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A test of the Acoustic Adaptation Hypothesis in three types of tropical forest: degradation of male and female Rufous-and-white Wren songs

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ABSTRACT
Many animals produce complex vocalizations that show pronounced variation between populations. The Acoustic Adaptation Hypothesis helps to explain this variation, suggesting that acoustic signals are optimized for transmission through different environments. Little is known about the transmission properties of female vocalizations because most studies of the Acoustic Adaptation Hypothesis have focused on male vocalizations of organisms living at temperate latitudes. We explored the relationship between environmental variation and the transmission properties of songs of Rufous-and-white Wrens, resident Neotropical songbirds where both sexes sing. Using playback, we broadcast and re-recorded elements of male and female songs from three populations of wrens living in three different forest habitats in Costa Rica. We measured four variables of the re-recorded sounds: signal-to-noise ratio, excess attenuation, tail-to-signal ratio and blur ratio. Our results show a significant difference between transmission characteristics of both male and female song elements across the three habitats, indicating that sounds transmit differently through different types of tropical forest. The population from which the broadcast sounds were recorded (source population) had little effect on sound transmission, however, suggesting that acoustic differences between these populations may not arise through acoustic adaptation to these habitats. Male and female elements showed similar transmission properties overall, although signal-to-noise ratio of male elements was influenced by source population, whereas blur ratio and excess attenuation of female elements were influenced by source population. Our study highlights the differences in transmission characteristics of animal sounds through different habitats, and reveals some sex differences in transmission properties.

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Introduction

Diverse animal taxa produce long-range acoustic signals that play an important role in mate attraction and resource defence (Bradbury and Vehrencamp 2011). Animal acoustic signals

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exhibit incredible diversity, and many signals vary geographically (Marler and Tamura 1964; Irwin et al. 2001; Campbell et al. 2010; Trefry and Hik 2010). Geographic variation in acoustic signals can play an important role during speciation when different populations develop divergent acoustic signals and then fail to recognize each other following secondary contact (Irwin et al. 2001). Given the role that acoustic divergence can play in evolution, understanding the forces that drive acoustic divergence remains an important area of research (Wilkins et al. 2013).

Habitat affects the evolution of acoustic signals (Morton 1975; Wiley and Richards 1978; Hunter and Krebs 1979; Hanford and Lougheed 1991; Dabelsteen et al. 1993; Boncoraglio and Saino 2007). This widely supported fact lead Morton (1975) to propose the Acoustic Adaptation Hypothesis: acoustic signals are optimized for transmission through the natural environment of the animals that produce them, and acoustic signals used for long-range communication should exhibit adaptations that minimize degradation and maximize transmission (Morton 1975; Marten et al. 1977; Boncoraglio and Saino 2007). A review by Boncoraglio and Saino (2007) found that song characteristics of forest and non-forest birds vary between habitats, providing further support that the Acoustic Adaptation Hypothesis may explain acoustic divergence between and within species (Hunter and Krebs 1979; Tubaro and Segura 1994; Slabbekoorn and Smith 2002). Other studies have found less support for the Acoustic Adaptation Hypothesis (Rothstein and Fleischer 1987; Date and Lemon 1993; Daniel and Blumstein 1998; Doutrelant et al. 1999; Trefry and Hik 2010), although it is noteworthy that a failure to find a relationship between habitat and acoustic characteristics does not mean that habitat does not affect animals' acoustic signals (Barker 2008). In addition to habitat, many other factors influence the evolution of acoustic signals, including morphology, phylogeny, physiology, sexual selection, social eavesdropping, predators, learning, founder effects, drift, and other aspects of the environment (e. g. humidity and ambient noise; Forrest 1994; Lynch 1996). These factors may act in concert and therefore the evolution of acoustic signals is necessarily complex, and likely to reflect interactions among these various factors (Forrest 1994; Wilkins et al. 2013).

Dense vegetation can cause significant problems for the transmission of acoustic signals (Bradbury and Vehrencamp 2011). In particular, leaves, branches, and tree trunks can degrade signals, changing sounds as they propagate through the environment (Richards and Wiley 1980; Dabelsteen et al. 1993; Badyaev and Leaf 1997). Degradation is expected to affect amplitude, frequency composition, and temporal patterns of sounds through processes that include scattering, atmospheric turbulence, boundary affects, reverberation, and dispersion (Richards and Wiley 1980; Dabelsteen et al. 1993; Bradbury and Vehrencamp 2011). Given the important role that habitat plays on the evolution of songs, testing the transmission properties of an animal's acoustic signal through its environment will provide further insight into the constraints that affect the evolution of signals.

Tropical species present exciting systems for studying the effects of habitat on acoustic signals, given the high diversity of habitat types, and the dramatic differences in habitats over relatively short distances (Stutchbury and Morton 2001). Population-level studies of broadly distributed species are especially revealing, because they provide the opportunity to examine characteristics of acoustic signals in animals that inhabit a diverse range of habitats (e.g. Hanford and Lougheed 1991; Slabbekoorn and Smith 2002). The high rates of philopatry and heightened habitat specialization that are common to many tropical bird species (Stutchbury and Morton 2008) suggest that tropical animals may be locally adapted to their habitats. Yet, most studies of the Acoustic Adaptation Hypothesis have been conducted on temperate species, and specifically on male song (Barker 2008). Tropical bird species are interesting from an acoustic perspective, given that females of many tropical bird species sing (Slater and Mann 2004), an uncommon phenomenon in north-temperate animals (Price et al. 2009). Studying the acoustic signals of female birds is important (Barker 2008), given that female song is an ancestral trait in birds (Odom et al. 2014), and many aspects of female song production and development remain poorly understood (Riebel 2003). Comparisons of male and female song characteristics offer a compelling area of research given that very few geographic-level comparisons have been made between male and female song characteristics (but see Mennill and Rogers 2006).

To investigate acoustic adaptation across both sexes and among different types of tropical habitats, we studied the transmission properties of songs of Rufous-and-white Wrens (*Thryophilus rufalbus*), a year-round resident of Central America and north-western South America. This species lives in a variety of forested habitats across its range (Stiles and Skutch 1989; Stotz et al. 1996). Interestingly, both male and female Rufous-and-white Wrens sing solo songs and produce coordinated duets by combining their solo songs (Mennill and Vehrencamp 2005). Both males and females possess song repertoires, singing up to 15 different song types (Harris et al. 2016), although male repertoires are larger than female repertoires (Mennill and Vehrencamp 2005). Male and female songs include similar characteristics, beginning with varied introductory elements, followed by a trill (the longest part of the song), and usually concluding with a single loud note that is often the highest frequency part of the song (Mennill and Vehrencamp 2005). Given that both sexes sing within this species, this system allows us to compare patterns between sexes and further our understanding of female song.

We used recordings of played-back songs to examine the transmission properties of both male and female Rufous-and-white Wren songs in three different populations in Costa Rica. Previous work has demonstrated that songs of Rufous-and-white Wrens vary geographically (Valderrama et al. 2007), and our ongoing research confirm that songs are variable between our three study populations (based on fine structural measurements, i.e. syllable length, bandwidth and dominant frequency of the trills). Our three study sites vary in habitat structure, vegetation density, and climate (Clark et al. 2002; Mata and Echeverria 2004), and therefore acoustic differences may reflect local adaptations at each site. We sought to test whether variation between songs among populations shows evidence of acoustic adaptation. Specifically, we explored the relationship between habitat and acoustic structure of male and female Rufous-and-white Wren songs, testing whether sound propagation varied with playback site (i.e. the location where sounds were broadcast and re-recorded) and source population (i.e. the location where the stimuli were recorded).

Methods

Study site

We conducted our experiment at three sites in Costa Rica: Sector Santa Rosa of the Guanacaste Conservation Area (10.8836°N, 85.7750°W, 300 m a.s.l.); Sector Rincon de la Vieja of the Guanacaste Conservation Area (10.8300°N, 85.3239°W, 1000 m a.s.l.); and the San Luis Valley of Monteverde at the University of Georgia Costa Rica field site (10.2380°N, 84.7970°W, 1100 m a.s.l.). Populations of free-living Rufous-and-white Wrens are found at all three sites. Playback sessions took place in 2013 on April 17–18 at San Luis, June 1–2 at Rincon de la Vieja, and June 11–12 at Santa Rosa during the onset of the breeding season at each population (birds breed earlier at San Luis than the other two sites; pers. obs.). All playback sessions were conducted between 0700 and 1100 h, a time period when this species is most vocally active (Mennill and Vehrencamp 2005). We conducted our experiment over a two-day period at each site, to ensure that weather conditions like temperature, relative humidity and wind were consistent throughout the experiment. Daily temperatures were consistent with mean monthly values at each of the sites (average temperature and relative humidity ranged from 23.0 °C and 72.6% at the montane forest site, 26.0 °C and 84.0% at the wet site and 27.3 °C and 76.0% at the dry forest site over the two day periods), and therefore we feel confident that the meteorological conditions are representative of conditions at each site during the appropriate time of year.

Our three study sites differ in both vegetation and precipitation (Clark et al. 2002; Mata and Echeverria 2004). (1) Santa Rosa (hereafter referred to as the "dry forest" site) is a tropical dry forest (following the Holdridge Life Zone classification system, Holdridge 1967) with a dry season that lasts from November to April and an intense rainy season from May to November (1876 mm on average/year from 1998 to 2013; NASA TRMM project). The understory at this dry forest site is relatively open (basal area = 25.0 m^2 Ha^{-1} for stems >10 cm; Gillespie et al. 2000) especially during the dry season, when the majority of shrubs in the understory are leafless. Vegetation density increases following the start of the rainy season. The canopy attains heights of approximately 20 m although some emergent trees reach heights of 30 m (Janzen 1983). (2) Rincon de la Vieja (hereafter referred to as the "wet forest" site) is a Premontane Moist-Wet Forest (Holdridge 1967), with a dry season from January to April (2057 mm average/year from 1998 to 2013; NASA TRMM project). This area is wetter than the lowland dry forest, but receives less precipitation than forests at higher elevations. This forest type is representative of many mid-elevation forests (~900 m elevation); the understory is relatively open, with fewer shrubs found here than in the dry forest (basal area = 31.2 m^2 Ha^{-1}; Heaney and Proctor 1990; basal area data are not available from our wet forest site, and this value is chosen for a comparison site in Costa Rica with similar vegetation, climate and altitude). The canopy attains heights of 25–30 m, and many large trees, including figs, dominate the forest (Janzen 1983). (3) San Luis field station at Monteverde (hereafter referred to as the "montane forest" site) is a Lower Montane Wet Forest (~1100 m elevation; Holdridge 1967), with a season of less precipitation lasting from January to April. This area receives greater precipitation than our other two sites (2706 mm average/year from 1998 to 2013; NASA TRMM project). The understory is densely vegetated by shrubs, ferns and palms (basal area = 62.0 m^2 Ha^{-1} for stems > 10 cm; Nadkarni et al. 1995) with epiphytes covering 50–70% of the tree trunks. Consequently, this habitat is much more dense than the understory at our other two sites (Janzen 1983). The canopy at the montane forest site reaches heights of 25–30 m, dominated by diverse large tree species.

Song type selection

For our playback stimuli, we used both male and female songs that we recorded from each of the three study populations in 2012. Recordings were collected using a solid-state digital recorder (PMD-660 Marantz; 44.1 kHz sampling rate; 16-bit accuracy; WAVE format) and a shotgun microphone (Sennheiser MKH70). To create our stimuli, we chose five of our highest quality songs from each population for each sex (each song used for the stimuli came from a different individual), using only songs with high signal-to-noise ratio (assessed visually based on sound spectrograms) and no overlap from other conspecific or heterospecific sounds. From those songs, we selected population-specific elements that were representative of elements that were most common in each population during our recording sessions. To create our final playback stimuli, we selected 18 male song elements (6 from each population, giving rise to 6 introductory, trill and terminal syllables overall; Figure 1) and 20 female song elements (6 from the montane and dry forest sites and 8 from the wet forest site, giving rise to 7 introductory, and terminal syllables, and 6 trill syllables, overall; we included 2 additional elements for wet forest females to reflect the diversity of female song elements in that population; Figure 1). We determined that six elements from each sex at each population was an appropriate number, given that the elements we selected for both male and female playback are representative of elements that are widespread and frequently used within each population. Our sample size (*n* = 18 elements for males and *n* = 20 elements for females) is comparable to previous transmission studies of species with intermediate to large song repertoires (Holland et al. 1998; Barker et al. 2009; Mockford et al. 2011). We isolated and filtered songs and elements using the "FFT filter" function of Audition software (version 3.0, Adobe Systems, San Jose, CA, USA); for each sound, we

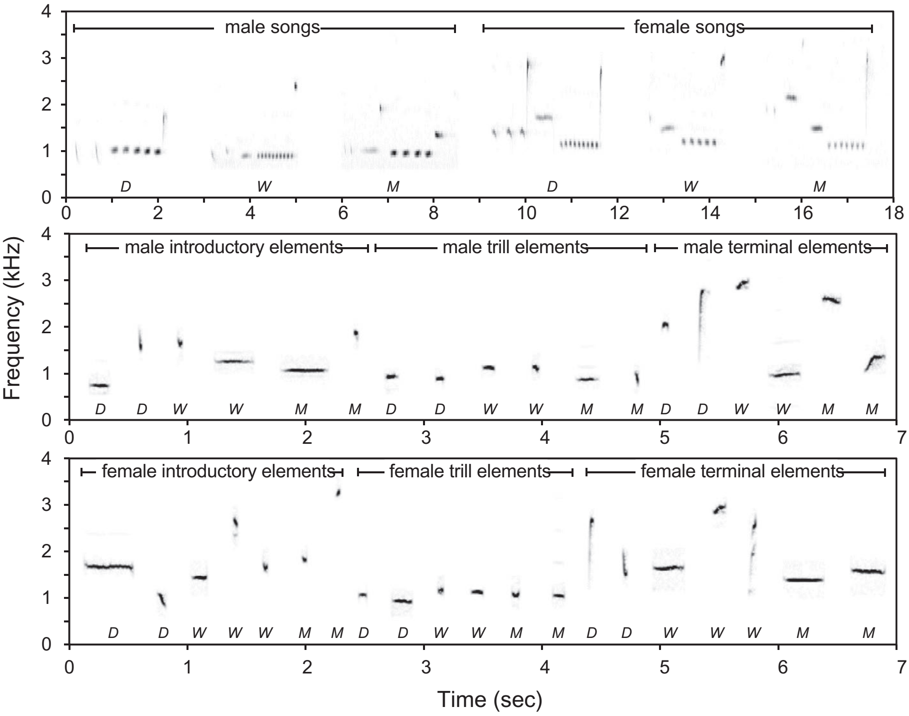

Figure 1. Sound spectrograms of example male and female Rufous-and-White Wren songs recorded from each of the three populations where playback experiments were conducted (top row). Sound spectrograms of example male song elements (second row) and female song elements (third row) used for playback during the transmission experiment. Letters indicate the population where the song or song element was recorded (D = dry forest, W = wet forest and M = montane forest).

used a different filter (see page 1 of supplementary material for information on the filters used to isolate each sound), given that each sound occupied a different bandwidth.

We focused our analysis on elements within the male and female songs, rather than entire songs, because we were interested in understanding how the degradation of single elements contributes to the degradation of entire songs. Examining elements separately from entire songs is important, given that the context in which sounds are broadcast can affect the acoustic properties; for example, reverberation is known to enhance both the length and amplitude of a sound, especially for the pure tone elements used by many forest birds, that change little in frequency (Slabbekoorn et al. 2002; Nemeth et al. 2006). While we present the results for elements only in this manuscript, we did analyse entire songs in another analysis, and we found that songs showed a similar pattern to elements (see supplementary material Tables S3–S7).

Using these prepared sounds, we created playback tracks by pasting the stimuli into a single file using Audition (Adobe Systems Inc., San Jose, CA). Each stimulus track included 5.0 s of silence at the outset (facilitating a measurement of background noise), followed by each of the sounds in succession, with 1.5 s of silence between each sound (preventing sounds from being overlapped by the end of the previous sound). Each playback stimulus was played five times in succession to maximize the chances of recording multiple examples of each element without overlap from background sounds. Each repetition was separated by 5.0 s of silence before the next repetition began.

Experimental set-up

At each of our three sites, we conducted our transmission experiment in three different Rufous-and-white Wren territories. We chose territories that were representative of the common vegetation at each site. Within each territory, we positioned both the speaker and microphone at a single height above ground (1.5 m). This height falls within the range of perch heights (1 to 5 m) male and female Rufous-and-white Wrens are most commonly observed using as song posts (Barker and Mennill 2009). We placed the microphone at four separate distances (5, 10, 20 and 40 m) from the speaker. We chose 20 m as one important distance based on a previous microphone array study that found 20 m to be the average distance separating male and female Rufous-and-white Wrens while performing duets (Mennill and Vehrencamp 2008). The maximum (40 m) and minimum (5 and 10 m) distances were chosen based on doubling and halving this average distance. Unlike previous studies (e.g. Barker et al. 2009; Sabatini et al. 2011), where playback was conducted along a linear transect, we distributed the four distances at different axes within each territory (as in Sandoval et al. 2015). By doing this, we attempted to include more of the birds' territories in our transmission tests, thus providing a more representative sampling of the effect of habitat on sound transmission. We chose these playback axes according to the cardinal points in all of the nine territories where we conducted our playback.

We broadcast sounds using an active loudspeaker (Anchor Audio, Minivox; frequency response 0.1–12 kHz), and re-recorded them using an omnidirectional microphone (Sennheiser ME62) and a solid-state recorder (PMD-660 Marantz; 44.1 kHz sampling rate; 16-bit accuracy; WAVE format), connected to a pre-amplifier (Sound Device MP-1: frequency response 0.02–22 kHz). Playback was broadcast at 75 dB (as measured at 1 m distance using a sound meter; Radio Shack model 33–2055 using C-weighting slow response), allowing us to match the sound pressure level that has been used in a previous study of Rufous-and-white Wrens songs (Barker et al. 2009). We increased the gain on our pre-amplifier to 18 and 28 dB for the 20- and 40-m trials, respectively, and we correct for these changes in gain by adding 18 and 28 dB to the appropriate analyses. Changing the gain was a critical component of these recordings, because the same recording levels could not be used to collect high-quality recordings for both the short and long transmission distances.

Sound analyses

As in most other transmission studies (e.g. Holland et al. 1998; Lampe et al. 2007; Barker et al. 2009), we used SigPro software (v 3.25; Pedersen 1998) to analyse the transmission properties of all recorded sounds. We compared recorded sounds at the four distances (5, 10, 20 and 40 m) against a model signal. The model signal used for comparison was obtained by broadcasting our male and female stimuli with the aforementioned playback and recording apparatuses, but with a separation distance of just 1.25 m at a height of 1.5 m on a flat dirt road in Sector Santa Rosa – i.e. an environment with no vegetation (in a 20-m radius) that could influence the transmission between the speaker and the microphone – on a calm morning with little or no background noise (e.g. wind). We then filtered and trimmed these recordings for the purpose of removing any potential tails or echoes introduced during the model signal recording. We used these model signals, rather than the original stimuli, to account for any noise that might have been introduced by the playback or recording equipment (as in Lampe et al. 2007, for example).

We compared degraded sounds to model sounds to obtain four measurements of degradation (for details see Dabelsteen et al. 1993; Holland et al. 2001): signal-to-noise ratio, tail-to-signal ratio, blur ratio and excess attenuation. We also measured background noise by sampling the background sound immediately prior to each stimulus recording (as described by Dabelsteen et al. 1993). We assumed that this background sound matched the noise overlapping our re-recorded playback sounds (Holland et al. 1998; Barker et al. 2009; Sabatini et al. 2011). Background noise was filtered within the same frequency ranges as the test sounds and then used to calculate signal-to-noise ratio and better understand how signal-to-noise ratio varied among our three forested sites, as described in Dabelsteen et al. 1993. Furthermore, we measured and compared background noise at each area, so that we could quantify the level of environmental noise at each site for each sound within its frequency range, given that past studies have shown that the background noise varies with frequency, that there are differences in the amount of ambient noise between forested habitats, and that these differences can affect sound degradation (Slabbekoorn et al. 2002).

For each sound, we analysed up to three re-recorded exemplars per distance along each transect, although in some instances, we were unable to measure three exemplars due to overlap by background noise. Due to windy conditions at Monteverde, we were only able to collect useful measurements for two of the three transects at 5, 10 and 20 m and only one of the three transects at 40 m; the remaining sounds were too heavily overlapped by background noise. After omitting these overlapped sounds, we were left with 1600 measurements for male song elements (2.47 ± 1.00 per distance in each transect; mean ± SE), and 1770 for female song elements (2.46 ± 1.01).

Statistical analyses

To analyse degradation of Rufous-and-white Wren sounds, we used linear mixed models. We analysed the sexes independently with separate models. We used the four sound degradation measurements (signal-to-noise ratio, blur ratio, tail-to-signal ratio and excess attenuation) as our response variables and ran each of the measurements in a model for each of the sexes (i.e. eight models in total). For each model, we had four independent variables: playback site (three levels corresponding to the three sites where we conducted playback), source population (three levels corresponding to the three populations where birds were recorded), distance (four levels, corresponding to the four distances between loudspeaker and microphone) and element type (three levels, because we were interested in seeing if there were differences in the degradation of introductory, trill and terminal elements; Mennill and Vehrencamp 2005). For our analysis, we examined main effects and two-way interactions for each model. We used Tukey *post hoc* tests to evaluate whether differences in means were significant. To analyse background noise (dB) during the transmission experiments, we ran two additional models, one for each sex. Like our models for sound degradation, we had four independent variables (playback site, source population, element type and distance), but for our background noise analysis, we examined only main effects.

To understand whether Rufous-and-white Wrens' song elements show local adaptation to the environment where the birds are found, we focused on the interaction playback site × source population. We focused specifically on this interaction, based on our expectation that elements that are adapted to their local environment should transmit more effectively (i.e. experience less degradation) at the playback site where they were originally recorded.

We report all values as mean ± SE. All analyses were performed in JMP (version 10.0; SAS Institute, Cary, NC, USA).

Results

Our transmission data reveal that playback site and source population had different effects on the degradation of male and female Rufous-and-white Wren song elements; transmission properties regularly showed a significant effect of playback site, but rarely showed a significant effect of source population. Below, we present detailed findings for male and then female song elements, describing the main effects followed by the interaction terms.

Males

For male song elements, signal-to-noise ratio, tail-to-signal ratio and excess attenuation were all significantly affected by playback site (Table 1); signal-to-noise ratio was higher at the wet and dry forest sites than at the montane forest site, tail-to-signal ratio was higher at the dry forest site than the other two sites, and excess attenuation was greater at both the wet and dry forest sites than the montane forest site (Figure 2). Signal-to-noise ratio was the only measurement that was significantly affected by source population (Table 1); elements recorded from the montane and wet forest sites had a higher signal-to-noise ratio than elements recorded from the dry forest site (Figure 3). All four sound degradation measurements were significantly affected by distance (Table 1); degradation increased

Table 1. Main effects and two-factor interactions for linear mixed models analysing male song elements for each of four measures of degradation of Rufous-and-white Wren song elements.

	Signal-to-noise ratio			Tail-to-signal ratio			Blur-ratio			Excess attenuation		
Male elements	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Model	39	109.18	**<0.001**	39	23.61	**<0.001**	39	7.1	**<0.001**	39	75.02	**<0.001**
Playback site	2	61.03	**<0.001**	2	15.78	**<0.001**	2	0.12	0.889	2	81.17	**<0.001**
Source population	2	11.33	**<0.001**	2	1.33	0.266	2	1.99	0.137	2	0.03	0.974
Distance	3	967.13	**<0.001**	3	222.03	**<0.001**	3	24.05	**<0.001**	3	749.43	**<0.001**
Element type	2	8.70	**<0.001**	2	2.77	0.063	2	3.58	**0.028**	2	13.48	**<0.001**
Playback site × source population	4	3.67	**<0.001**	4	0.17	0.951	4	0.53	0.715	4	2.30	0.057
Playback site × distance	6	36.88	**<0.001**	6	4.72	**<0.001**	6	2.36	**0.029**	6	37.36	**<0.001**
Playback site × element type	4	12.74	**<0.001**	4	1.65	0.158	4	2.29	0.058	4	2.37	0.051
Source population × distance	6	1.53	0.165	6	0.99	0.432	6	0.68	0.665	6	1.26	0.275
Source population × element type	4	21.35	**<0.001**	4	11.45	**<0.001**	4	4.85	**0.001**	4	4.67	**0.001**
Distance × element type	6	2.27	**0.034**	6	0.46	0.838	6	3.22	**0.004**	6	2.01	0.062

The significance of bold values is ($p < 0.05$).

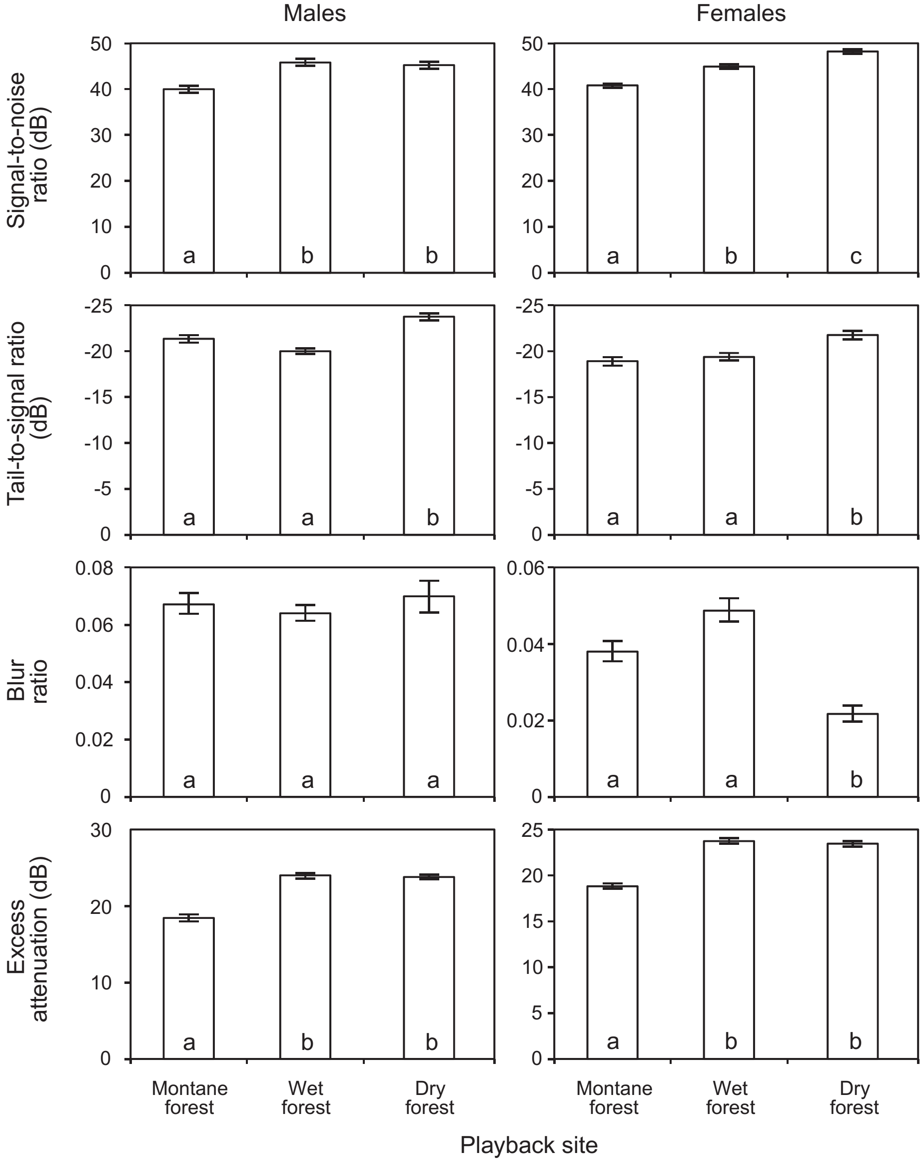

Figure 2. Four measurements of sound degradation of rufous-and-white wren song elements at each of three different playback sites in Costa Rica, both for males (left column) and females (right column). Error bars are standard errors of the mean, and bars with different letters indicate that values are significantly different from each other in *post hoc* tests.

as distance from the speaker increased (Table S1). Three of the four sound degradation measurements (signal-to-noise ratio, blur ratio and excess attenuation) showed significant variation with element type (Table 1); signal-to-noise ratio was higher for introductory and terminal elements than trill elements, blur ratio was higher for terminal elements than either introductory or trill elements, and excess attenuation was higher for introductory elements, than either terminal or trill elements (Figure 4).

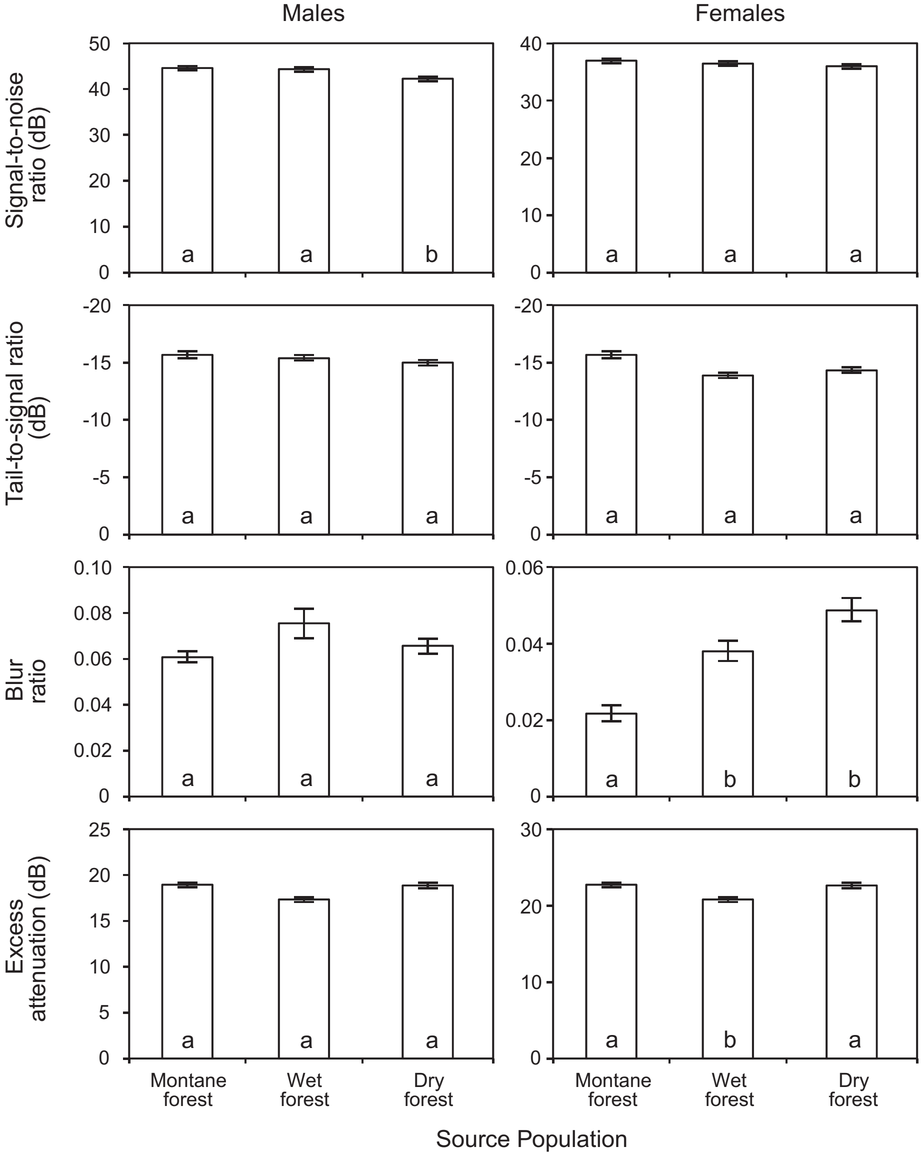

Figure 3. Four measurements of sound degradation of rufous-and-white wren song elements based on the source population (where a sound was recorded), both for males (left column) and females (right column). Error bars are standard errors of the mean, and bars with different letters indicate that values are significantly different from each other in *post hoc* tests.

All four sound degradation measurements showed significant interaction effects in our analysis of male song elements, especially for the interactions between playback site × distance (Table S1) and source population × element type (Table 1). Signal-to-noise ratio of elements for the interaction playback site × distance was significantly higher at shorter distances (both 5 and 10 m) at the wet and dry forest sites, and lowest at the furthest distances (20 and 40 m) at the montane forest site (Table S1). Like the patterns observed for signal-to-noise ratio, tail-to-signal and blur ratio were higher for elements at the furthest

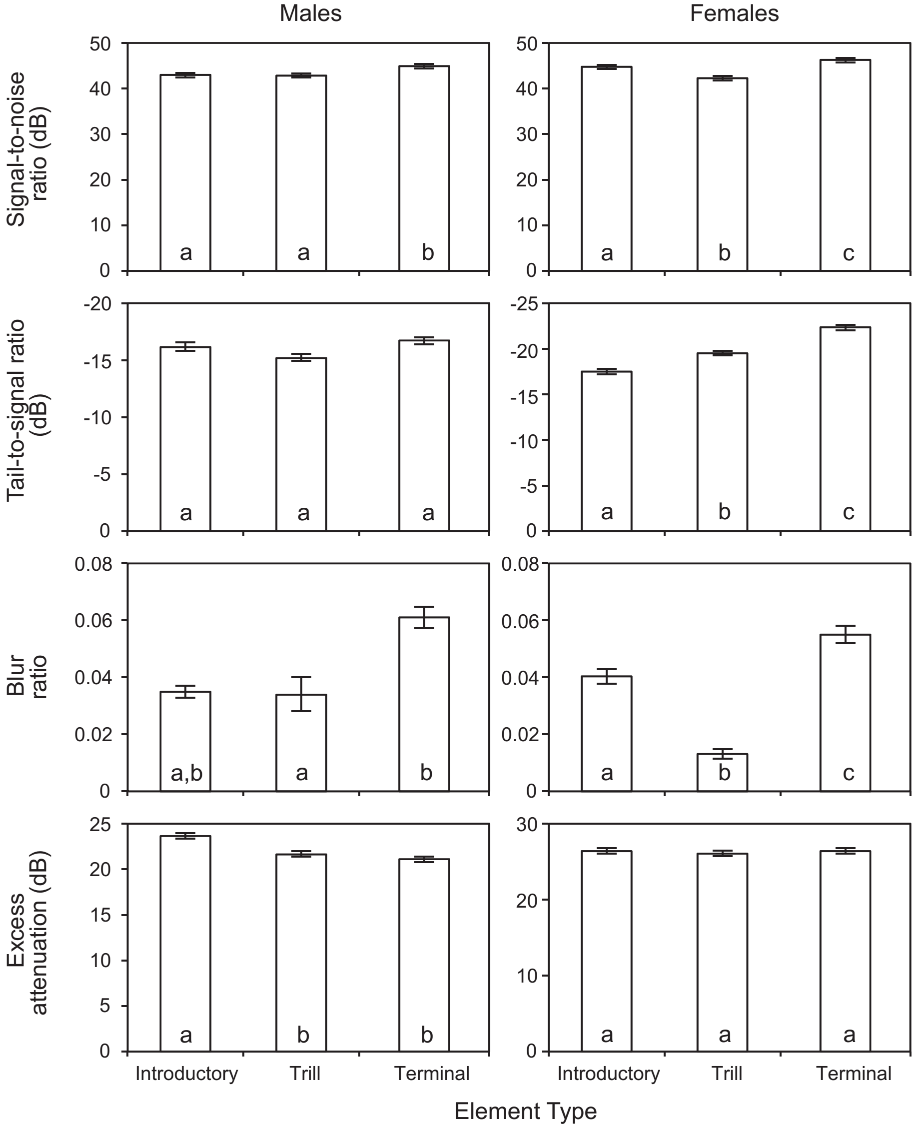

Figure 4. Four measurements of sound degradation of rufous-and-white wren song elements based on element type for males (left column) and females (right column). Error bars are standard errors of the mean, and bars with different letters indicate that values are significantly different from each other in *post hoc* tests.

distances at all three sites, while excess attenuation was greatest at the furthest distances at the wet and dry forest sites, with the lowest values being observed at the shortest distances at the montane forest site. For the interaction between source population × element type, the majority of element types recorded from both montane and wet forest sites had a higher signal-to-noise ratio than element types recorded from our dry forest site (Table S2). Tail-to-signal ratio was lower for terminal and introductory elements from the montane and wet forest sites, while tail-to-signal ratio was highest for trill elements recorded from the

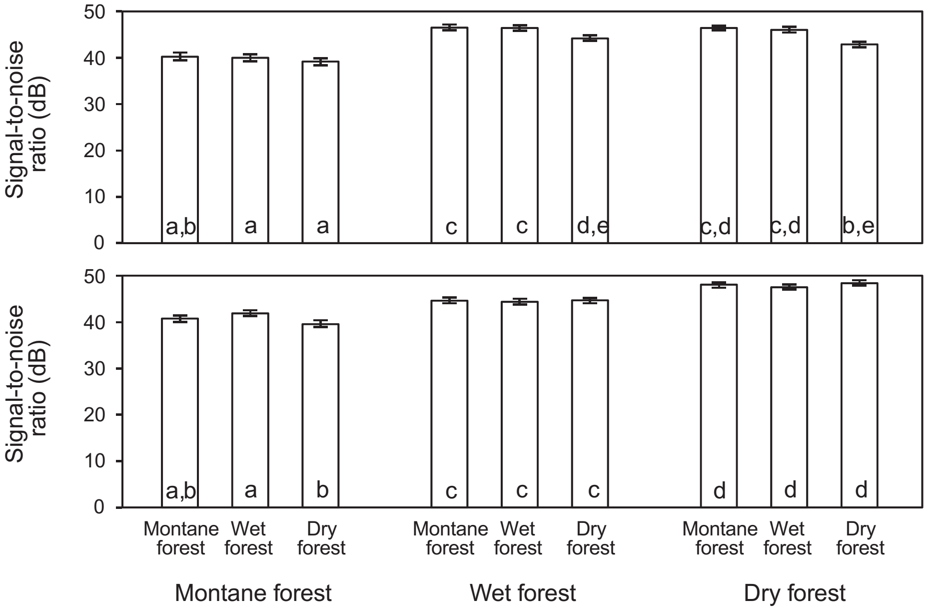

Figure 5. Signal-to-noise ratio measurements of Rufous-and-white Wren song elements showing the interaction of playback site × source population for males (top) and females (bottom). Error bars are standard errors of the mean, and bars with different letters indicate that values are significantly different from each other in *post hoc* tests.

montane and wet forest sites and introductory and terminal elements recorded from the dry forest site. Wet forest terminal and trill elements along with dry forest terminal elements showed a lower blur ratio than dry forest trill elements. Finally, excess attenuation was significantly higher for montane and wet forest introductory elements than trill or terminal elements from the same populations (Table S2). Only a single interaction (signal-to-noise ratio) was significant for the interaction playback site × source population; however, sounds did not show significantly less degradation at the sites where they were recorded (i.e. the degradation of elements recorded at the dry forest was not lower than elements recorded at our wet and montane forest sites, when played at our dry forest site; Figure 5). Elements recorded from montane and wet forest sites had a higher signal-to-noise ratio at the wet and dry forest sites, while signal-to-noise ratio of elements (from all three populations) played at the montane forest site had the lowest signal-to-noise ratio values. Signal-to-noise ratio was the only variable to show a significant relationship for the interaction between playback site × element type, where introductory and trill elements played at the montane forest site had the lowest signal-to-noise ratio values from all others (Table S1). There were no significant effects for the interaction source population × distance, while distance × element type affected signal-to-noise ratio and blur ratio only. For signal-to-noise ratio, elements at the closest distances (5 m) had a higher signal-to-noise ratio than elements at the farthest distances (40 m). Meanwhile terminal elements at farther distances (20 and 40 m) had a significantly higher blur ratio than all other element types, while trill and introductory elements at shorter distances (5 and 10 m) had the lowest blur ratio values (Table S1).

Table 2. Main effects and two-factor interactions for linear mixed models analysing female song elements for each of four measures of degradation of Rufous-and-white Wren song elements.

	Signal-to-noise ratio			Tail-to-signal ratio			Blur-ratio			Excess attenuation		
Female elements	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Model	39	126.55	**<0.001**	39	80.45	**<0.001**	39	32.29	**<0.001**	39	58.93	**<0.001**
Playback site	2	84.78	**<0.001**	2	27.36	**<0.001**	2	8.48	**<0.001**	2	50.30	**<0.001**
Source population	2	0.27	0.763	2	3.09	**0.046**	2	9.59	**<0.001**	2	7.83	**<0.001**
Distance	3	1073.53	**<0.001**	3	527.32	**<0.001**	3	88.86	**<0.001**	3	574.27	**<0.001**
Element type	2	25.99	**<0.001**	2	59.99	**<0.001**	2	24.71	**<0.001**	2	0.99	0.373
Playback site × source population	4	5.78	**<0.001**	4	1.69	0.151	4	1.74	0.140	4	0.60	0.660
Playback site × distance	6	28.53	**<0.001**	6	9.20	**<0.001**	6	8.17	**<0.001**	6	12.67	**<0.001**
Playback site × element type	4	15.12	**<0.001**	4	0.93	0.448	4	1.57	0.179	4	1.10	0.356
Source population × distance	6	0.51	0.804	6	1.09	0.368	6	5.57	**<0.001**	6	1.26	0.274
Source population × element type	4	33.29	**<0.001**	4	242.51	**<0.001**	4	68.90	**<0.001**	4	1.06	0.374
Distance × element type	6	1.54	0.162	6	2.33	**0.030**	6	4.21	**<0.001**	6	1.11	0.355

The significance of bold values is ($p < 0.05$).

Females

For female song elements, sound degradation was significantly affected by the majority of the main effects (Table 2). Signal-to-noise ratio, tail-to-signal ratio, blur ratio and excess attenuation were all significantly affected by playback site. Female elements showed a higher signal-to-noise ratio and tail-to-signal ratio, lower blur ratio, and experienced greater excess attenuation at the dry forest site, while elements played at the montane forest site exhibited a lower signal-to-noise ratio and tail-to-signal ratio, higher blur ratio, but experienced less excess attenuation (Figure 2). Source population affected tail-to-signal ratio, blur ratio and excess attenuation (Table 1). While *post hoc* tests revealed no differences among sites for tail-to-signal ratio, female elements recorded from the montane forest site had a lower blur ratio than elements from the other two populations; elements recorded from the dry and montane forest showed greater excess attenuation than elements recorded from the wet forest (Figure 3). Like male elements, all four measurements were affected by distance, and elements showed greater degradation at the furthest distances (Table S2). Lastly, three of the four measurements (signal-to-noise ratio, tail-to-signal ratio and blur ratio) were affected by element type (Table 2), and terminal elements had a higher signal-to-noise ratio, higher tail-to-signal ratio and higher blur ratio than both introductory and trill elements (Figure 4).

Half of the interactions showed significant effects in our analysis of female song elements (Table 2). Signal-to-noise ratio was the only measurement that showed a significant pattern for playback site × source population, where elements had a significantly higher signal-to-noise ratio when played at our dry forest site than at our montane and wet forest sites, and elements played at wet forest site had a significantly higher signal-to-noise ratio than elements at our montane forest site (Figure 5). However, as we observed for males, degradation of non-local elements was not significantly greater than that of local elements outside of the populations where they were recorded. All four degradation measurements were significant for the interaction playback site × distance (Table S2); song elements experienced significantly greater degradation as distance from the speaker increased, similar to patterns observed for males. Signal-to-noise ratio was significant for playback site × element type (Table S2), and elements had a significantly higher signal-to-noise ratio at the dry forest site, followed by the wet and montane forest sites (Table S2). Only blur ratio showed a significant effect for the interaction between source population × distance; elements from the wet and dry forest sites at the furthest distances had a higher blur ratio than elements from the montane forest site at all distances (Table S2). Signal-to-noise ratio, tail-to-signal ratio, and blur ratio were significant for source population × element type, where signal-to-noise ratio was significantly lower for trill elements from all populations than the majority of terminal and introductory elements (Table S2). Tail-to-signal ratio was lower for terminal elements recorded from our montane forest site, while introductory elements from our montane forest site have the longest tails. Greater blur ratio was exhibited by terminal elements from the dry and wet forest sites than introductory and trill elements (Table S2). Finally, blur ratio was the only measurement significant for element type x distance, and revealed that terminal and introductory elements at the furthest distances (20 and 40 m) experienced a higher blur ratio than trill elements at all distances (Table S2).

Table 3. Main effects and two-factor interactions for the linear mixed models analysing comparisons of background noise during male and female song elements.

	Male song elements			Female song elements		
	df	*F*	*p*	df	*F*	*p*
Model	39	26.02	**<0.001**	12	32.92	**<0.001**
Playback site	2	6.99	**0.001**	2	7.47	**0.001**
Source population	2	0.11	0.899	2	0.20	0.822
Distance	3	155.39	**<0.001**	3	189.64	**<0.001**
Element type	2	1.71	0.182	2	1.87	0.155

Background noise

Transmission experiments for both male and female song elements showed that background noise varied by site (Table 3). Background noise at the montane forest site was significantly higher than at the wet and dry forest sites, which were not significantly different from one another (Table S7). Source population did not show a significant effect for background noise levels for either male or female elements (Table 3), while distance significantly affected both male and female songs, where background noise increased with distance between the loudspeaker and the microphone (Table S7).

Discussion

Using a sound-transmission experiment, we tested the influence of habitat on the transmission of male and female Rufous-and-white Wren song elements in three different types of tropical forest, thereby testing predictions of the Acoustic Adaptation Hypothesis. We found that playback site affects the transmission of both male and female elements, and we found significant differences in background noise levels among sites. Source population (i.e. the location where songs were recorded) had little effect on degradation, given that only four of eight degradation measurements were significant (i.e. signal-to-noise ratio for male elements and tail-to-signal ratio, blur ratio and excess attenuation for female elements). Furthermore, the interaction playback site × source population did not suggest that song elements are locally adapted, given that elements did not experience less degradation at their respective sites (e.g. dry forest song elements did not experience less degradation at the dry forest site in comparison to elements recorded at our wet or montane forest sites; Figure 5). Overall, Rufous-and-white wren songs appear to be optimized for transmission through forested habitat in comparison to open habitats (Barker et al. 2009), but our data reveal that their song elements are not specifically adapted for transmission through different types of tropical forests. We conclude that habitat influences sound transmission of both male and female songs, but that sounds in these three study populations do not show strong evidence of acoustic adaptation to the three different habitats.

Playback site

The Acoustic Adaptation Hypothesis predicts that the signals of animals living in densely vegetated habitats should be adapted for transmission through these habitats (Richards and Wiley 1980; Badyaev and Leaf 1997). Support for the Acoustic Adaptation Hypothesis is mixed (Ey and Fisher 2009); many studies have demonstrated support for the hypothesis

(Hunter and Krebs 1979; Tubaro and Segura 1994; Perla and Slobodchikoff 2002; van Dongen and Mulder 2006; Derryberry 2009), whereas other studies have failed to show support (Rothstein and Fleischer 1987; Date and Lemon 1993; Daniel and Blumstein 1998; Doutrelant et al. 1999; Trefry and Hik 2010). In our study, we found that playback site had a significant effect on the degradation of both male and female acoustic signals. Environmental differences such as vegetation density, atmospheric absorption and ambient noise all affect sound transmission (Brumm and Naguib 2009), and differences in these factors between our three sites surely played a role in the transmission properties we described. We observed greater degradation at the montane and wet forest sites than at the dry forest site with regards to tail-to-signal ratio and blur ratio of both male and female elements. Vegetation density and rainfall are higher at the montane and wet forest sites than the dry forest site, where the habitat is more open (Nadkarni et al. 1995; Gillespie et al. 2000). Densely forested habitats result in greater degradation because there are more leaves, stems, branches, and trunks, thereby increasing the effect of reflection, refraction, and diffraction on sound waves (Naguib 2003).

In contrast to the pattern for tail-to-signal ratio and blur ratio, excess attenuation was significantly lower at the montane forest site than at the wet and dry forest sites, for both male and female elements. While vegetation density does affect excess attenuation, other factors such as atmospheric scattering and turbulence, as well as boundary interference, also affect attenuation (Brumm and Naguib 2009). Humidity and temperature are known to affect the attenuation of sounds, and sounds experience less attenuation in humid air and when temperatures are cooler (Ingård 1953; Griffin 1971). Among the three study sites, the montane forest site receives the largest amount of annual rainfall; humidity is greater (an average of 91% throughout the year; Johnson et al. 2005) and temperatures are cooler (mean = 20.7 °C; www.worldclim.org) than at the other two sites (by comparison the average humidity in the dry forest ranges from 20 to 60% during the dry season and temperatures are warmer; mean = 24.8 °C; Janzen 1988; Clark et al. 2002; Mata and Echeverria 2004). Therefore, climate differences among sites may contribute to the differences in excess attenuation we observed, as has been suggested in the previous studies (Morton 1975; Nottebohm 1975), although we are aware of no studies that have tested the effect of climate differences between sites on sound transmission.

Signal-to-noise ratio of both male and female elements was significantly higher when sounds were played at the wet and dry forest sites than at the montane forest site. These differences may be attributable to the much noisier environment at our montane forest site, an idea that was directly supported by our comparisons of background noise (Table S7). Conditions at the montane forest site were much windier than at the other two sites and wind produces low-frequency noise in the range of 0.1–1.0 kHz (Bradbury and Vehrencamp 2011). The added background noise masked some of the elements used for playback during our experiment, especially those produced around 1.0 kHz (e.g. the introductory and trill elements of many male and some female songs are produced at this frequency; Mennill and Vehrencamp 2005). Additionally, within highland tropical forests, there is a considerable amount of background noise in the high-frequency spectrum (Ryan and Brenowitz 1985; Slabbekoorn and Smith 2002). Animals like cicadas call continuously, with this noise band beginning around 2 kHz and extending up to 5 kHz (Slabbekoorn 2004). A recent study by Hart et al. (2015) found that birds avoided temporal overlap with cicadas, suggesting that biotic noise (from sources including cicadas) may influence the frequency and timing of avian vocal signals. Many of the female elements and songs recorded and used for this experiment are produced at ≥3 kHz. Since these sounds fall within the range of high-frequency noise, female sounds are at risk of being masked by cicada advertising calls, and background noise differences between sites may explain why we observed a higher signal-to-noise ratio for female sounds played at the dry forest site (Slabbekoorn 2004).

Source population

Source population had little influence on the degradation of male or female Rufous-and-white Wren elements. Only male elements showed a significant effect of source population for signal-to-noise ratio, where male elements recorded at the montane forest and wet forest sites showed less degradation than elements recorded at our dry forest site (i.e. higher signal-to-noise ratios), but for no other degradation measurements. Many animals increase signal-to-noise ratio to compensate for noisy environments (Brumm and Slabbekoorn 2005). For instance, abiotic features such as wind and fast-flowing rivers produce low-frequency noise (0.1–1.0 kHz for wind noise, up to 4 kHz for aquatic noise, Slabbekoorn 2004; Bradbury and Vehrencamp 2011) that can mask signals in this range. Background noise differences among sites likely contributed to the higher signal-to-noise ratio observed for male elements from the wet and montane forest sites. For example, species living next to water produce vocalizations at higher frequencies to avoid having their vocalizations masked by the noise produced by streams (Martens and Geduldig 1990). By comparison, there is less low-frequency ambient noise at the dry forest site during the breeding season, where there is little or no moving water, and conditions are less windy. The reduced background noise may explain why broadband elements are commonly used in songs at the dry forest site where males often terminate songs using broadband elements (e. g. the second male terminal element in the second row of Figure 1; 17 of 40 of song types recorded in 2012–13 included broadband terminal elements). By comparison, male elements (especially terminal elements, e.g. the fourth and fifth male terminal elements in the second row of Figure 1) from our wet and montane forest sites tend to be more tonal (Figure 1; only 2 of 35 song types at our wet forest site, while only 8 of 33 song types at our montane forest site included broadband terminal elements), suggesting that males use these elements over broadband signals because they are masked less easily by ambient noise. Differences in signal-to-noise ratio of elements for male Rufous-and-white Wrens could be indicative of local adaptation, but could also represent phenotypic plasticity. For instance, Red-wing Blackbirds (*Agelaius phoenicius*) make short-term modifications to their songs by increasing their signal tonality when exposed to low-frequency white noise (Hanna et al. 2011). Evidence from this study and others (Slabbekoorn and Peet 2003; Mockford et al. 2011; Parris and McCarthy 2013; Gough et al. 2014) have demonstrated the high plasticity in birds that learn their songs, where individuals are able to modify their songs in the presence of increased noise to stand out in their environment.

Female elements did not show differences in signal-to-noise ratio, in contrast to the pattern observed for males. However, we did observe significant differences for the other three degradation measurements; these results may indicate local adaptations for female elements. Tail-to-signal ratio was significant in our overall model, but did not show any differences among populations. Female elements from the montane forest site had a lower blur ratio overall than elements recorded from the other two sites. This is likely due to the fact that vegetation density is higher at the montane forest site, suggesting that female elements from this population are adapted for transmission through dense vegetation. Finally, we found small differences for the excess attenuation of female elements, with sounds recorded from the wet forest site showing less excess attenuation than sounds recorded from the montane and dry forest sites. These differences may be indicative of local adaptation, given that excess attenuation was highest at the wet forest site (although not significantly different than excess attenuation at our dry forest site). This result aligns with predictions of the Acoustic Adaptation Hypothesis, given that we would expect sounds from each of the three sites to be optimized to their respective sites.

Element type

Both male and female elements showed similar degradation patterns, suggesting that song elements have evolved under similar influences for both sexes. Nevertheless, it is worthwhile to note that degradation was not equal across all element types. For example, trill elements exhibited a lower signal-to-noise ratio (possibly because they are produced at lower frequencies than other elements and therefore more likely to be masked by background noise) than introductory and terminal elements, but experienced less blurring. It would be reasonable to predict that trill elements would experience less blurring, given that trill elements have lower frequencies and are more tonal than introductory or terminal elements (Figure 1) and therefore should experience less degradation (Brown and Hanford 2000; Slabbekoorn et al. 2002). Our results for the interaction between element and distance supported this prediction; we observed little variation in the blurring of trill elements as transmission distance increased for both sexes. In contrast, terminal elements showed a higher blur ratio than did trill elements, and blur ratio increased with distance for terminal elements. However, both males and females appeared to compensate for this by singing terminal elements that had a higher signal-to-noise ratio (Table S2). By comparison, introductory elements fell in between terminal and trill elements with regards to signal-to-noise ratio and blur ratio, but male introductory elements experienced greater excess attenuation, while female introductory elements showed a greater tail-to-signal ratio; this suggests that trills are likely more important for long-distance communication (given that they experience less degradation over further distances, Barker et al. 2009), whereas introductory elements and terminal elements are likely most important over shorter distances and potentially used by receivers to locate individuals at closer ranges (Morton 1986). Additionally, these elements may aid receivers in determining the signaller’s identity (Bee et al. 2001; Sandoval et al. 2014), given that these components of the song are highly variable (unpublished data).

Male vs. female transmission

Sex of the signaller may play a role in the attenuation and degradation of animal signals, but to date the Acoustic Adaptation Hypothesis has primarily been tested only on male acoustic signals (Morton 1975; Boncoraglio and Saino 2007). The differences we found between the sexes in the degradation of song elements (i.e. source population significantly affected the signal-to-noise ratio of males vs. blur ration and excess attenuation for females) may reflect differences in communication strategies between sexes (Langmore 1998). Given that females tend to be less conspicuous than males when singing (females produce fewer songs, and sing primarily from lower perches in the understory; Topp and Mennill 2008; Barker and Mennill 2009), and that female songs degrade faster as distance increases (Barker et al. 2009), this suggests that male songs and singing behaviour are likely better adapted for transmitting longer distances than females (Barker and Mennill 2009; Barker et al. 2009). Furthermore, duetting is an important aspect of the vocal behaviour in this species (Mennill and Vehrencamp 2005), and while the average distance between pairs when performing duets is approximately 20 m, the majority of duets are produced between 0 and 10 m (Mennill and Vehrencamp 2008). These observations suggest that female signals are not adapted to maximize transmission distance but rather optimized to communicate through dense vegetation over shorter distances with their breeding partners, especially since female song is known to play a role in coordinating breeding activities (Ritchison 1983; Sonnenschein and Rayer 1983). At all three sites, we have observed females producing songs and calls at the nest during nest building, and from the nest while incubating eggs or brooding young (Kovach 2013). Given that females vocalize so much near or at the nest, they risk drawing the attention of potential predators from afar. Therefore, female signals may be quieter and experience greater degradation with increasing distance because broadcasting loud far-reaching signals could be detrimental to their fitness. The Acoustic Adaptation Hypothesis often assumes that animal vocalizations are adapted to maximize transmission range while minimizing degradation (Boncoraglio and Saino 2007); however, differences in the transmission properties of males and females (Barker et al. 2009) may reflect different life history traits.

Past studies have emphasized the role that culture has on the evolution of songs through forces that include selection, learning biases and drift (Lynch 1996; Podos and Warren 2007). Importantly, song transmission properties may affect learning, especially in the light of a recent study by Peters et al. (2012) that suggested young birds preferentially learn the least-degraded songs. As mentioned previously, terminal elements at both our wet forest and montane forest sites tend to be more tonal (e.g. the third through fifth male terminal elements in the second row of Figure 1) than at our dry forest site, where birds use terminal elements with sharp rising or falling frequency sweeps (e.g. the second male terminal element in the second row of Figure 1). Differences in the transmission properties of different element types could explain element differences among our three sites; ongoing research will explore differences in elements among these and other sites.

Conclusion

Our study does not suggest that acoustic variation among the three populations of Rufous-and-white Wrens has been driven heavily by acoustic adaptation to three different tropical forest environments. While previous research makes it clear that these birds' songs are adapted for transmission through forests vs. fields (Barker 2008), our current work does not suggest that they are specifically adapted to different types of forest. In our study, playback site (in particular ambient noise) played an important role in the transmission and degradation of both male and female elements. In contrast, source population had a weak effect on the degradation of elements for both males and females. Furthermore, the interaction between playback site and source population did not suggest local adaptation, given that song elements did not transmit better at their respective sites. While male and female elements showed similar patterns of degradation, we did observe a few important differences.

For example, male elements appeared to be optimized to transmit most efficiently through their environment, given that we found elements recorded from populations where ambient noise is higher had a higher signal-to-noise ratio. In contrast, female elements showed no differences in signal-to-noise ratio among sites. However, we did observe that source population affected blur ratio and excess attenuation of female elements. Elements recorded from the montane forest site (the habitat with the highest vegetation density) had a lower blur ratio, suggesting that these elements are optimized for transmission through densely vegetated habitat. While our observations of male and female elements do not suggest local adaptations, they may be indicative of plastic modifications, but further studies are necessary to support this idea. Importantly, this study emphasizes the transmission differences between sexes, which is likely reflective of behavioural and life history differences between sexes. Whereas male song elements are likely maximized for long-range transmission, this does not seem to be the case for female songs; female song elements seem to be optimized for transmission through dense vegetation. This is important given that females often sing from the densely vegetated understory and will also sing songs when they are concealed in their nests. Future studies should continue to compare male and female songs and singing strategies to not only increase our understanding of the function of female song (Riebel 2003) but to better understand the behaviour and ecology of birds overall.

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