than male trills (Figure 5). In addition to the previous interactions, the speaker height \times transect interaction was significant for all measures except TSR, demonstrating that microhabitat differences influence the effect that speaker height has on degradation. The microphone height \times transect interaction was significant for EA, TSR and BR, indicating that the influence of microphone height on degradation is also dependent on the specific habitat conditions. The distance \times sex interaction significantly influenced SNR and BR, while the speaker height \times sex interaction significantly affected SNR and TSR. For both interactions, the two significantly affected degradation measures showed opposite patterns. That is, while males had higher SNR than females at all distances, there was a larger sex difference at a distance of 5 m than at 40 m (Figure 2b), whereas there was a smaller difference between the BR of male and female trills at 5 m than at 40 m (Figure 2d). Similarly, male and female trills showed similar SNR at a speaker height of 1 m, and male trills were higher at 5 m and 7 m (Figure 3b), whereas there was a larger sex difference in TSR at 1 m than at 5 m and 7 m (Figure 3c). The remaining interactions were significant for one or no measures.

Degradation of terminal syllables

Only a few main effects significantly affected the propagation of terminal syllables (Tables 1–4), which is probably related to the relatively small number of terminal syllables analyzed. Distance had a significant effect on all four measures, such that degradation generally increased with distance, although the difference between 20 m and 40 m was non-significant for EA and BR (Figure 2). Speaker height and microphone height did not significantly

affect any measures. Female terminal syllables had significantly higher SNR, but also showed higher TSR, than males; EA appeared somewhat higher for females than males but this trend was not significant (Figures 2–4). Transect significantly affected SNR and TSR. All other main effects were non-significant.

Only a small number of interactions significantly affected terminal syllable degradation (Tables 1–4). The speaker height \times transect interaction and the sex \times transect interaction were both significant for three measures; EA, SNR and BR for the former, and EA, TSR and BR for the latter. The first interaction indicates that variation in microhabitat influences the effect of speaker height on degradation of terminal syllables. The second shows that microhabitat influences whether female terminal syllables will be more or less degraded than male terminal syllables. The interaction between distance and sex was significant for SNR, such that female terminal syllables had slightly higher SNR than male terminal syllables at 10 m and 20 m, but had much higher SNR at 40 m (Figure 2b). The speaker height \times sex interaction was significant for SNR, where male terminal syllables showed a consistent SNR across all speaker heights, but female syllables, while maintaining a higher SNR for all heights, showed a lower SNR at a 5 m speaker height as compared to 1 m or 7 m (Figure 3b). The microphone height \times sex interaction was significant for EA only, such that the difference between EA of male and female terminal syllables was greater at 5 m than at other microphone heights (Figure 4a).

Background noise

Background noise levels did not vary significantly with any of the main effects, although the effect of microphone height approached significance (Table 5). There was slightly more background noise at microphone heights of 5 m and 7 m than at 1 m, likely because the 1 m microphone was farther away from the noise generated by wind rustling leaves in the canopy. Several interactions affected background noise levels, probably due to variation in wind conditions over the course of each trial and between trials at different transects (Table 5). For example, the background noise level increased greatly at 20 m and 40 m for transect 2 (mature forest), which was due to increased wind later in that particular morning. In some other transects, the background noise level was constant over the course of the trial. Effects involving sex may relate to the frequency difference between male and fe-

Table 5. Mixed-model ANOVA table for background noise, pooled across introductory syllables, trills and terminal syllables, with main effects and two-factor interactions ($N = 3599$).

	df	<i>F</i>	<i>p</i>
Distance	3	1.78	0.21
Speaker height	2	0.33	0.73
Microphone height	2	4.11	0.06
Sex	1	5.23	0.08
Transect	4	1.54	0.24
Distance × speaker height	6	8.32	<0.001
Distance × microphone height	6	0.54	0.78
Distance × sex	3	4.04	0.007
Distance × transect	10	350.18	<0.001
Speaker height × microphone height	4	0.18	0.95
Speaker height × sex	2	13.74	<0.001
Speaker height × transect	8	64.01	<0.001
Microphone height × sex	2	0.05	0.95
Microphone height × transect	8	1.99	0.04
Sex × transect	4	16.50	<0.001

male songs and, therefore, the background noise corresponding to element-specific filters. The remaining interactions were not easily interpretable.

Discussion

Rufous-and-white wren songs showed pronounced degradation as they propagated through a neotropical forest. Song degradation in this species is affected by the distance between signaller and receiver, the song post height of the signaller, the perch height of the receiver, the sex of the signaller and the microhabitat conditions through which the songs are propagating. Consistent with expectations and with previous transmission studies (e.g., Dabelsteen et al., 1993; Balsby et al., 2003; Lampe et al., 2007), rufous-and-white wren songs became more degraded as the distance between signaller and receiver increased. Additionally, many of the interactions involving distance were significant, suggesting that the degradation of rufous-and-white wren song over distance is influenced by other factors pertaining to the signaller, the receiver, and the microhabitat conditions. Below we explore the details of these findings from the perspective of signallers and receivers by

first discussing the results and implications, and then comparing our findings to other transmission studies.

Signaller perch height and song degradation

Speaker height, on its own, affected excess attenuation (EA) only and suggests that a singing rufous-and-white wren maximizes song transmission when singing from a perch height of 5 m or 7 m rather than 1 m. However, the optimal signaller height depends on other factors and seems to increase with distance. If the intended receiver is close to the signaller, a perch height of 5 m is optimal, while 5 m and 7 m would both be good for communicating over intermediate distances. If the receiver is farther away (e.g., 40 m), the optimal perch height is 7 m because the signal-to-noise ratio (SNR) of trills and terminal syllables is greater at this height compared to 1 m or 5 m, when travelling over this distance. This variation indicates that rufous-and-white wrens can reduce song degradation by choosing to sing from particular heights.

Our results show a relationship between signaller perch height and receiver perch height. While this result may largely be due to increased distance when the speaker and microphone heights were very different, there is also some evidence suggesting that some song post heights are better than others. The least degradation occurs when the signaller and receiver are perched at or near the same height, with EA lowest at 5 m, SNR highest at 1 m, and tail-to-signal ratio (TSR) and blur ratio (BR) lowest at 5 and 7 m. SNR may be highest near the ground if the predominant noise source, wind, is higher near 5 m and 7 m, as was suggested in our analysis of background noise. The most degradation occurs when signallers are perched at 1 m and receivers are perched at 7 m, which is probably due to the combined effect of a greater propagation distance, and the fact that songs travelling diagonally through a forest likely encounter more vegetation than those travelling horizontally through a more open forest layer, especially in very stratified forests.

The optimal song post height was similar for male and female rufous-and-white wrens. Although the interaction between speaker height and sex was significant for some measures, the overall pattern across all three song components indicated that both males and females benefit from singing at a height of 5 m as compared to 1 m or 7 m. Microhabitat conditions influenced the effect of speaker height on the degradation of rufous-and-white

wren songs, with a greater influence on trills and terminal syllables than on introductory syllables. Although a song post height of 5 m appeared to result in less song degradation overall, the optimal song post height was somewhat specific to particular habitat conditions. For example, there was a slight transmission advantage of singing from 5 m in transect 1 (field) and transect 4 (mature) while 7 m was clearly superior in transect 2 (mature), and there was no great advantage of either height in transect 3 (regenerating) or 5 (regenerating). These subtle differences may arise because of the variation in the structure of the midstory and understory across our transects. Despite the fact that the continuous canopy layer started above 7 m in all locations, there was substantial variation in the sizes and foliage density of the understory trees.

The results regarding signaller height indicate that the active choice of specific perch heights by rufous-and-white wrens may help to extend their communication range. The optimal song post height appears to be in the range of 5 m and 7 m, with the specific height determined by the structure of vegetation. Rufous-and-white wren songs will be detected and recognized best if the receiver is close to the sending bird and if they are perched at the same height. Overall, these findings are consistent with previous studies which suggest that perching higher in a forest can reduce song degradation and increase the active space of a singing bird (e.g., Dabelsteen et al., 1993; Mathevon et al., 1996; Holland et al., 1998; Mathevon et al., 2005). This effect has largely been attributed to the fact that elevated perches avoid thick undergrowth, and one study has explicitly shown that the optimal perch height changes with leaf phenology, such that the ideal perch height decreases when canopy leaves appear (Blumenrath & Dabelsteen, 2004). In the forests of Santa Rosa where we conducted our study, however, the 5 m and 7 m speakers were within a stratum of the understory dominated by the leafy vegetation of small trees that do not reach the subcanopy, whereas the 1 m speaker was often above any small plants growing on the forest floor but below the thicker growth of the small understory shrubs and trees, so the disadvantage from singing at 1 m in our study cannot necessarily be explained in the same way as previous studies. It may be that songs emitted from 1 m have to travel through the undergrowth vegetation to reach the higher receiver heights, and it may also be related to the destructive influence of the ground effect. Although complex and dependent on multiple factors such as signaller and receiver heights, distance, and sound frequency, the ground effect typically results in disruption of low frequency sounds as they interact with the ground (Marten et al., 1977; Embleton, 1996; Catchpole & Slater, 2008).

Receiver perch height and song degradation

Microphone height, on its own, did not affect degradation of rufous-and-white wren songs, although it did interact with other factors, indicating that the height a receiving bird perches at can influence how much degradation it perceives in songs given by conspecifics. The optimal listening post height depends on the distance between signaller and receiver although not in any regular way, and it also depends on whether recognition is necessary or whether detection will suffice. When signallers and receivers are close together, a receiver perch height of 5 m results in less degradation than a perch height of 1 m or 7 m. The reverse appears to be true at intermediate distances; receiver perch heights of 7 m and 1 m seem to result in better song detection although songs may be less recognizable to a listener perched at 1 m due to increased temporal distortion (e.g., BR). There was no clear advantage of receiver height at far distances because introductory syllables and trills appeared loudest to a receiver perched at 5 m, while terminal syllables were best heard from 1 m or 7 m. Taken together, these results suggest that rufous-and-white wren songs may possess a structure that permits the detection (if not recognition) of songs by receivers perched at different heights.

As discussed above, the interaction between signaller height and receiver height shows that listening birds will best detect and recognize conspecific songs when perched at the same height as singing birds. Additionally, the interaction between microphone height and sex had some slight effects on degradation. The results are mixed, but seem to suggest that rufous-and-white wrens should perch at 7 m when listening to male signallers, but should perch at 1 m or 5 m when listening to female signallers. As with speaker height, microhabitat has some influence on the effect that microphone height has on degradation of rufous-and-white wren songs, with a greater influence on introductory syllables and trills than on terminal syllables. There was no clear pattern in which receiver heights resulted in less degradation, even within a given microhabitat, since some microphone heights led to low degradation values for some measures but higher values for other measures, all within a given transect.

The overall conclusion regarding receiver height is that rufous-and-white wrens can only subtly modify their perception of conspecific songs by varying their own perch height. The optimal receiver perch height varies slightly with the sex of the signaller and the distance between the signaller and receiver, as well as the microhabitat. These results stand in contrast to many

previous studies which suggest that receiver perch height has a large influence on song reception (e.g., Dabelsteen et al., 1993; Holland et al., 1998; Balsby et al., 2003), even larger than the influence of signaller perch height (e.g., Mathevon et al., 2005). However, it is important to recognize that the habitat where we conducted our transmission study (a fully foliated neotropical forest) was markedly different from the habitat used in other transmission studies (often involving temperate forests, prior to annual leaf out) and this habitat variation may contribute to different effects of receiver height on sound transmission. It may also be that by having syllable types that degrade differently under various conditions, rufous-and-white wren songs are structured in a way that enables detection by receivers across all three perch heights that we measured, and that listening birds may need to vary their perch height repeatedly in order to minimize degradation and increase recognition of conspecific songs at different distances and under different habitat conditions.

Sex of signaller and song degradation

Male rufous-and-white wren songs generally appeared less degraded than female songs, although female terminal syllables had a higher signal-to-noise ratio (SNR) than male terminal syllables. The finding that female songs showed greater degradation than male songs may be explained if male and female songs were differently influenced by the process of normalizing songs, which may have occurred if female introductory and trill sections are quieter, relative to terminal syllables, than the corresponding sections in male songs. The pattern regarding SNR may be related to the fact that the predominant noise occurring during this experiment (i.e., wind) was low frequency, and female songs have slightly higher frequency components than male songs (Mennill & Vehrencamp, 2005). Therefore, female songs may show a higher SNR for terminal syllables than male songs because there is less background noise in the frequency of female songs, specifically terminal syllables. For the majority of other measures, female songs were usually more degraded than male songs.

Male and female rufous-and-white wren songs showed similar patterns with respect to signaller perch height, although the significant interaction between sex and speaker height suggests that there are some differences with respect to certain measures and certain song elements. Most notably, male and female songs show different patterns in the TSR of trills and terminal syllables, and in the BR of all three song components, with respect

to speaker height. However, when all song components and all degradation measures are taken into account, the overall pattern suggests that both males and females experience an advantage of singing from a height of 5 m, as previously stated.

As discussed above, the optimal perch height for a receiving bird may depend on the sex of the singing bird; a receiver should perch at 7 m when listening for male songs, and 1 m or 5 m for female songs. However, male songs will generally be less degraded than female songs at all receiver heights. There were no clear patterns regarding the combined effect of sex and microhabitat on rufous-and-white wren song degradation. In three transects, introductory syllables and trills showed opposite patterns, such that male introductory syllables experienced less degradation than female introductory syllables but male trills experienced more degradation than female trills, or vice versa, within the same transect. Introductory syllables were the most variable between transects and for different measures with respect to sex. The overall conclusion is that male songs generally transmit better than female songs, but that some syllables, particularly female introductory and terminal syllables, may be especially good at avoiding excess attenuation and blurring under certain microhabitat conditions.

This study represents the first detailed comparison of the degradation of male and female songs. Female song is very common in tropical passerines, and yet little is known about its function (Langmore, 1998; Slater & Mann, 2004). Duetting is also fairly common in tropical birds, and although more is known about this behaviour than about female song *per se*, our understanding of this widespread and diverse behaviour is still far from complete (Hall, 2004). Male and female rufous-and-white wrens show significant differences in the structure of their songs, and in their singing and duetting behaviour (Mennill & Vehrencamp, 2005; Topp & Mennill, 2008), implying different functions of song for the different sexes. When listening to free-living rufous-and-white wrens, female songs sound quieter than male songs, although this has not yet been formally quantified (Mennill & Vehrencamp, 2005). Our finding that female songs show more degradation than male songs suggests one possible reason why female songs appear quieter than male songs, since we normalized male and female songs to the same level based on the loudest part of their songs (usually the terminal syllable). That female songs experience a higher level of degradation may be related to the frequency difference between male and female songs, but could also be due

to some particular characteristic of female songs that has not yet been identified.

Microhabitat and song degradation

Habitat may influence birds' songs over evolutionary time, as proposed in the acoustic adaptation hypothesis, such that birds' songs may be structured to transmit maximally in their particular habitats (Rothstein & Fleischer, 1987; Brown & Handford, 2000). Evidence supporting this idea comes from studies across species, and some evidence within species as well (reviewed in Slabbekoorn, 2004; Barker, 2008; Catchpole & Slater, 2008). Our study in Santa Rosa involved three habitats, including mature humid forest, regenerating forest, and a treeless field. The differences in vegetation structure between the mature and regenerating forests are evident at a larger scale, but variability between our transects (even those within the same forest type) was large. We, therefore, included transect as a random factor, to investigate how variable microhabitat conditions can influence the effect of other factors on song degradation, and were unable to perform post hoc tests. However, the interactions of transect with sex and distance greatly affected all measures of song degradation, and can be used to understand some effects of microhabitat on the degradation of rufous-and-white wren songs.

The largest apparent difference in song degradation was between the field transect and the four forest transects. In the open field habitat, EA of trills appeared much higher, SNR of introductory and terminal syllables appeared lower, and BR of trills appeared lower, in comparison to the forested transects (Figure 5). BR was likely higher in the forest because there was more vegetation to cause scattering, refraction, and reverberation (Blumenrath & Dabelsteen, 2004; Slabbekoorn, 2004). This may in turn explain why EA was lower in the forest, if the temporal distortion of trill syllables filled the silences between syllables and reinforced the trill amplitude to reduce EA, as has been suggested for the tails of narrow frequency bandwidth syllables (Slabbekoorn et al., 2002; Nemeth et al., 2006). In the open field, the trills appeared to have little temporal distortion, and a lower TSR as well, thereby leading to increased EA. The low SNR in this transect was likely due to a combination of high EA and higher winds than occurred during most of the forest trials. Our results suggest that songs were somewhat less attenuated in the forest habitats where rufous-and-white wrens are found than in the open field habitat where rufous-and-white wrens are absent.

The remaining results were difficult to interpret due to a lack of consistency between forest types. For example, rufous-and-white wren songs are probably easiest to hear (i.e., showed the least EA and had highest SNR) in transect 3 (regenerating), transect 4 (mature), and transect 5 (regenerating), and seemed to be the least temporally distorted (i.e., had the lowest TSR and BR) in transect 1 (field) and transect 4 (mature), despite the fact that transect 1 and 4 were very different habitat types, and transect 2 and 4 were both within the mature forest. It, therefore, appears that microhabitat conditions on the scale of individual territories have more of an influence on rufous-and-white wren song degradation than the larger classification of forest type, although a transmission study with more than two transects within a forest type might help to clarify any patterns that may exist.

Conclusions

Rufous-and-white wren songs show complex transmission properties that are affected by signaller and receiver characteristics, as well as microhabitat conditions. Female songs show greater degradation than male songs, suggesting one possible reason why female songs appear to sound quieter than male songs in the field. This has implications for the functions of male and female songs as well, since it suggests that female songs may have evolved primarily for short-range communication rather than long-range communication. By changing their perch height, both males and females, as signallers and receivers, can influence the transmission of their own songs and to a much lesser extent, the reception of conspecific songs. Males and females both benefit from singing from intermediate heights that occur slightly above the densest layer of undergrowth, and from more elevated heights that at times place them in the branches of subcanopy trees, rather than from much lower heights below or in the midst of the undergrowth. Perch height has less of an effect for receivers than signallers, and suggests that birds listening to male conspecifics may benefit from perching at 7 m while those listening to female conspecifics may be better to perch at 1 m or 5 m. While all three song components showed fairly similar patterns of degradation in response to the independent factors, there is some evidence that trills may yield a special benefit to rufous-and-white wrens for communicating over long distances. Trills can accumulate temporal distortion through reverberations, and although this distorts the time pattern of the individual trill syllables, it may

also reduce excess attenuation and increase signal detectability over long distances (providing that enough tail energy overlays subsequent trill syllables). Rufous-and-white wren songs appear to show more attenuation in an open field than in all four forested habitats, suggesting that their songs are better adapted for communicating in their native habitat than in a non-native field habitat. Although we completed two trials in each of two different forest habitats, our results were not consistent between transects within a given forest type. It, therefore, appears that the microhabitat conditions on the level of the individual territory are more important for influencing the degradation of rufous-and-white wren song than the larger forest structure. This in turn suggests that rufous-and-white wren songs may not be specifically adapted to their microhabitat conditions, since they must learn songs from neighbours (who necessarily live in different territories with presumably different microhabitats). Our study enhances the current understanding of song transmission, specifically with reference to tropical habitats, and it sheds new light onto the influence of sex on song transmission.

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