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EFFECTIVE COMMUNICATION IN TROPICAL FORESTS: SONG TRANSMISSION AND THE SINGING BEHAVIOUR OF RUFOUS-AND-WHITE WRENS (*THRYOTHORUS RUFALBUS*)

by

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A Thesis

Submitted to the Faculty of Graduate Studies

through Biological Sciences

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Windsor, Ontario, Canada

2008

Canada

Declaration of Co-authorship and Previous Publication

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is a result of joint research, as follows:

I am the sole author of the introductory chapter, Chapter 1. I am the principle author for the research presented in the data chapters, Chapters 2, 3, and 4. All three data chapters are co-authored with my supervisor, Dr. Daniel Mennill. In all cases, the key ideas, experimental execution, data analysis, interpretation, and writing were performed primarily by me. Dr. Daniel Mennill contributed through the provision of financial and logistical assistance, sharing in the research design, and providing feedback and editorial input during the writing of all three chapters.

Chapter 2 is a result of joint research undertaken by myself and my supervisor, Dr. Daniel Mennill, in collaboration with Dr. Torben Dabelsteen from the University of Copenhagen, Denmark. Dr. Torben Dabelsteen provided me with essential software for this research, the skills to use the software, and financial support to visit his university and learn about the software. He also provided feedback on the interpretation and writing for this chapter. For these reasons, he shares co-authorship on Chapter 2.

Chapter 2 is written in the format of the journal Behaviour, and was submitted for publication on 7 July 2008. Chapter 4 is written in the format of the journal Animal Behaviour, and was submitted on 8 July 2008.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis.

I certify that, with the above qualification, this thesis and the research to which it refers is the product of my own work.

II. Declaration of Previous Publication

This thesis includes a substantial portion of one original paper that has been previously published in a peer reviewed journal, as follows:

Thesis Chapter	Publication Citation	Publication Status
Chapter 1	Barker, N.K. 2008. Bird song structure and transmission in the Neotropics: Trends, methods and future directions. Ornitologia Neotropical 19: 175-199	Published

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Abstract

This thesis examines sound transmission and the communication behaviour of Neotropical Rufous-and-white Wrens. A song transmission experiment revealed strong effects of distance, signaller perch height, and sex on song degradation, minor effects of receiver perch height, and mixed effects of microhabitat. An examination of fine structure of Rufous-and-white Wren song in relation to habitat did not show a strong effect of microhabitat on song structure, although it did quantitatively validate the use of song type classes in this species. A field study of perch height selection in Rufous-and-white Wrens showed that they use elevated song posts, which were shown to provide a song propagation benefit. Males perch higher than females, which may be related to a more active territorial defence or mate guarding role for male song. This is the first sound transmission-based investigation of effective communication in both sexes of a tropical duetting species.

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Chapter 1

Introduction

Introduction

Bird song plays an important role in territory defence and mate attraction (Catchpole & Slater 2008). Song structure is significant because it acts in both species and individual recognition, and may also be important for reproductive divergence (Baker & Boylan 1999, reviewed in Slabbekoorn & Smith 2002) and hybridization prevention (reviewed in Slabbekoorn & Smith 2002). Song structure is shaped by proximate and ultimate mechanisms such as bill morphology (e.g. Podos 2001), body size (e.g. Ryan & Brenowitz 1985), and sexual selection (e.g. Vallet & Kreutzer 1995). However, bird song must transmit effectively through the environment before it can be shaped by any other selective pressures (Wiley & Richards 1982). Some characteristics of bird song are thought to differ between tropical and temperate habitats (Morton 1996, Stutchbury & Morton 2001), although no systematic study has been conducted thus far. With differences in their physical environment as well as behavioural ecology, it would not be surprising to find that birds in the tropics exhibit different patterns of variation in song structures and singing behaviours than temperate species. This thesis is focussed on patterns in song transmission, song structure, and singing behaviour in a Neotropical duetting songbird: the Rufous-and-white Wren. In this introductory chapter, I review the important background concepts necessary to understand the contents of the three data chapters in this thesis.

Tropical versus temperate

The concepts of "tropical" and "temperate" are often presented as dichotomous. As geographical regions, they are divided on a map by the Tropics of Capricorn and Cancer, but the actual division is more gradual. The dichotomy is therefore somewhat artificial in its

oversimplification; "tropical" and "temperate" represent two ends of a spectrum of variation in latitude, climate, and other features. A complete picture of tropical to temperate variation should include studies of intermediate latitude, but a false dichotomy is useful because it helps to highlight differences between the regions of maximum contrast.

In general, tropical habitats differ most dramatically from temperate habitats in terms of climate and seasonality; tropical regions have rainy and dry seasons whereas temperate regions have winter, spring, summer, and fall. Patterns in flowering, fruiting, and insect abundance are more variable in the tropics than in temperate habitats. Birds living in tropical habitats experience different selective pressures from those in temperate habitats, and they exhibit contrasting behavioural ecologies (Stutchbury & Morton 2001). Differences in breeding season and migratory behaviours, stemming primarily from climatic differences, influence other behaviours such as territoriality, mating system, and communication (Stutchbury & Morton 2001, 2008). The tropics exhibit greater species diversity and the majority of bird species are found in the tropics; approximately 80% of songbirds (order: Passeriformes) breed in tropical regions (Stutchbury & Morton 2001). These facts have prompted Morton (1996) and Stutchbury & Morton (2001) to suggest that it might be more reasonable to consider the behavioural ecology of tropical birds as the standard, and temperate species as divergent, which stands in contrast to the prevalent world view. While many studies regarding the structure and transmission of tropical bird song have been conducted, the amount of research dedicated to temperate species is disproportionately high. Research regarding tropical bird song in relation to habitat contributes to our understanding of bird song, avian behavioural ecology, and the important associations between birds and their physical environments.

Song structures are shaped by multiple evolutionary factors

Birds' species-specific songs evolve as a compromise between multiple selective forces that can sometimes work in opposition. For example, some birds may be under intense selective pressures on beak size due to food availability (e.g. Gibbs & Grant 1987) which may then affect song structure by constraining the speed of trilled notes (e.g. Podos 2001, Ballentine 2006). Sexual selection can also influence song structure if female birds prefer specific features in male songs (e.g. Vallet & Kreutzer 1995, Ballentine *et al.* 2004). Additional factors including body size, territory size, population density, and intended receivers will also influence song structure (Lemon *et al.* 1981, Cosens & Falls 1984, Calder 1990, Nemeth *et al.* 2001, 2006). Phylogeny can have an impact as well, by constraining the variation between closely related species. Lastly, the habitat a species lives in can influence song structure, if certain song features transmit more effectively in certain habitats and thereby lead to better communication between conspecifics.

Signal distortion: Attenuation and degradation

Animal communication involves the transmission of information-carrying signals from senders to receivers. As these signals propagate through the natural environment, they are distorted from their original structure by several processes. Bird song is no exception and is often modified extensively by the time it travels from a sending individual to a receiving one. Modifications that occur to a song as it is transmitted may interfere with a receiver's ability to detect or recognize the signal. Detection requires that a receiver can determine the presence or absence of a signal, while recognition requires the receiver to discriminate between numerous different signals (Wiley & Richards 1982). Attenuation and degradation

are the two major forces affecting sound transmission. *Attenuation* is the decrease in signal strength that occurs with increasing distance from the sender, and is often perceived as a decrease in amplitude. *Degradation* is the distortion of the "spectral, temporal, and structural characteristics" of a sound (Slabbekoorn 2004b) by processes of reverberation, refraction, and irregular amplitude fluctuations (Wiley & Richards 1978, 1982, Bradbury & Vehrencamp 1998, Slabbekoorn 2004b), although sometimes this word is used to refer to all changes to a sound that occur during transmission (including excess attenuation; e.g. Dabelsteen *et al.* 1993, Holland *et al.* 1998).

Attenuation: *Spherical spreading* is the reduction of sound intensity by 6 dB with every doubling of distance from the sound source. Spherical spreading causes global attenuation, where all frequencies of a sound are decreased by the same amount. Attenuation in excess of that caused by spherical spreading is called *excess attenuation*, and occurs through various forces such as absorption and scattering. *Absorption* is when sound energy is converted to other forms of energy (i.e. heat) during propagation though a medium (e.g. air). *Scattering* occurs when sounds are reflected by obstacles such as leaves, branches, or atmospheric disturbances. Absorption and scattering both cause frequency-dependent attenuation, where higher frequency sounds attenuate faster than lower frequency sounds. There are complex interactions between sender height, distance to receiver, the sound's frequency, and other factors that influence the degree to which a sound is attenuated (Wiley & Richards 1978). Sounds produced near or at ground level and travelling over long distances interact with the ground, selectively attenuating specific frequencies. The exact pattern of attenuation depends on the height that the signal is produced at, the height of the receiver, the distance between sender and receiver, and the substrate over which the sound is

propagating (i.e. bare ground versus vegetation-covered). In some instances, low frequency

sounds (less than 1-2 kHz) experience a great increase in attenuation when they are produced

from within 1 m of the ground (e.g. Marten *et al.* 1977, Ellinger & Hödl 2003), while in other

instances, higher frequencies experience greater attenuation (Embleton 1996). The overall

conclusion regarding attenuation seems to be that low frequency sounds propagate better than

high frequency sounds although there are some situations when this rule does not apply

(Marten & Marler 1977, Marten *et al.* 1977, Wiley & Richards 1978, Ellinger & Hödl 2003).

Degradation: There are two main forms of sound degradation. *Reverberations* are

caused when sound is reflected off surfaces to create a "sound tail" of multiple echoes after a

sound. They are often associated with closed habitats because the presence of many thick tree

trunks and branches causes extensive reflections. *Irregular Amplitude Fluctuations* are

caused when sound is refracted by atmospheric turbulence; the resulting distortion is

perceived as fluctuations in a sound's intensity, which can mask the amplitude fluctuations in

the original signal (Wiley & Richards 1978). Irregular amplitude fluctuations are often

associated with open environments, where solar radiation warms pockets of air to create

turbulence and stratification in air temperature. The term *blurring* has been used to refer to

the collective effects of frequency-dependent attenuation and degradation (reverberations and

irregular amplitude fluctuations) on amplitude and frequency patterns (e.g. Dabelsteen *et al.*

1993, Mathevon *et al.* 2005).

Habitat and vocal signals: The acoustic adaptation hypothesis

The founding research relating sound transmission to avian communication (e.g.

Morton 1975, Gish & Morton 1981, Nottebohm 1985), as well as the proposition that birds

will best learn the songs they hear most clearly (Hansen 1979), prompted the formulation of the *acoustic adaptation hypothesis*. This hypothesis suggests that evolution has favoured acoustic signals that are structured to maximize their transmission in a given environment (Rothstein & Fleischer 1987, Brown & Handford 2000). In other words, birds' songs should match their habitats, so as to travel the greatest distance with minimal attenuation (decrease in signal strength with distance) and degradation (temporal and structural distortion). Additional terms such as environmental adaptation hypothesis (Date & Lemon 1993), local adaptation hypothesis (Brown *et al.* 1995), and environmental selection hypothesis (Bosch & de la Riva 2004) have also been used to refer to the selection pressure that the physical environment can exert on strategies for acoustic communication, but acoustic adaptation hypothesis is the most prevalent term in avian communication studies. General predictions from this hypothesis suggest that bird songs should be lower pitched, less frequency-modulated, and have fewer rapidly repeated elements in closed (i.e. forest) habitats than in open (e.g. grassland) habitats, because the songs of closed habitat birds are generally subject to more reverberation and frequency-dependent attenuation than those of open habitat birds (Richards & Wiley 1980, Wiley & Richards 1982). Numerous studies have tested these predictions and the match between song and habitat using various methods (e.g. Wiley 1991, Date & Lemon 1993, Slabbekoorn *et al.* 2002, Seddon 2005, Nemeth *et al.* 2006, Lijtmaer & Tubaro 2007). Some findings support the predictions (e.g. Morton 1975, Anderson & Conner 1985, Wiley 1991, Badyaev & Leaf 1997, Bertelli & Tubaro 2002, Tubaro & Lijtmaer 2006) while others fail to do so (e.g. Lemon *et al.* 1981, Handford & Lougheed 1991, Date & Lemon 1993, Williams & Slater 1993). A recent meta-analysis showed that song frequency variables were consistent with predictions of the acoustic adaptation hypothesis, but the

single temporal variable included in the analysis was not (Boncoraglio & Saino 2007). Collectively, these and other studies have demonstrated some general relationships between habitat, song structure and sound transmission.

Trends in song structure and transmission: How is song related to habitat?

There are clear differences in the frequency and temporal structure of bird song between open and closed habitats, but differences between tropical and temperate habitats are far less obvious. Bird species living in closed habitats tend to have lower frequency songs than those in more open habitats (Morton 1975, Wiley 1991, Tubaro & Lijtmaer 2006), a difference that is more pronounced in the tropics (Wiley & Richards 1982, Wiley 1991). One explanation for this frequency difference is that open and closed habitat birds experience differential selective pressures. While there is an overall pressure for birds to produce low pitched songs because lower frequency sounds attenuate less than higher pitched sounds (Konishi 1970), birds in closed habitats may experience especially strong selection for low frequency songs because trees and foliage cause extensive scattering and absorption leading to greater excess attenuation of high frequencies than lower frequencies (Wiley & Richards 1982). There may be a wider range of acceptable song frequencies in open habitats because selection pressures are relaxed in the absence of sound-scattering foliage (Wiley & Richards 1982, Wiley 1991, Nemeth *et al.* 2001). Ambient noise likely also plays a role: birds may be under selective pressure to produce songs that are not overlapped by wind or insect noises (Ryan & Brenowitz 1985). Insects such as cicadas (Homoptera: Cicadidae) produce extensive high frequency ambient noise (Ellinger & Hödl 2003, Slabbekoorn 2004b), wind noise is predominantly low frequency (Brenowitz 1982, Ryan & Brenowitz 1985,

Slabbekoorn 2004b) and other biotic factors such as amphibians or mammals produce noise

of low to intermediate frequencies (reviewed in Slabbekoorn 2004a, 2004b). There is some

evidence that high frequency noise is more common in forest habitats, particularly in the

tropics, whereas lower pitched wind noise is more prevalent in open habitats (Ryan &

Brenowitz 1985, Waser & Brown 1986, Slabbekoorn 2004a, 2004b). Therefore, differential

selective pressures may be exerted on birds in closed and open habitats to produce low and

high frequency songs, respectively, to avoid being masked.

Birds living in closed habitats have different song structures than those living in more

open habitats. Grassland birds tend to have songs with faster trills (e.g. Handford &

Lougheed 1991), a greater prevalence of side bands and buzzes (e.g. Wiley 1991), more

notes, and broader bandwidths (e.g. Tubaro & Lijtmaer 2006). In contrast, forest species tend

to have pure-tonal songs (e.g. Morton 1975) with fewer notes, longer notes, and longer

intervals between notes (e.g. Badyaev & Leaf 1997, reviewed in Wiley & Richards 1982).

This trend of slower trilled tonal songs in closed habitat species is true in both tropical

species (Morton 1975, Ryan & Brenowitz 1985) and temperate species (Richards & Wiley

1980, Wiley 1991, but see Boncoraglio & Saino 2007). These structural characteristics are

thought to be adaptive for avian communication. In a dense forest, reverberations will blur

the temporal structure of repetitive frequency modulation and rapid amplitude modulation in

songs but whistled tonal notes will be less distorted (Richards & Wiley 1980, Brown &

Handford 2000). In open habitats, irregular amplitude fluctuations mask low rates of

amplitude modulation, so trills may be adaptive because the redundancy created in their rapid

rate of amplitude and frequency modulation ensures that information is still received

(Richards & Wiley 1980).

No studies have explicitly compared tropical and temperate bird songs, despite the several surveys that have been conducted within tropical habitats (Morton 1975, Ryan & Brenowitz 1985, Seddon 2005) and temperate habitats (Richards & Wiley 1980, Wiley 1991, Sorjonen 1986). However, there is some evidence that suggests differences in songs between the two habitats. For example, when comparing the findings of two similar studies (Morton 1975, Wiley 1991), tropical forest species appear to sing lower frequency songs than temperate forest species, though no such difference is apparent between tropical and temperate grassland species. Tropical forest birds concentrate the energy of their songs into low frequencies (mean frequency emphasized is 2.1 kHz; Morton 1975), while temperate forest birds have a higher average dominant frequency (frequency of maximum amplitude is 4.2 kHz; Wiley 1991). Many tropical forest species are described as having simple tonal songs that change little in frequency (Morton 1975) and some researchers state that these narrow frequency bandwidth songs are typical of species that live in dense tropical forests (Slabbekoorn *et al.* 2002). These potential frequency and structural differences between tropical and temperate forest habitats may relate to stronger selection pressures on tropical species to produce low frequency, narrow frequency bandwidth sounds as a strategy of avoiding excess attenuation and degradation caused by dense tropical habitats. Tropical bird species may be subject to stronger selection to maximize the distance their songs travel because they have larger territories than those of their temperate counterparts (Terborgh *et al.* 1990), and birds that sing at low frequencies could be at a selective advantage because their songs travel farther to mates or rival conspecifics. Additionally, there may be further advantages for tropical forest species to use narrow frequency bandwidth notes if reverberations enhance the signal efficiency of these songs (Slabbekoorn *et al.* 2002, Nemeth

et al. 2006). Lastly, ambient noise may also create an advantage for low pitched, narrow frequency bandwidth songs. The biotic environment in tropical forests is varied and noisy; insects such as crickets (Orthoptera: Gryllidae), katydids (Orthoptera: Tettigoniidae), and cicadas produce a great deal of ambient noise in the frequency range of 3.15-12.5 kHz, with most of it concentrated around 4-8 kHz (Ellinger & Hödl 2003, Slabbekoorn 2004a, 2004b). Birds in tropical forests may experience especially strong selection to produce songs within the window of relative quiet (1-4 kHz) to avoid masking from the intense ambient noise created by tropical insects, although this will depend on the particular habitat (e.g. Slabbekoorn 2004a, 2004b).

While there is a sufficient amount of evidence to suggest that the acoustic adaptation hypothesis holds true in many situations, there are many reasons why we might find evidence that directly contradicts its predictions. Firstly, the acoustic adaptation hypothesis focuses on maximizing long-distance signals; broadcasting as far as possible with minimal attenuation and degradation to enhance detection and recognition by receivers. There are, however, situations in which maximizing a signal might not be necessary or desirable, in which case a signal may be adapted for optimal, rather than maximal distances (Lemon *et al.* 1981, Aubin *et al.* 2004, Nemeth *et al.* 2006). It may be, for example, that intended receivers (neighbours or mates) are nearby, or that a degraded signal is adequate for its intended purpose (Aubin *et al.* 2004, Kroon & Westcott 2006) or even beneficial if the degraded signal keeps information from unintended eavesdroppers (Mennill et al. 2002). It could also be that some signals are designed to minimize variability in transmission quality rather than maximize distance travelled (Brown & Handford 1996, 2000, 2003). Additionally, some amount of signal alteration can actually be useful to birds if it is advantageous to know how far away

neighbouring birds are, because degradation can act as a distance and location cue (Richards 1981, Morton 1982, Morton 1986).

The second reason we might predict deviation from the predictions of the acoustic adaptation hypothesis is that many factors influence the evolution of song structure beyond the natural environment. For example, larger birds may produce lower pitched songs (e.g. Bowman 1979, Ryan & Brenowitz 1985, Bertelli & Tubaro 2002), beak size and shape constrains temporal features of songs (e.g. Podos 2001, Seddon 2005, Ballentine 2006, reviewed in Podos & Nowicki 2004), phylogeny can constrain variation and subsequent evolution of song (e.g. Laiolo & Rolando 2003, Rheindt et al. 2004), territory size, population density and intended receiver (i.e. close-range or long-range) will influence how far a signal must travel (e.g. Wiley & Richards 1978, Lemon et al. 1981, Calder 1990, Aubin et al. 2004, Nemeth et al. 2006), the presence of related sympatric species may lead to character displacement in songs (e.g. Bowman 1979, Irwin 2000, Slabbekoorn & Smith 2002), and sexual selection can exaggerate certain song features if they are preferred by females (e.g. Vallet & Kreutzer 1995, Ballentine et al. 2004). These factors may counterbalance acoustic adaptation.

Thirdly, there are several approaches to studying song structure and transmission, and innumerable variations within each approach. Inconsistencies between methods can explain some variation in the results of studies testing the acoustic adaptation hypothesis.

Types of studies: Focal studies, surveys, and transmission studies

Studies that test the predictions of the acoustic adaptation hypothesis and the effects of sound transmission on the structure of bird song can be split into three major categories:

1) sound transmission studies; 2) surveys; and 3) focal species studies. Generally, sound

transmission studies are aimed at understanding the transmission of sound through different

environments; surveys compare song characteristics of many species between categories of

habitat; and focal species studies concentrate on habitat-related song differences in one or a

few species.

Sound transmission studies: The study of sound transmission and its implications

for avian communication was largely founded by transmission studies conducted in the 1970s

(e.g. Chappuis 1971, Morton 1975). The general method for conducting a study of this type

is to broadcast synthetic noises from a speaker and re-record them from a variety of distances

at one or more heights. The resulting *observation* sounds are then compared to the *model*

sounds, which can be either the original broadcasted stimuli or close-range re-recordings.

Using re-recordings as model sounds is preferable, because this helps control for possible

distortion caused by the broadcasting and recording process (e.g. Morton 1975, Dabelsteen *et*

al. 1993). Model sounds are compared to the transmitted sounds to ascertain the extent of

attenuation and degradation. The same experimental setup can be used in multiple habitats,

and then attenuation, reverberation, and other sources of distortion can be measured in

relation to various factors.

Survey studies: Sound transmission studies have revealed that signals experience

differential attenuation and degradation dependent on the structure of the habitat they

propagate through. The predictions of acoustic adaptation hypothesis were developed with

this central idea in mind: birds requiring their long-distance signals to be received by distant

conspecifics should have songs structured to transmit efficiently and accurately through their

native environment (Brown & Handford 2000). Several researchers have used large- and

small-scale surveys to investigate whether this prediction holds true. These studies involve

relating the songs or calls of several species to the habitats in which these species live. When

conducting survey studies, investigators collect recordings of bird songs from various

habitats, conduct fine structural measurements on these songs, and then compare song

structure between habitat classes. Surveys differ in the number and type of species,

geographic area and habitats considered, as well as the inclusion of other factors that might

influence song, such as body size, beak morphology, or phylogeny.

Focal species studies: In focal species studies, researchers investigate a single

species or a few closely-related species, either to give insight regarding that particular species

or to use it as a model species which helps explain general principles of avian

communication. Focal species studies can be split into four general categories: (1)

Descriptive studies; (2) Song transmission studies; (3) Reciprocal transmission studies; (4)

Playback and response studies. Combining more than one of these approaches into one study

is common and useful.

Descriptive studies: Generally, researchers measure various frequency and temporal

parameters of songs from birds of one or a few species living in different habitats and then

compare these characteristics to see if conspecifics from various habitats sing different songs.

Birds' songs are recorded in multiple habitat types, measured with sound analysis software,

and then compared between habitats. Like surveys, researchers measure multiple fine

structural features of songs and then relate them to habitat classes or ecological variables.

Song transmission studies: The stimuli in song transmission studies are songs or song

elements from one or more species, but the experimental design is similar to that of sound

transmission studies. The stimuli songs are broadcast and re-recorded under various

conditions to generate observation sounds, which are then compared to the model sounds (either the original recordings, or songs re-recorded at very short distances). The goal is to compare the effects of distance, height of song and listening posts, different habitats, or other factors on the propagation of particular species' songs.

Reciprocal transmission studies: Reciprocal transmission experiments determine how bird songs from various locations transmit in native and foreign habitats. They provide a test of the acoustic adaptation hypothesis by assessing the match of songs to habitats; a bird's song should be adapted for the habitat in which it lives, so if a conspecific song from a different habitat propagates better than the native song, it suggests that the native song does not meet the predictions of the acoustic adaptation hypothesis. The methods are similar to those of song transmission, except the propagated songs or song elements are collected from multiple habitats, and the experiment is replicated in those same habitats.

Playback and response studies: Playback studies introduce a behavioural element to studies of song propagation in the natural environment. This technique involves assessing birds' reactions to various playback stimuli to determine if they recognize the differences between songs. Often a control song and a degraded song are used, where degraded can mean re-recorded at various distances, altered in the frequency domain to simulate attenuation of higher frequencies, or altered in the time domain to create or simulate reverberations.

Tropical songbirds: Female song and duetting

The most common definition of "bird songs" states that they "tend to be long, complex, vocalizations produced by males in the breeding season" (Catchpole & Slater 2008), but as many authors have pointed out, this definition leaves out half the story (e.g.

Slater & Mann 2004). The authors of this widespread definition wrote it from a temperate-biased perspective; it is true that song is a primarily male activity in the temperate region, but it is quite common to find female song in tropical regions (Langmore 1998, Slater & Mann 2004). Female solo song has been largely neglected, although there has been some research on duet singing (Slater & Mann 2004). Duetting, defined as "overlapping bouts of vocalizations given by paired individuals such that their elements within those bouts have a high level of alternation, or a low coefficient of variation of the intervals between their elements, or both" (Hall 2004, adapted from Farabaugh 1982), has been documented in over 220 bird species (Farabaugh 1982). This number, representing $\geq 3\%$ of avian species, is likely to be a vast underestimate, based on preliminary research (Mennill, unpubl. data). Because female song and duetting occur in a variety of unrelated bird taxa, these behaviours must have evolved several times, a more parsimonious explanation than the alternative that they have been lost multiple times (Slater & Mann 2004). It therefore stands to reason that some aspects of tropical life history are associated with female song, duetting, or both (Slater & Mann 2004).

Based on the small amount of research that has been conducted, female song appears to function in territorial defence, mate guarding, mate attraction, and coordination of breeding activities, and tends to be associated with high levels of female-female competition and year-round territoriality (Langmore 1998). In many tropical species, especially insectivores, year-round territoriality is common (Kunkel 1974, Stutchbury & Morton 2001), breeding seasons are longer (Stutchbury & Morton 2001), and parental investment may be higher than temperate species (Stutchbury & Morton 2001, Slater & Mann 2004). Stutchbury & Morton (1995, 2001) have also suggested that extra-pair copulations by males are less

frequent in tropical birds. Taken together, these factors suggest lower levels of sexual selection, greater pair commitment, and extensive sex-role convergence in tropical birds (Slater & Mann 2004). Sex-role convergence is thought to be one of the primary factors favouring female song in tropical bird species (Stutchbury & Morton 2001, Slater & Mann 2004). Female song may also be involved in breeding synchrony; there are few external cues for breeding (i.e. changes in day length and temperature) in tropical regions, so it may be that song by both pair members ensures that their breeding activities are synchronized (Slater & Mann 2004).

Up to twelve hypotheses for avian duetting have been proposed, many of which are similar to those for female song. Duet singing has been suggested to function primarily in maintaining contact between pair members, mate guarding, paternity guarding, ensuring reproductive synchrony, joint resource defence, and signalling commitment (reviewed in Hall 2004). These can be simplified into a smaller number of categories: acoustic contact, pair bonding, territory defence, and sexual conflict. Dense tropical forests may restrict visibility, in which case cooperative duets would be useful in maintaining acoustic contact and localizing mates (Thorpe 1963). Pair bonding is accomplished through cooperative duets, if members are signalling commitment to one another (Wickler 1980). Pairs may duet cooperatively to defend their territories or resources against intruders (Seibt & Wickler 1977). Lastly, duetting may also have a role in sexual conflict if individuals reply to their mates' songs to prevent extra-pair copulations, thereby functioning as a mate or paternity guard (Sonnenschein & Reyer 1983).

Rufous-and-white Wrens

In this thesis, I explore sound transmission and communication behaviour in Rufous-and-white Wrens (*Thryothorus rufalbus*), a Neotropical duetting species of medium-sized, non-migratory songbirds in the family Troglodytidae. There are five subspecies of Rufous-and-white Wrens, collectively ranging from southern Mexico through Central American into Colombia and Venezuela. Our study site is in Sector Santa Rosa of the Area de Conservación Guanacaste (10°40'N, 85°30'W), in which our study species (subspecies *Thryothorus rufalbus castonanotus*) lives in areas of mature humid forest as well as late-successional regrowth forest. Rufous-and-white Wrens are insectivores, feeding primarily on the ground among the leaf litter (Ahumada 2001).

While a detailed study has yet to be published, the ongoing study of this species by Mennill et al. demonstrates that this species is relatively long-lived and maintains long pair-bonds. Several pieces of evidence collected during the on-going long-term study of our population provide support for this statement: (1) two males in the population were observed during six consecutive field seasons (male 1: 2002-2007, male 2: 2003-2008); (2) one pair was observed defending the same territory from 2002-2006; and (3) survivorship from the 2005 field season to the 2006 field season was 76.7% (Mennill et al. unpubl. data). Rufous-and-white Wrens maintain year-round territories that are relatively large for passerines (regularly ≥ 100 m long in our study site; Mennill & Vehrencamp in press). Males and females show similar territorial behaviour; territories delineated by male songs are similar in size to those delineated by female songs (Osmun Honours thesis).

The breeding season for Rufous-and-white Wrens is from April until at least mid-August and possibly later. The date of the first egg laid within a breeding season is associated

with the onset of the rainy season in May (Topp & Mennill 2008), and I have observed pairs actively attempting to re-nest following predation events well into August. Pairs share parental duties such as nest-building and nestling-feeding, but only females incubate eggs and brood nestlings. They are socially monogamous and it is not yet clear whether they are genetically monogamous, although females have been observed making forays into adjacent territories prior to egg-laying (Mennill & Vehrencamp in press).

Rufous-and-white Wren song

Both male and female Rufous-and-white Wrens sing, and pairs combine their songs to form duets (Mennill & Vehrencamp 2005). Songs in this species have a generally stereotyped song structure, although there is some variation between subspecies (Valderrama *et al.* 2007). Within our study population (subspecies: *Thryothorus rufalbus castonanotus*), male and female songs both follow a very consistent structure, comprised of introductory, trill, and terminal sections (Mennill & Vehrencamp 2005). The introduction section appears to be the most variable, and can include between one and six notes, which range from short or long pure-tonal syllables of various frequencies to very quick wide bandwidth syllables (Mennill & Vehrencamp 2005). The trill section contains between two and 35 pure-tonal syllables within a very narrow frequency range that are repeated in relatively quick succession, although there is some variability in the spacing between subsequent trill syllables (Mennill & Vehrencamp 2005). The terminal section is often the loudest part of Rufous-and-white Wren songs, and it most often consists of one wide bandwidth syllable, although some songs have tonal terminal syllables (Mennill & Vehrencamp 2005).

While male and female songs are similar, there are significant differences in the fine structure of their songs that allow for sex differentiation by ear in the field, or later using spectrograms. Males have more repeated syllables in their trills, female songs are higher frequency, and female songs often appear quieter than male songs, although this is difficult to quantify (Mennill & Vehrencamp 2005). Males sing more than females, and only males show a pronounced peak in singing at dawn (Mennill & Vehrencamp 2005, Topp & Mennill 2008). Males and females also show differences in the seasonal pattern of their singing behaviour: males sing most around the onset of the rainy season, which coincides with the female fertile period, while females sing most early in the year, prior to breeding (Topp & Mennill 2008).

Both males and females have repertoires of distinct song types that can be identified based on differences in their temporal and frequency features; males usually have larger repertoires than females (Mennill & Vehrencamp 2005). Rufous-and-white Wrens sing with eventual variety, where they repeat a given song type several times before switching to another song type (Mennill & Vehrencamp 2005). Males sing more repeats of a given song before switching than females do (Mennill & Vehrencamp 2005). Song sharing is very common in our population, where every bird shares several song types with other birds in the population (Mennill & Vehrencamp 2005).

Rufous-and-white Wren duets are formed when a male and female contribute at least one song within ≤ 1.0 s of each other. Duets are loosely coordinated in time, and range from simple duets (one song from each sex), to sandwich duets (one song from one pair member, surrounded by two songs from second pair member), to complex duets (more than one song from both pair members; Mennill & Vehrencamp 2005). Substantial evidence suggests that duets in this species are multi-purpose and that the function depends on the context in which

they occur (Mennill & Vehrencamp in press). Duets appear to be involved in maintaining acoustic contact, pair bonding, cooperative territory defence, and mate guarding (Mennill 2006, Topp & Mennill 2008, Mennill & Vehrencamp in press).

Effective communication in tropical forests: Song transmission, song structure, and singing behaviour in Rufous-and-white Wrens

There is substantial evidence that birds rely on a variety of techniques to enhance communication within their habitats, as shown through surveys and various focal species studies. In my thesis, I used multiple methods to assess the techniques used by Rufous-and-white Wrens. In Chapter 2, I present results of a song transmission experiment designed to assess the effects of propagation distance, song post height, receiver height, sex, and habitat on the degradation of Rufous-and-white Wren song. In Chapter 3, I present analyses of the fine structure of Rufous-and-white Wren songs in relation to habitat in a descriptive study. In Chapter 4, I quantify the perch heights that Rufous-and-white Wrens choose during particular activities, in order to assess whether they utilize song posts that enhance communication. My research provides a comprehensive analysis of the song structure and singing behaviour of Rufous-and-white Wrens, particularly in relationship to sound transmission and effective communication. This research also represents the first thorough examination of song transmission and singing behaviour for both sexes in a duetting species.

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Chapter 2

Degradation of Rufous-and-white Wren songs in a tropical forest:

Effects of sex, perch height, and habitat

Chapter 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 maximize 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 were more degraded in open field than forest habitats, but microhabitat conditions within the forest exerted a strong influence on song degradation. These findings match previous studies showing an effect of distance, song post height, and habitat, but stand in contrast to previous studies that show a strong effect of receiver perch height. This study represents the first detailed investigation of differences in song transmission between males and females.

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 defence,

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; Holland et al., 1998; Nemeth et al., 2001; Balsby et al., 2003; Blumenrath & Dabelsteen, 2003; Mathevon et al., 2005; 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 impact the ability of conspecifics to detect, recognize, and localize each other (Richards, 1981; Dabelsteen et al., 1993; Naguib, 1996; Aubin et al., 2004). 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 (Nemeth et al., 2006; Slabbekoorn et al., 2002).

Previous research has shown that sound degradation increases with distance (e.g. Dabelsteen et al., 1993; Holland et al., 1998; Balsby et al., 2003; Mathevon et al., 2005; Lampe et al., 2007), is affected by the perch height of signallers as well as receivers (e.g. 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; Stutchbury & Morton,

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). Solos and duet songs in this species are

multi-functional and context-dependent, and previous research has shown a connection with

territorial defence, mate and paternity guarding, coordination of breeding activities, as well

as bonding and maintaining acoustic contact within pairs (Mennill & Vehrencamp, 2005;

Mennill, 2006; Topp & Mennill, 2008; Mennill & Vehrencamp, in press). Male and female

songs are very similar; nearly all songs in our population consist of a variable number of

introductory syllables, a trill of repeated syllables, and a loud terminal syllable (Mennill & Vehrencamp, 2005). However, males have larger repertoires and higher song outputs than females (Mennill & Vehrencamp, 2005; Topp & Mennill, 2008), 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).

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 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 different 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 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 from our Santa Rosa site, regardless of song type. We bandpass filtered all songs (highpass frequency: 500 Hz; lowpass frequency: 4000 Hz); 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 normalized to -1 dB. The final test sequence had 30 songs from rufous-and-white wrens in the Santa Rosa population, with 10 males and 8 females contributing in different ways. Each song was repeated four times, with 5 seconds between different song types. We analyzed 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). This subset was chosen to represent the variation within the test sequence.

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 RadioShack Realistic 33-4050 sound level meter), reflecting the natural amplitude of rufous-and-white wren song. Recording levels were held constant throughout the experiment. 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 distance: 19.2 ± 2.2 m across 525 duets recorded from 19 pairs; Mennill & Vehrencamp, in press). The remaining distances were chosen by halving or doubling this distance, resulting in final (horizontal) distances of 5 m, 10 m, 20 m, 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 broadcasted

from speakers 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 specially designed program SIGPRO (Pedersen, 1998), and followed an established analytical protocol (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 filtering the sound with an element-specific filter and tightly cropping the sound to eliminate background noise (Filters: a: 0.80-1.04 Hz; b: 0.55-1.25 Hz; c: 0.904-1.68 Hz; d: 0.646-1.335 Hz; e: 1.11-3.3 Hz; f: 0.894-1.189 Hz; g: 0.59-1.10 Hz; h: 0.66-1.87 Hz; i: 0.62-0.98 Hz; j: 0.61-1.16 Hz; k: 0.86-1.12 Hz; l: 0.90-1.09 Hz; m: 0.85-1.23 Hz; n: 0.61-0.82; o: 1.25-1.98 Hz; p: 0.69-1.20 Hz; q: 1.13-3.20 Hz; r: 0.72-1.23 Hz; s: 0.60-1.30 Hz; t: 1.18-

1.706 Hz; u: 0.85-1.17 Hz; v: 1.00-1.46 Hz; w: 0.99-1.20 Hz; x: 0.81-0.91; 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 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 maximize 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, this was sometimes not possible due to singing birds, wind, or other spontaneous noises during the playback of the test sequence. Due to high winds and technical problems, we were unable to complete the 40 m trials for transect 1 (field) and

transect 3 (regenerating forest). For analyses of introductory syllables and trills, sample sizes were very large, despite missing values: 2998 for introductory syllables and 2960 for trills. For 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; for the reasons outlined above, the sample size for the terminal syllable analysis was 759.

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. The model used for introductory syllables and trills was identical: 4 distances (5 m, 10 m, 20 m, 40 m) x 3 speaker heights (1 m, 5 m, 7 m) x 3 microphone heights (1 m, 5 m, 7 m) x 2 sexes x 5 transects (1 field, 2 mature, 2 regenerating). The model used for terminal syllables was slightly different: 3 distances (10 m, 20 m, 40 m) x 3 speaker heights (1 m, 5 m, 7 m) x 3 microphone height (1 m, 5 m, 7 m) x 2 sexes x 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 $\text{Log}_{10}(x)$ 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 attached to an Anchor Audio Minivox PB-25 speaker. We controlled the speaker height by attaching it to a rope that hung over a branch, and stabilizing the speaker with two additional ropes anchored close to the ground. 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, Inc., California) and assembled the test sequence in SYRINX-PC (J. Burt, Washington). 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 the independent factors.

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). 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 was approaching 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 x transect interaction, the speaker height x microphone height interaction, and the sex x transect interaction. The first interaction shows that the pattern of degradation over distance depends on specific microhabitat conditions found in each transect. 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 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 x 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 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 (Figures 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 much 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 (Figures 2 – 4). 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. 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 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 x transect and speaker height x 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 affects whether female trills experience more or less degradation than male trills (Figures 2 – 4). In addition to the previous interactions, the speaker height x 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 x 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 x sex interaction significantly influenced SNR and BR, while the speaker height x 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 sample size for terminal syllables in this study. 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 x transect interaction and the sex x 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 have more or less degradation 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 x 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 x sex interaction was significant for EA only, such that there 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 was approaching 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 female 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 height of the signaller, the 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 three of the transects, while 7 m was superior in the remaining two transects. 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 extend their communication range. The optimal song post height appears to be in the range of 5 m and 7 m, and the specific height will be 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 listener perch height of 5 m results in less degradation than a perch 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. 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 somewhat of an 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 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 have 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 occured 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 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 in 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 quantified (Mennill & Vehrencamp, 2005). Our finding that female songs experience 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, 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 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 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 was lower, and BR of trills was very low, in comparison to the forested transects. BR was likely low because there was little vegetation to cause

scattering, refraction, and reverberations (Blumenrath & Dabelsteen, 2004; Slabbekoorn, 2004). This may in turn explain why EA was very low, 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 showed very 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 show that songs were somewhat less degraded 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.

Overall 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 a much lower height 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 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 degradation 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, which in turn suggests that rufous-and-white wren songs cannot be specifically adapted to the microhabitat conditions in their own territory, 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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Table 1. Mixed-model ANOVA table for excess attenuation (EA) of introductory syllables, trills, and terminal syllables, with main effects and two-factor interactions. A dashed line separates main effects from interactions.

	Introductory N=2998			Trill N=2960			Terminal N=759		
	df	F	p	df	F	p	df	F	p
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 x speaker height	6	1.48	0.18	6	5.26	<0.001	4	2.20	0.07
Distance x microphone height	6	4.76	<0.001	6	12.47	<0.001	4	2.87	0.02
Distance x sex	3	0.26	0.86	3	1.56	0.20	2	0.72	0.49
Distance x Transect	10	6.51	<0.001	10	6.60	<0.001	5	1.88	0.10
Speaker height x microphone height	4	10.74	<0.001	4	4.11	0.003	4	2.13	0.08
Speaker height x sex	2	3.19	0.04	2	0.10	0.91	2	0.13	0.88
Speaker height x transect	8	1.56	0.13	8	3.13	0.002	6	3.74	0.001
Microphone height x sex	2	3.36	0.04	2	0.16	0.85	2	5.54	0.004
Microphone height x transect	8	2.35	0.02	8	2.61	0.008	6	0.96	0.45
Sex x transect	4	43.15	<0.001	4	9.81	<0.001	3	12.14	<0.001

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. A dashed line separates main effects from interactions.

	Introductory N = 2970			Trill N = 2938			Terminal N = 759		
	df	F	p	df	F	p	df	F	p
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 x speaker height	6	3.53	0.002	6	4.84	< 0.001	4	10.99	< 0.001
Distance x microphone height	6	3.10	0.005	6	6.46	< 0.001	4	1.08	0.37
Distance x sex	3	6.24	< 0.001	3	4.24	0.005	2	7.20	0.001
Distance x Transect	10	62.10	< 0.001	10	88.85	< 0.001	5	32.84	< 0.001
Speaker height x microphone height	4	17.81	< 0.001	4	16.23	< 0.001	4	2.22	0.07
Speaker height x sex	2	2.92	0.054	2	3.92	0.02	2	5.97	0.003
Speaker height x transect	8	8.37	< 0.001	8	12.72	< 0.001	6	17.54	< 0.001
Microphone height x sex	2	1.55	0.21	2	0.23	0.79	2	1.97	0.14
Microphone height x transect	8	1.05	0.40	8	1.16	0.32	6	0.85	0.53
Sex x transect	4	4.97	0.001	4	9.09	< 0.001	3	1.60	0.19

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. A dashed line separates main effects from interactions.

	Introductory N=2940			Trill N=1180			Terminal N=757		
	df	F	p	df	F	p	df	F	p
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 x speaker height	6	1.35	0.23	6	2.78	0.01	4	0.60	0.66
Distance x microphone height	6	1.40	0.21	6	3.61	0.002	4	0.89	0.47
Distance x sex	3	1.51	0.21	3	0.92	0.43	2	0.83	0.44
Distance x Transect	10	4.62	<0.001	10	3.12	0.001	5	1.87	0.10
Speaker height x microphone height	4	2.89	0.02	4	2.85	0.02	4	1.32	0.26
Speaker height x sex	2	0.75	0.47	2	3.16	0.04	2	0.51	0.60
Speaker height x transect	8	0.66	0.73	8	0.79	0.61	6	1.32	0.24
Microphone height x sex	2	1.49	0.23	2	1.72	0.18	2	1.16	0.32
Microphone height x transect	8	0.97	0.46	8	2.30	0.02	6	1.20	0.30
Sex x transect	4	2.54	0.04	4	3.07	0.02	3	2.70	0.05

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

	Introductory N = 2998			Trill N = 2960			Terminal N = 759		
	df	F	p	df	F	p	df	F	p
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 x speaker height	6	2.91	0.008	6	5.41	< 0.001	4	0.05	1.00
Distance x microphone height	6	4.19	< 0.001	6	5.93	< 0.001	4	1.72	0.14
Distance x sex	3	0.63	0.60	3	5.28	0.001	2	0.28	0.76
Distance x Transect	10	6.13	< 0.001	10	16.02	< 0.001	5	1.24	0.29
Speaker height x microphone height	4	9.09	< 0.001	4	4.97	0.001	4	0.60	0.66
Speaker height x sex	2	2.27	0.10	2	0.70	0.50	2	1.11	0.33
Speaker height x transect	8	1.06	0.39	8	2.48	0.01	6	2.12	0.05
Microphone height x sex	2	3.72	0.02	2	0.38	0.68	2	1.88	0.15
Microphone height x transect	8	2.32	0.02	8	2.54	0.009	6	0.69	0.66
Sex x transect	4	3.45	0.008	4	10.73	< 0.001	3	2.86	0.04

Table 5. Mixed-model ANOVA table for background noise, pooled across introductory syllables, trills, and terminal syllables, with main effects and two-factor interactions. A dashed line separates main effects from interactions.

	N = 3599		
	df	F	P
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 x speaker height	6	8.32	< 0.001
Distance x microphone height	6	0.54	0.78
Distance x sex	3	4.04	0.007
Distance x Transect	10	350.18	< 0.001
Speaker height x microphone height	4	0.18	0.95
Speaker height x sex	2	13.74	< 0.001
Speaker height x transect	8	64.01	< 0.001
Microphone height x sex	2	0.05	0.95
Microphone height x transect	8	1.99	0.04
Sex x transect	4	16.50	< 0.001
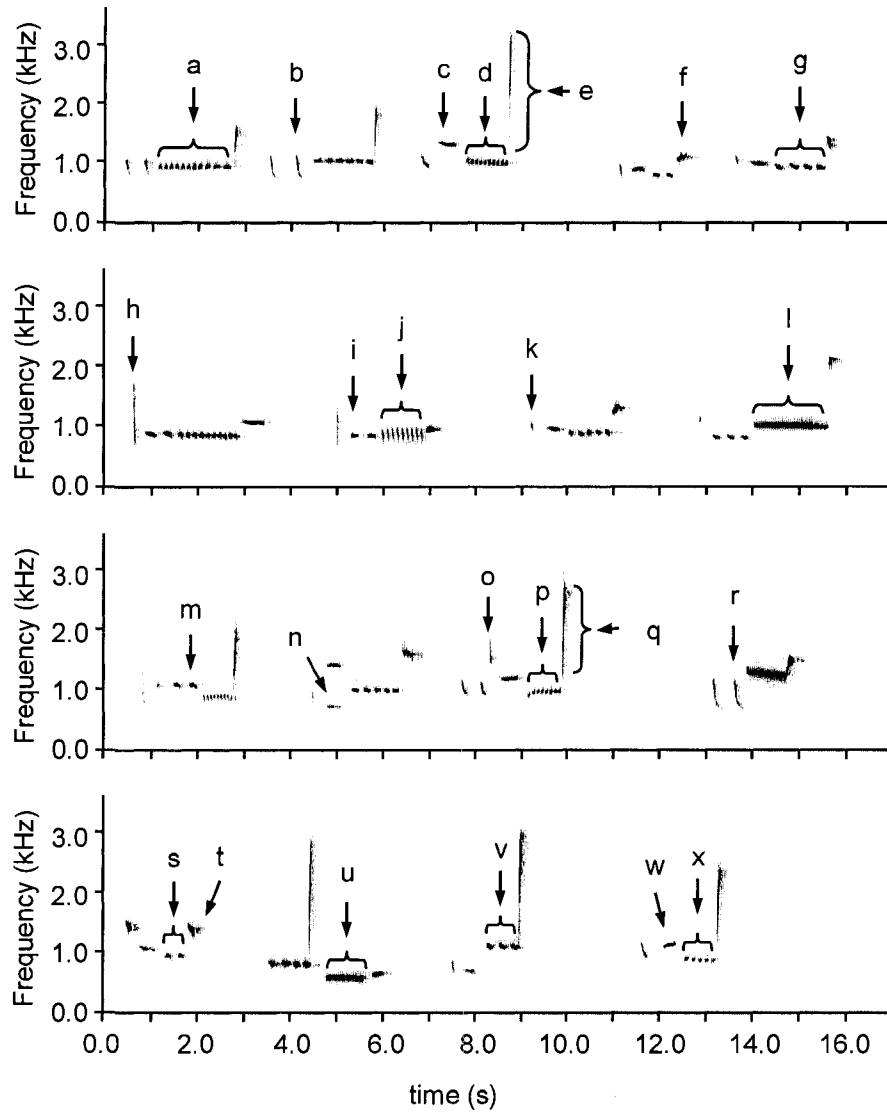
Figure 1. Spectrograms of seventeen rufous-and-white wren songs. Lowercase letters above each spectrogram refer to the individual song elements that were analyzed in this study, with elements a – l from males and elements m – x from females. Introductory syllables, trills, and terminal syllables as defined in Mennill & Vehrencamp, 2005.
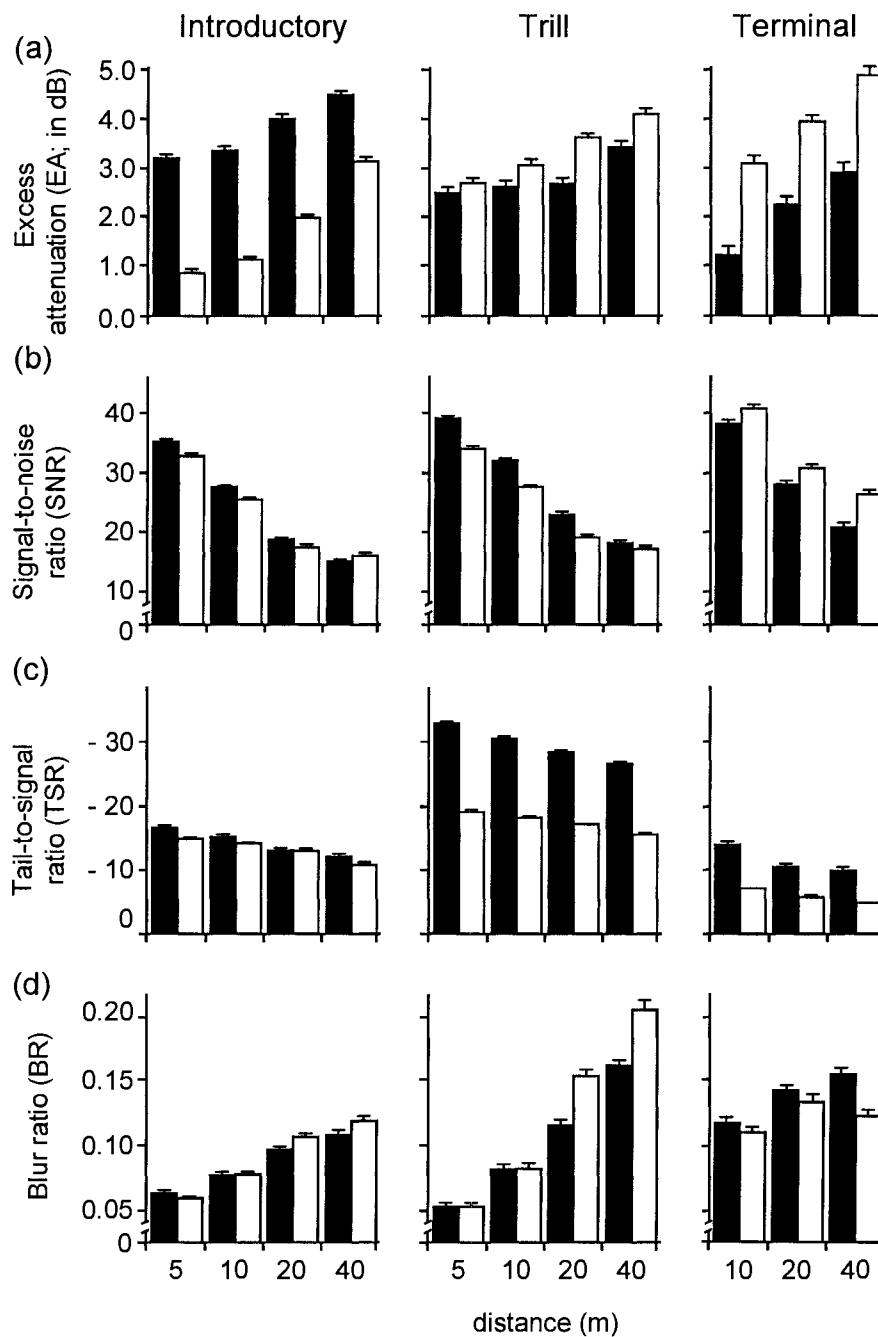
Figure 2. Interaction effect of distance and sex on four degradation measures (black: male; white: female). Error bars denote standard errors of the means.
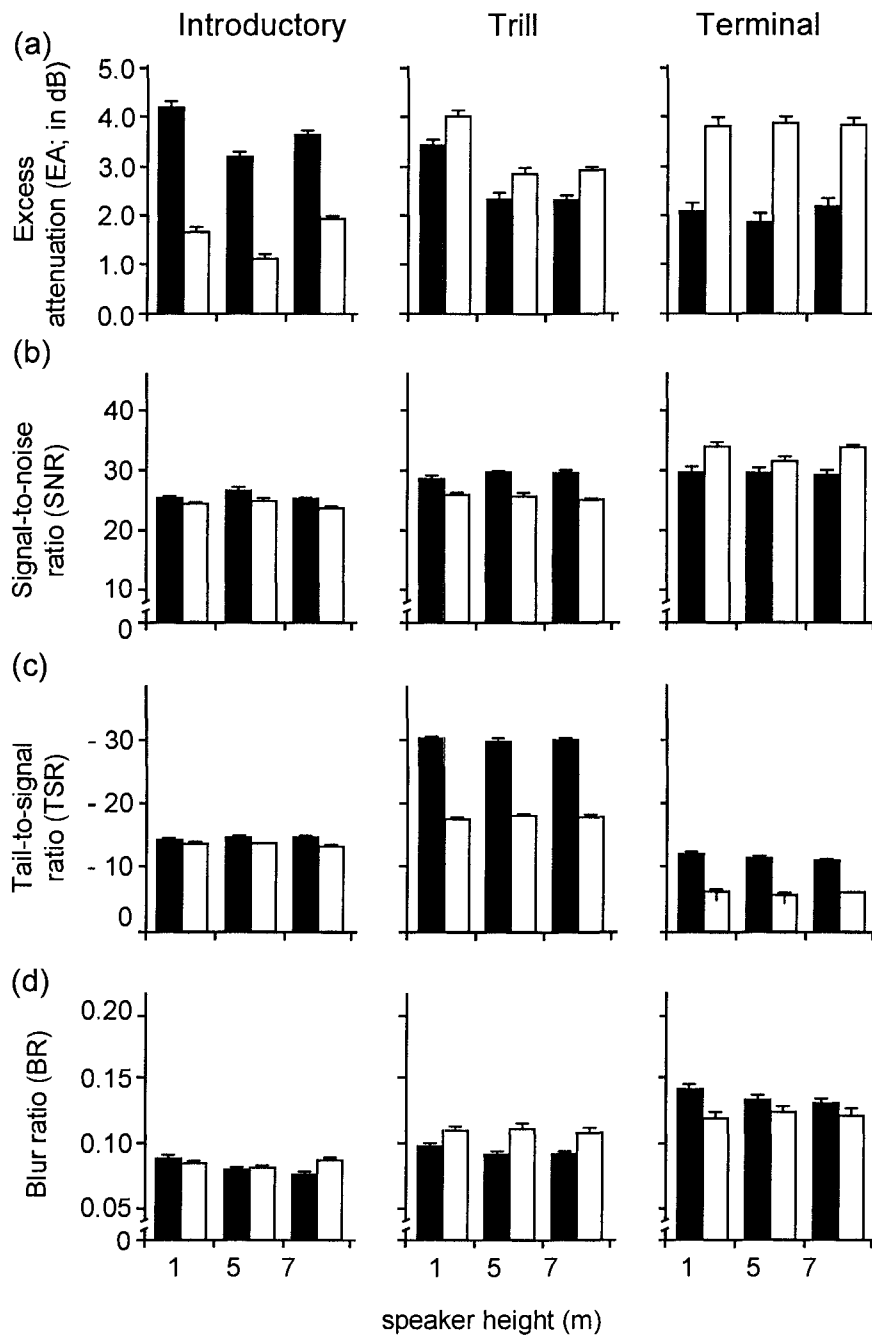
Figure 3. Interaction effect of speaker height and sex on four degradation measures (black: male; white: female). Error bars denote standard errors of the means.
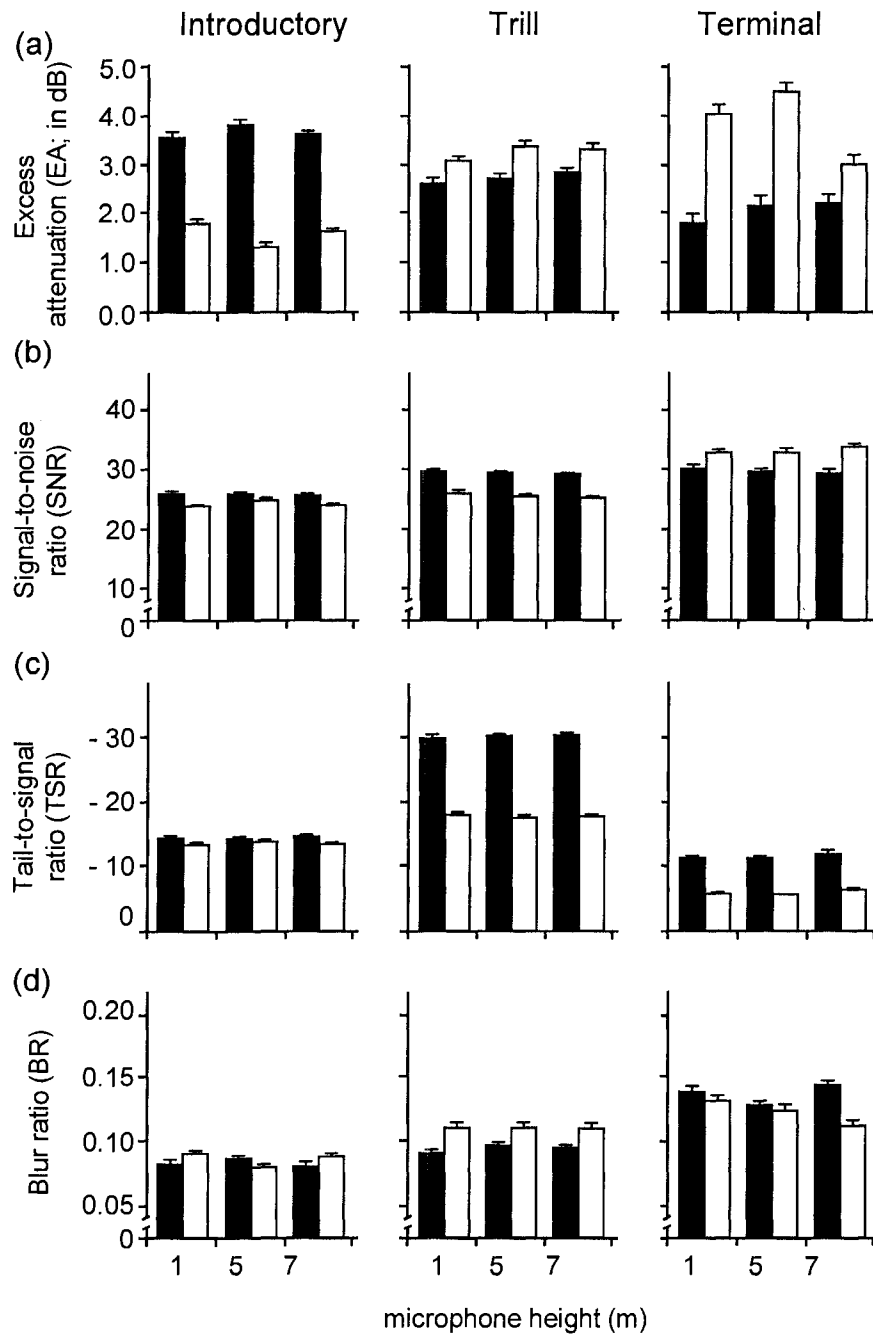
Figure 4. Interaction effect of microphone height and sex on four degradation measures (black: male; white: female). Error bars denote standard errors of the means.

Chapter 3

Structure of Rufous-and-white Wren song in a tropical forest:

Is there a link between habitat and song structure?

Chapter Summary

Song structure has been shown to be related to specific habitat characteristics in several bird species. An association between song and habitat may be adaptive if it enables birds to efficiently communicate signals in the face of habitat specific obstacles to communication. We investigated the relationship between song structure and habitat in Rufous-and-white Wrens (*Thryothorus rufalbus*), a Neotropical passerine, in an area of forest in Costa Rica. First, we compared the vegetation characteristics in two forest types within our study site (mature and regenerating). Discriminant analysis showed that the habitats were somewhat different, where regenerating forests had more grasses, a lower density of large diameter trees, and a thinner and lower canopy layer. Second, we quantified and compared different classes of song types for the wrens that inhabit these forests. Canonical discriminant analysis accurately predicted song class based on fine structural measurements, where the most important distinguishing features were length and rate of the middle trill portion of the song, and the complexity and frequency of the introductory portion of the song. Lastly, we evaluated the association between song structure and habitat by relating habitat and song class to three principal components summarizing song structure. Song structure was significantly affected by song class, but was largely unaffected by habitat and the interaction between habitat and song class, although the terminal syllables appeared to be lower frequency and longer in regenerating forests than mature forests. Our results did not show a strong relationship between song structure and habitat in Rufous-and-white Wrens. We propose that the mature and regenerating forests were not sufficiently structurally different, or that the two habitats were so close together that Rufous-and-white Wrens dispersed across habitat boundaries thereby minimizing the evidence of any selective effect of habitat.

Introduction

Like all aspects of animal communication, acoustic signals are affected by their transmission through the natural environment. Specifically, sounds experience attenuation (the decrease in signal strength with increasing distance) and degradation (distortion of temporal resolution and amplitude patterns; Wiley and Richards 1982, Slabbekoorn 2004). The acoustic adaptation hypothesis proposes that evolution has favoured acoustic signals that are structured to maximize their transmission through the signaling animal's environment (Rothstein and Fleischer 1987, Brown and Handford 2000). Species may benefit from an association between vocal signals and habitats if songs that transmit further allow them to more easily attract social partners, solicit extra-pair copulations, defend large territories, or coordinate breeding activities with partners (Richards 1985). Alternatively, the song-habitat match may not actually be adaptive in the sense that it enhances reproductive fitness, and may instead simply be the result of young birds learning those songs which they hear most clearly, which will be the songs that are structured for maximal transmission in particular habitats (Hansen 1979). If this latter situation is true, the relationship should only arise in birds that learn their songs, and should therefore be limited to oscine passerines, hummingbirds, and parrots.

Numerous sound and song transmission studies have elucidated what types of sounds are well suited for transmission in specific environments, allowing for predictions to be made regarding the acoustic adaptation hypothesis (Morton 1975, Marten et al. 1977, reviewed in Boncoraglio and Saino 2007, Bradbury & Vehrencamp 1998). Long-distance vocalizations should be low frequency, because they attenuate less than higher frequency sounds (Konishi 1970); this is especially true of animals living in dense forests because of increased

attenuation of higher frequencies through scattering by trees and foliage (Aylor 1972, Marten et al. 1977, Martens 1980). In forests, where reverberations blur the temporal structure of repetitive frequency modulations and rapid amplitude modulations, animal vocalizations should be simple and tonal, with adequate spacing between song elements to avoid distortion caused by echoes (Richards and Wiley 1980, Wiley and Richards 1982). In contrast, irregular amplitude fluctuations, which are more prevalent in open habitats, tend to mask low rates of amplitude modulation, so the redundancy created by repetitive trills may help ensure that information is received (Richards and Wiley 1980). Ambient noise may further influence vocalizations; high pitched ambient noise from insects and frogs may drive selection for low frequency songs in forests, while low pitched wind noise may select for higher frequency songs in open habitats (Ryan and Brenowitz 1985, Slabbekoorn 2004), although this will vary between habitats, depending on the communities of organisms therein.

Multi-species surveys as well as focal species studies have been used to examine these specific predictions of the acoustic adaptation hypothesis, and some have found supporting evidence (surveys: Morton 1975, Wiley 1991, Cosens and Falls 1984, Badyaev and Leaf 1997, Seddon 2005, Tubaro and Lijtmaer 2006; focal species studies: Bowman 1979, Hunter and Krebs 1979, Shy 1983, Anderson and Conner 1985, Slabbekoorn and Smith 2002b, Kopuchian et al. 2004, Nicholls and Goldizen 2006; meta-analysis: Boncoraglio and Saino 2007), while others have found conflicting results (surveys: Lemon et al. 1981, Blumstein and Turner 1995, Laiolo and Rolando 2003, Rheindt et al. 2004; focal species studies: Handford and Lougheed 1991, Date and Lemon 1993, Williams and Slater 1993, Date and Lemon 1993, Tubaro and Segura 1995, Hylton and Godard 2001; meta-analysis: Boncoraglio and Saino 2007). Generally, multi-species surveys tend to provide

more support for the acoustic adaptation hypothesis than focal species studies, suggesting that species as a whole have songs which are adapted for transmission within their habitats but that within a species, habitat-related variation from one population to the next is less common.

Many studies of the acoustic adaptation hypothesis, particularly surveys, have been carried out in temperate regions rather than the tropics, although there are some exceptions (e.g., Morton 1975, Handford and Lougheed 1991, Slabbekoorn and Smith 2002, see Barker 2008 for a review). Some tropical research has added an interesting perspective to the predictions of the acoustic adaptation hypothesis. For example, while reverberations have generally been considered detrimental for signal transmission, there is evidence suggesting that reverberations may actually enhance song transmission in rainforests (Slabbekoorn et al. 2002, Nemeth et al. 2006). When narrow frequency bandwidth notes experience reverberations, the tails of the notes increase note length, and may reinforce the note itself to reduce attenuation (Slabbekoorn et al. 2002, Nemeth et al. 2006). These findings suggest additional explanations for tropical birds having simple songs composed of widely spaced tonal notes and provide further evidence that there is much more to be learned about sound transmission and acoustic adaptation in tropical forests.

In this study we investigate associations between variation in fine structure of songs and habitat by exploring the songs and habitat of Rufous-and-white Wrens (*Thryothorus rufalbus*) in a forest in Costa Rica. Our study site, in Sector Santa Rosa, Area de Conservación Guanacaste, is a mosaic of forests of different ages, and Rufous-and-white Wrens live in forests that appear to have different structures, including sections of mature humid forest and regenerating forest. Each bird in our study population has a repertoire of

different song types, which are shared between individuals and can be grouped into classes of song types based on similar structures that are consistent across many birds within our study population (Mennill and Vehrencamp 2005). Here we explore the association between the fine structure of Rufous-and-white Wrens songs and habitat characteristics. First, we compare the vegetation characteristics of the two apparently different sections of forest to assess variation in vegetation structure. Second, we use fine structural measurements of songs to analyze and compare the degree of difference between the various song classes. Lastly, we combine the information from habitat and song comparisons to evaluate the association between habitat and song structure.

Methods

Field techniques

Rufous-and-white Wrens are resident Neotropical passerines ranging from Mexico to Colombia and Venezuela. Our study took place in Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W). Within this site, Rufous-and-white Wrens inhabit areas of mature humid forest and regenerating late successional forest. From 5 May to 13 August 2007, we conducted behavioural observations and focal recordings of Rufous-and-white Wrens in 10 territories; 3 territories were in the humid forest and 7 were in the regenerating forests (5 territories in one continuous area, and 2 in another continuous area approximately 1 km away from the other 5). Males in all 10 territories were given a unique combination of three coloured bands and one metal numbered band. Although both sexes produce song, song output is much higher for males than females (Mennill & Vehrencamp

2005, Topp & Mennill 2008) and we therefore focus on the vocal behaviour of males in this study.

We focally recorded birds between approximately 0500 and 0630 hours each morning. These recordings captured the first songs of the morning (usually starting at or after 0500 hours) and the peak in singing that represents the dawn chorus. All recordings were made using Marantz PMD 660 solid-state digital recorders with Sennheiser ME66/K6 or ME67/K6 directional shotgun microphones. We made efforts to record an example of each song type from each of the focal males at as close a distance as possible to ensure good quality recordings of all songs in their repertoires.

Vegetation measurements

We quantified vegetation characteristics in regenerating and mature areas by sampling random points within each bird's territory. Points were selected using a random number table containing numbers between 1 and 100, which determined the number of steps walked away from the nest in a direction determined through a second random number table containing the cardinal directions. At each point we divided the surrounding area into quarters using the four cardinal directions, and took the following measurements: (1) the number of plants (ferns, vines, trees/seedlings, shrubs, or grasses) over a height of 0.5 m within a 1 m radius circle surrounding the point; (2) the distance to and diameter of the nearest tree with a diameter at breast height (DBH) greater than 10 cm in each of the four quarters; (3) the height of the canopy above the point, measured with a clinometer; (4) the height of the lowest branches of the continuous vegetation layer extending down from the canopy; and (5) a count of how many dominant tree species comprised the canopy in the area above the point.

We took digital photographs (Canon PowerShot S3 IS) to quantify vegetation density; one photo was taken pointing straight up at the canopy from a height of 1 m above the forest floor at each point, and one photo was taken pointed horizontally in each of the four cardinal directions. For the horizontal photos, we placed a 1 m tall pole (painted with 10 cm tall bands of red and white) 5 m away from the camera. We used these photos to assess foliage density, as estimated by the percentage of the pole covered by foliage (leaves, twigs, vines, etc.). We estimated canopy cover from the canopy photos by converting the photos to black and white (i.e. foliage was converted to black; the sky was converted to white) and calculating the proportion of the photo composed of black pixels using Photoshop (Adobe Systems, Inc., San Jose, California).

Song and repertoire structure

Rufous-and-white Wren songs are composed of three sections: (1) a variable introductory section; (2) a trill of repeated syllables (syllable defined as a continuous trace on a sound spectrogram); and (3) a terminal section containing one loud, high frequency syllable (Figure 1). These sections can be quite variable and are combined to form distinct song types, which can be distinguished by ear and spectrographic analysis. Birds have repertoires of different song types (males: 10.8 ± 0.7 songs; females: 8.5 ± 0.7 songs; Mennill & Vehrencamp 2005) and sing them with eventual variety. A male's repertoire is typically evident after 300-400 songs (Mennill & Vehrencamp 2005), which can be collected in a few mornings of recordings, and we believe that we observed the full repertoires of each of the males in this study.

Beyond classifying an individual bird's songs into song types, we can also group different song types into population-level song type classes. We grouped songs into different classes based on similarities in time and frequency characteristics, as well as syllable structure, which are all evident from visually examining spectrograms and listening to the songs. The resulting song classes appear quite distinct (Mennill & Vehrencamp 2005), and yet there is also heretofore overlooked variation within song classes; two males may produce songs of the same song type class that show subtle differences, and an individual male can have more than one song type in his repertoire that fits into a given song type class (Figure 2). To examine and compare the song classes on a quantitative level, we performed canonical discriminant analysis on fine structural measurements of songs.

Fine structural measurements

We performed fine structural measurements on three examples of each song type sung by each of the 10 males, and calculated an average for each measurement (for three out of 113 songs we were only able to measure one or two examples). We attempted to measure all songs in each male's evident repertoire, and were able to do this in seven of 10 cases; the remaining songs were not of high enough quality to measure. Overall, our repertoire sampling ranged from 53% to 100%, with an average of 92% of a male's repertoire sampled.

We measured 27 song parameters for each song (letters refer to labels in Figure 1): Number of syllables in the introduction; number of types of syllables in the introduction (types defined as syllables that share similar frequency and length characteristics); (a) average length of introductory syllables; frequency of maximum amplitude (FMA) of the introduction; (b) length of introduction; (c) minimum frequency of the introduction; (d)

maximum frequency of the introduction; bandwidth of the introduction (maximum -

minimum frequency); (e) frequency difference between the trill and last introductory

syllable; number of syllables in the trill; (f) average length of trill syllables; FMA of the trill;

(g) length of the trill; (h) minimum frequency of the trill; (i) maximum frequency of the trill;

bandwidth of the trill; (j) average inter-syllable interval for the trill; trill rate (length of trill /

number of trill syllables); FMA of the terminal syllable; (k) length of the terminal syllable;

(l) minimum frequency of the terminal syllable; (m) maximum frequency of the terminal

syllable; bandwidth of the terminal syllable; number of syllables in the whole song; number

of types of syllables in the whole song; FMA of the whole song; and (n) length of the whole

song (see Figure 1).

Prior to measuring fine structure of songs, we bandpass filtered all songs (highpass

frequency: 500 Hz; lowpass frequency: 3500 Hz) and used the lasso selection tool of

Audition (Adobe Systems, Inc., San Jose, California) to apply additional spot filtering and

remove heterospecific background sounds that were not removed with the bandpass filter.

Due to the variation in amplitude between the different sections of Rufous-and-white Wren

songs, we normalized each introductory syllable, whole trills, and each terminal syllable

individually to facilitate automatic parameter measurements and to ensure comparability

between measurements of different syllable types. We measured the FMA of each section

and of the entire song in Audition prior to normalizing; all other variables were measured

using the automatic parameter measurement tool in Avisoft SASLab Pro (R. Specht, Berlin,

Germany) or calculated from measurements. We measured songs in Avisoft with a frequency

resolution of 43 Hz and a temporal resolution of 0.73 ms (FFT length: 102 points; 19% frame

size).

Statistical analyses

We used canonical discriminant analysis on the vegetation measurements outlined above to determine if the mature and regenerating forests were substantially different from each other. This analysis used all 11 measurements and all 27 sampling points. We used canonical discriminant analysis on the fine structural measurements outlined above to determine if the songs could be reliably classified into the correct population-level song type class. For this analysis, we omitted songs belonging to rare classes (those classes for which we had examples from fewer than three males), resulting in 91 songs in 9 classes included (11 songs in 6 classes were omitted). For the canonical analysis of the song classes, we used a cross validation technique. First, we performed discriminant analysis using a randomly selected subset of 80% of all measured songs to construct discriminant functions. Then, we tested the accuracy of assigning songs to the correct song class with the remaining 20% of songs. We report the accuracy of the discriminant analyses as the percentage of songs assigned to the correct song class for this 20% of songs.

Before comparing song structure to habitat, we performed a principal components analysis to summarize all song measurements that related to frequency or temporal structure (since the acoustic adaptation hypothesis has explicit predictions regarding those characteristics; measurements omitted were the number of types of syllables in introduction and song, and the frequency difference between trill and last introductory syllable) into a smaller number of composite variables. This principal components analysis therefore used 24 fine structural measurements on all 102 songs; following *varimax* rotation, the first three

rotated factors explained 58% of the variation, and these three components (PC1, PC2, and PC3) were used in further analyses. PC1 explained 22% of the variance in the song measurements and showed strong positive loading from the length of the introduction and the number of syllables in the introduction, trill, and whole song, and showed strong negative loading from the length of trill syllables, the trill inter-syllable interval, and the trill rate; larger values of PC1 therefore represent songs with many syllables and fast trills (Table 1). PC2 explained 19% of the variance in song measures and showed positive loading from the length of the terminal syllable, and strong negative loading from the FMA, minimum frequency, maximum frequency, and bandwidth of the terminal syllable, as well as the FMA of the whole song; since the terminal syllable is nearly always the loudest component of a song, larger values of PC2 therefore correspond to long, low frequency and narrow bandwidth terminal syllables. PC3 explained 17% of the variance in the song measures and showed positive loading from the frequency of the introduction, and strong negative loading from the FMA, minimum frequency, and maximum frequency of the trill, as well as the length of the trill; larger values of PC3 therefore correspond to songs with higher frequency introductions and short, low frequency trills (see Table 1 for a detailed account of the contribution of each song measure).

We determined the effect of habitat on song structure using three factorial ANOVAs, each with the same model, one for each of the song principal components. Habitat, with two levels (mature and regenerating) was one factor, and population-level song type class, with nine levels (one for each of the song classes separated in the discriminant analysis), was the second factor. The inclusion of song class allowed us to account for the variation within any individual bird's repertoire (a repertoire of 10 different song types accounts for a large

proportion of variation in the three song principal components). For each of the three

ANOVAs, we assessed effect size (E.S., as partial eta-squared) and observed power for each

factor and interaction.

Discriminant analyses and principal components analysis were performed using JMP

6.0 (SAS Institute, Cary, NC) and we performed our ANOVA (including estimates of effect

size and observed power) using SPSS 16.0 (SPSS Inc., Chicago, IL). All tests are two-tailed

and use a significance level of $\alpha = 0.05$.

Results

Habitat

Habitat measurements demonstrated that forest structure was fairly different between mature

and regenerating regions of our study site. Canonical discriminant analysis separated

regenerating sites from mature sites with 93% accuracy (10 of 10 mature sites and 15 of 17

regenerating sites were classified correctly; Figure 3). Regenerating sites had high canonical

scores, corresponding with a high number of grasses, a large distance to the bottom of the

canopy layer, a small distance to the top of the canopy layer, and a large distance between

trees with DBH of 10 cm or greater (Table 2). Consequently, our vegetation measurements

indicate that our *a priori* distinction between mature and regenerating sections of the forests

within Sector Santa Rosa of the Area de Conservacion Guanacaste is a meaningful one.

Song classes

Population-level song type classes are distinct, as indicated by canonical discriminant

analysis; the nine most common song classes in our study population were separated from

each other with high accuracy (Figure 4). Discriminant analysis with cross-validation predicted song class with 94% accuracy (17 of 18 songs in the cross-validation group were classified to the correct song class). The first canonical axis showed positive loading from trill rate and the average syllable length and inter-syllable interval for trills, and negative loading from the number of syllables in the introduction, trill, and whole song; it therefore separated songs with a few, widely-spaced, longer syllables from those with many shorter syllables. The second canonical axis showed positive loading from the minimum frequency of the introduction; it therefore separated songs with low frequency introductory syllables from those with high frequency introductory syllables. The third canonical axis showed positive loading from the length of the introductory section, length of introductory syllables, and number of different types of introductory syllables, as well as the FMA and maximum frequency of the terminal syllable, and the FMA of the whole song; it therefore separated songs with short, simple introductions and low frequency terminal syllables from those with longer, more complex introductions and higher frequency terminal syllables (see Table 3 for a detailed account of the contribution of each song measure).

Song versus habitat

We used principal components analysis to summarize fine structural variation between songs, in order to compare the relationships between population-level song-type class, habitat, and fine structure of songs. Song class had a highly significant influence on PC1, PC2, and PC3 (Table 4), demonstrating, unsurprisingly, that the fine structure of Rufous-and-white Wren songs significantly varies between song classes. Habitat showed significant variation with PC2, but not PC1 or PC3 (Table 4), indicating that the terminal syllable differed between the

two forests but most other song features did not. Songs in the regenerating forest had terminal syllables that were longer, lower frequency, and narrower-bandwidth than those in the mature forest. The interaction between song class and habitat was non-significant for all three principal components (Table 4), indicating that the differences in song structure between mature and regenerating forests did not vary across the different song types.

Discussion

The mature and regenerating forests that comprise our study site show differences in habitat structure, such that the regenerating forest have more grasses, a thinner and lower canopy layer, and a lower density of large trees. The song classes we developed to classify different song types of Rufous-and-white Wrens living within these forests are statistically differentiable by discriminant analysis. Our analysis of variation in song structure demonstrates that while song structure varies with song class, it does not generally vary with habitat, although the terminal syllables of Rufous-and-white Wren songs appear to vary subtly between the two forests. Consequently, our results provide evidence that some aspects of the fine structure of male Rufous-and-white Wren songs are different between the two habitats, although most aspects of their songs are not.

Discriminant analysis separated most vegetation sampling points into their respective forests, but was not 100% accurate. This lack of accuracy may be due to a number of reasons. First, it may be that the vegetation structures are actually fairly similar between the two forests. Both forests were exposed to some form of disturbance (e.g. cutting, burning, grazing, and farming; Janzen 1988) at some point in the past 400 years and it is difficult to determine the degree to which a forest is pristine versus late successional without a highly

comprehensive study (Janzen 1988). It is therefore possible that these two forests are mostly

different in age, and are therefore not extremely distinct from each other in terms of habitat

structure. A more likely reason for why the separation between the two forests was not

complete is that our sampling may not have been extensive enough. There can be substantial

variation between different sampling points when using the point-sampling method that we

used; a large sample size is required to overcome this variability and accurately reflect the

forest being sampled (Lindsey et al. 1958). Lastly, it is also possible that our measurements

did not accurately assess the characteristics that would be most useful in differentiating the

two forests. For example, species composition, size of leaves and branches in the understory,

and foliage density in the more open midstory might have differed between the two forests,

and some of these characteristics could affect sound transmission, but we did not quantify

these features in this study.

Our canonical analysis separated the two forests based on habitat characteristics that

we would predict for regenerating and mature sections of Sector Santa Rosa, Area de

Conservacion Guanacaste. The regenerating forest had more grasses than the mature forest,

which is consistent with previous accounts of succession in tropical dry forests (e.g. Kennard

2002). The regenerating forest also had a greater distance between trees with DBH greater

than 10 cm, indicating either a decreased density of trees overall, or a decreased density of

large trees. Murphy and Yugo (1986) found that younger tropical dry forests have a large

number of small stems, and our findings are consistent with this. It is not surprising that we

found that the canopy in the regenerating forest was lower than in the mature forest, since

regenerating forests are necessarily composed of younger trees, which are shorter than

mature trees. That the vertical spread of the canopy is lower in regenerating forests is less

clearly interpretable, but may relate to the fact that canopy trees in the mature forest are larger and therefore their branches have more of a spread in all directions, including vertically. Also, regenerating tropical forests have been referred to as having a "monolayered upper canopy" (Ewel 1980), so a thin canopy layer may be a common feature in younger, regenerating forests. Overall, our results are consistent with what we would expect to be different between similar forests of different ages.

An examination of the fine structure of different song classes using discriminant analysis validated our previously qualitative classification of song types into different classes. Prior to this study, Rufous-and-white Wren songs were examined spectrographically as they were compared between individuals to determine if they were structurally similar enough to be considered the same type (Mennill & Vehrencamp 2005). However, this study shows that songs can be individually identified as belonging to particular classes of songs, which allows for a new approach to assessing song sharing between individuals. It also gives further credibility to the ability of researchers to identify the different song types within an individual Rufous-and-white Wren's repertoire, since both that level of classification and the classification of song types into song classes were hitherto based largely on qualitative assessments. More importantly, the significant discrimination between song classes allowed us to include population song class as a factor in our analysis relating song structure to habitat, which helped us control for variability. A given bird's repertoire will contain songs that fit into several song classes, and therefore a full repertoire may encompass a large amount of the variation in song structure. If we were to analyze song structure on the level of the bird (rather than individual song), any patterns would have been masked by this large variability. We think that this is an important method to utilize when relating song structure

to other factors, and suggest that it be used in future research of this type. Strategies used in previous studies range from using a single example of each song type (e.g. Williams & Slater 1993) to including each song in an individual's repertoire as a separate observation (e.g. Hunter & Krebs 1979). Our method provides increased consistency and control of variability within the repertoires of specific males, and is likely to benefit studies regarding fine structure of songs.

The fine structure of Rufous-and-white Wren songs varied with population-level song-type class. This is not surprising, since the inclusion of song class was used to help control for variability between different songs. Habitat, for the most part, had little influence on song structure, although songs in the regenerating forest had longer, narrower-bandwidth, and lower frequency terminal syllables than those in the mature forest. Narrow frequency bandwidth notes accumulate and are reinforced by reflected echoes, increasing note length and decreasing excess attenuation (Slabbekoorn et al. 2002, Nemeth et al. 2006). Having songs with narrow bandwidth, pure tonal terminal syllables may be adaptive for Rufous-and-white Wrens living in regenerating areas of forest if it helps reduce the excess attenuation that might occur from the greater number of grasses, or the lower canopy. It is also possible, however, that this apparent association between habitat and terminal syllable structure is spurious, reflecting small-scale dialects that developed in our population due to the distance between the most distant ends of the study site (up to 4 or 5 km).

There may be many reasons why we did not detect a stronger effect of habitat on song structure in Rufous-and-white Wrens. First, it may be that our habitats were not different enough to show the effect that habitat has on song structure. There is substantial geographic variation in this species (Valderrama et al. 2007), which could be related to habitat structure

or could just be a result of geographic distance and drift (reviewed in Kroodsma 2004). A study comparing the structure of songs from geographically close locations with very substantial habitat differences, and/or geographically distant locations with very similar habitat characteristics will be an important future test of acoustic adaptation hypothesis in this species.

Second, it may be that the structure of songs in this species is not related to habitat at all, meaning that our finding relating the structure of the terminal syllable to habitat is spurious. There are a number of selection forces acting to shape species-specific structure of songs. For example, sympatry can lead to character displacement in songs (e.g. Bowman 1979, Irwin 2000, Slabbekoorn & Smith 2002a), and sexual selection can exaggerate certain song features if they are preferred by females (e.g. Vallet & Kreutzer 1995, Ballentine et al. 2004). Within our study site, Rufous-and-white Wrens are sympatric with a very closely-related congener, the Banded Wren (*Thryothorus pleurostictus*), which has a somewhat similar song structure (Molles & Vehrencamp 1999, Mann et al. unpubl. data). Also, research has shown that females of some species prefer quickly trilled syllables, and larger or more complex repertoires (e.g. Catchpole 1986, Hiebert et al. 1989, Ballentine et al. 2004). It therefore could be that the structure of Rufous-and-white Wren songs is more strongly influenced by character displacement (to avoid hybridization with Banded Wrens) or by sexual selection (if females prefer a diverse repertoire and songs with specific features such as rapid trills) than habitat.

Third, although habitat may have the potential to shape song structure in Rufous-and-white Wrens, it is possible that a combination of learning and dispersal overrides acoustic adaptation within our population. We would expect to see an effect of habitat if birds learn

(or modify) their songs after dispersing from their natal territory and settling into a new one. Conversely, if birds learn songs from their parents or close neighbours and then disperse to other areas for breeding, they may settle in habitat different from their natal one but still sing songs from their natal habitat, thereby complicating acoustic adaptation. Learning and dispersal has not yet been investigated in this species, although we do have some interesting observations suggesting that they learn songs and disperse over moderate distances. We know that neighbours share more songs than more distant birds (Mennill & Vehrencamp 2005). This pattern could occur either if birds learn their songs early and then disperse over very short distances or if they learn their songs from neighbours upon settling in their new territories. We also have records of two birds (one male, one female) that were banded as nestlings and recaptured as adults. The male's adult territory was 1.4 km from his natal territory, and the female's adult territory was 700 m from her natal territory. The mature and regenerating forests we studied were greater than 700 m apart, but at their closest points they were less than 1.4 km apart, so it is possible that males (and perhaps females) could disperse across forest boundaries.

A review of previous descriptive focal species studies shows some patterns among studies that do not report differences in song structure between habitats. The methodological feature most often associated with a lack of evidence for acoustic adaptation is a relatively short distance between sampling sites (e.g. Williams & Slater 1993, Hylton & Godard 2001), although significant associations between song structure and habitat have been found between sites of relatively close distance (4.5 km; Anderson & Conner 1985). Most studies that found significant variation of song with habitat structure were conducted over very large scales, sometimes covering large portions of continents (e.g. Hunter & Krebs 1979, Shy

1983, Handford & Lougheed 1991, Tubaro & Segura 1994). A second feature associated with a lack of evidence for acoustic adaptation is forest similarity between the sampled sites, where forests may appear different and have substantially different species compositions, but the physical characteristics that affect sound transmission are not different (e.g. Slabbekoorn & Smith 2002b). Our two forests were less than 1 km apart at their closest points, and although the forests were somewhat different from each other, it is possible that our lack of strong evidence for acoustic adaptation is a consequence of these two factors.

One additional habitat-dependent factor we did not consider here is that of ambient noise. Several studies have suggested that the ambient noise present in a habitat can exert selection pressures on song structure (e.g. Slabbekoorn & Smith 2002b, Dingle et al. 2008). We did not quantify ambient noise in this study, but we are aware of several sources of loud noise. Wind generates loud, primarily low frequency noise as it rustles leaves in the forest canopy. Howler monkey (*Alouatta palliata*) vocalizations are also very loud and low frequency and these monkeys commonly vocalize at the same time that Rufous-and-white Wrens perform their dawn chorus. Cicadas (Homoptera: Cicadidae) are very loud and high frequency and some species sing at a time that coincides with the Rufous-and-white Wren dawn chorus while others start singing later in the morning. In addition to these specific noise sources, there are other heterospecific vocalizations, such as those from frogs or other birds, which occasionally overlap Rufous-and-white Wren songs in time and frequency. Rufous-and-white Wren songs are quite low frequency for passerine bird songs, but most of the trills appear to be of higher frequency than the very low frequency howler monkey vocalizations. The trills are also lower frequency than cicadas although the higher frequency introductory and terminal syllables are sometimes masked by cicadas and other high-frequency

heterospecific vocalizations. Perhaps these sources of ambient noise have selected for the frequency of trills we observe in our population of Rufous-and-white Wrens.

In this study, we investigated the structure of Rufous-and-white Wren songs between mature and regenerating forests in Costa Rica. We did not find a very strong effect of habitat on song structure, which could be because there is actually no relationship between habitat structure and song structure in Rufous-and-white Wrens, because the habitats were not different enough to have a strong effect, or because a combination of song learning and dispersal overrides any acoustic adaptation that does occur. Our results did suggest an association between habitat and terminal syllable structure, such that terminal syllables appeared to be lower frequency, narrower bandwidth, and longer in the regenerating forest than in the mature forest, but this may be a result of drift and micro-dialects. Our examination of forest structure may be useful for future research in this study site, and our detailed analysis of song classes is helpful for future Rufous-and-white Wren research. Furthermore, our method of incorporating song class will be useful for any studies relating song structure to other factors since it provides an example of how to deal with birds that have repertoires of songs.

Acknowledgments

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Table 1. Correlation coefficients for song measurements significantly contributing to the first three *varimax*-rotated principal components when including 24 song measurements and 102 Rufous-and-white Wren songs. PC1, PC2, and PC3 were included in further analyses. Bold indicates a significant correlation.

Song measure	PC1 r	PC1 P	PC2 r	PC2 P	PC3 r	PC3 P
IN-AvgSyllableLength	-0.07	0.51	**-0.37**	**< 0.001**	**0.41**	**< 0.001**
IN-Bandwidth	**0.49**	**< 0.001**	**0.20**	**0.04**	0.15	0.12
IN-FMA	0.11	0.29	-0.12	0.24	**0.28**	**0.004**
IN-Length	**0.69**	**< 0.001**	-0.15	0.14	0.13	0.21
IN-MaxFreq	**0.41**	**< 0.001**	**0.23**	**0.02**	**0.28**	**0.005**
IN-MinFreq	**-0.31**	**0.002**	0.13	0.18	**0.51**	**< 0.001**
IN-NumSyllables	**0.79**	**< 0.001**	-0.04	0.69	-0.08	0.42
TR-AvgInterSyllableInterval	**-0.78**	**< 0.001**	**0.30**	**0.002**	0.15	0.14
TR-AvgSyllableLength	**-0.83**	**< 0.001**	0.07	0.50	-0.11	0.28
TR-Bandwidth	**0.37**	**< 0.001**	-0.04	0.71	**0.24**	**0.01**
TR-FMA	0.02	0.84	**-0.26**	**0.008**	**-0.80**	**< 0.001**
TR-Rate	**-0.85**	**< 0.001**	**0.25**	**0.01**	0.04	0.70
TR-Length	-0.14	0.16	-0.02	0.84	**-0.71**	**< 0.001**
TR-MaxFreq	0.12	0.22	**-0.26**	**0.009**	**-0.70**	**< 0.001**
TR-MinFreq	-0.16	0.11	**-0.21**	**0.04**	**-0.82**	**< 0.001**
TR-NumSyllables	**0.72**	**< 0.001**	-0.09	0.37	**-0.47**	**< 0.001**
TE-Bandwidth	**0.36**	**< 0.001**	**-0.67**	**< 0.001**	**0.20**	**0.05**
TE-FMA	0.08	0.45	**-0.95**	**< 0.001**	-0.14	0.16
TE-Length	0.01	0.95	**0.58**	**< 0.001**	0.02	0.81
TE-MaxFreq	**0.20**	**0.05**	**-0.93**	**< 0.001**	-0.13	0.20
TE-MinFreq	-0.13	0.20	**-0.68**	**< 0.001**	**-0.45**	**< 0.001**
SONG-FMA	0.11	0.27	**-0.89**	**< 0.001**	-0.14	0.17
SONG-Length	**0.42**	**< 0.001**	0.08	0.40	**-0.47**	**< 0.001**
SONG-NumSyllables	**0.79**	**< 0.001**	-0.08	0.42	**-0.45**	**< 0.001**
% Variance	22.3		18.6		16.6	

Table 2. Correlation coefficients for vegetation measurements significantly contributing to the canonical variable in discriminant analysis by forest type, using 11 measurements and 27 sampling points.

Vegetation measure	r	P
NumGrasses	0.74	< 0.001
HtCanopyTop	-0.54	0.004
AvgDistToTree	0.41	0.03
HtCanopybottom	0.41	0.04

Table 3. Correlation coefficients for song measurements significantly contributing to the first three canonical variables in discriminant analysis by population song class, using 27 song measurements and a randomly-selected 80% of the 91 songs. Bold indicates significant correlations.

Song Measure	Can1		Can2		Can3	
	r	P	r	P	r	P
IN-AvgSyllableLength	**0.42**	**< 0.001**	**0.45**	**< 0.001**	**0.62**	**< 0.001**
IN-Bandwidth	**-0.26**	**0.03**	0.16	0.18	0.05	0.69
IN-Length	**-0.27**	**0.02**	0.08	0.51	**0.58**	**< 0.001**
IN-maxFreq	-0.16	0.16	**0.32**	**0.005**	-0.01	0.93
IN-MinFreq	**0.37**	**0.001**	**0.67**	**< 0.001**	**-0.23**	**0.05**
IN-NumSyllables	**-0.56**	**< 0.001**	-0.03	0.80	**0.47**	**< 0.001**
IN-NumTypesSyllables	0.06	0.62	0.12	0.31	**0.77**	**< 0.001**
TR-AvgInterSyllableInterval	**0.54**	**< 0.001**	**0.41**	**< 0.001**	**-0.44**	**< 0.001**
TR-AvgSyllableLength	**0.62**	**< 0.001**	-0.22	0.06	**-0.38**	**0.001**
TR-Bandwidth	-0.21	0.07	0.12	0.30	**0.27**	**0.02**
TR-FMA	**-0.32**	**0.006**	**-0.36**	**0.002**	**0.25**	**0.03**
TRMinusINFreqDiff	**-0.34**	**0.003**	**-0.24**	**0.04**	0.18	0.14
TR-Rate	**0.62**	**< 0.001**	0.10	0.40	**-0.45**	**< 0.001**
TR-Length	0.09	0.45	**-0.46**	**< 0.001**	0.01	0.91
TR-MaxFreq	**-0.39**	**0.001**	**-0.35**	**0.002**	**0.33**	**0.004**
TR-MinFre	-0.22	0.06	**-0.38**	**0.001**	0.14	0.25
TR-NumSyllables	**-0.78**	**< 0.001**	-0.07	0.53	**0.32**	**0.005**
TE-Bandwidth	0.08	0.48	-0.06	0.64	**0.36**	**0.002**
TE-FMA	**0.32**	**0.007**	**-0.33**	**0.004**	**0.58**	**< 0.001**
TE-Length	-0.13	0.27	**0.32**	**0.005**	-0.12	0.31
TE-MaxFreq	0.20	0.09	**-0.27**	**0.02**	**0.59**	**< 0.001**
TE-MinFreq	0.20	0.09	**-0.34**	**0.003**	**0.45**	**< 0.001**
SONG-FMA	0.19	0.11	**-0.32**	**0.006**	**0.50**	**< 0.001**
SONG-Length	-0.19	0.11	-0.16	0.17	**0.40**	**< 0.001**
SONG-NumSyllables	**-0.81**	**< 0.001**	-0.06	0.61	**0.37**	**0.001**
SONG-NumTypesSyllables	0.03	0.80	0.22	0.07	**0.66**	**< 0.001**
% Variance	30.2		24.9		19.0	

Table 4. Results of ANOVA on the effect of population-level song class and habitat structure on male Rufous-and-white Wren songs.

Factor	df	PC1				PC2				PC3			
		F	P	E.S	Power	F	P	E.S.	Power	F	P	E.S.	Power
Song class	8, 73	43.69	<0.001	0.83	1.00	17.22	<0.001	0.65	1.00	19.23	<0.001	0.68	1.00
Habitat	1, 73	0.15	0.70	0.002	0.07	6.05	0.02	0.08	0.68	3.03	0.09	0.04	0.41
Song class* Habitat	8, 73	1.78	0.10	0.16	0.72	1.23	0.29	0.12	0.53	1.13	0.35	0.11	0.49
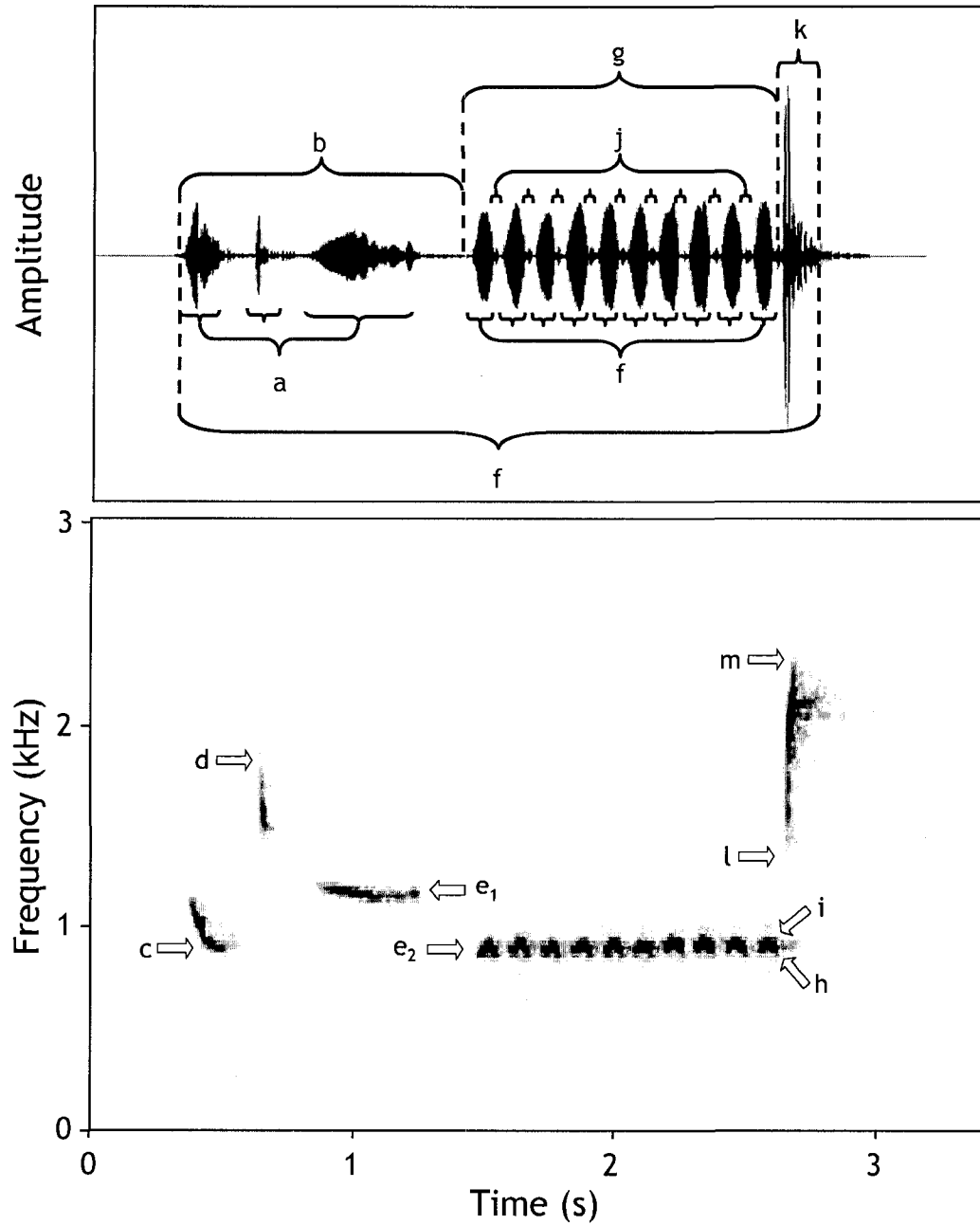
Figure 1. Waveform and spectrogram depicting a Rufous-and-white Wren song, highlighting the song sections and some of the 27 song measurements used in this study. See text for measurement descriptions.
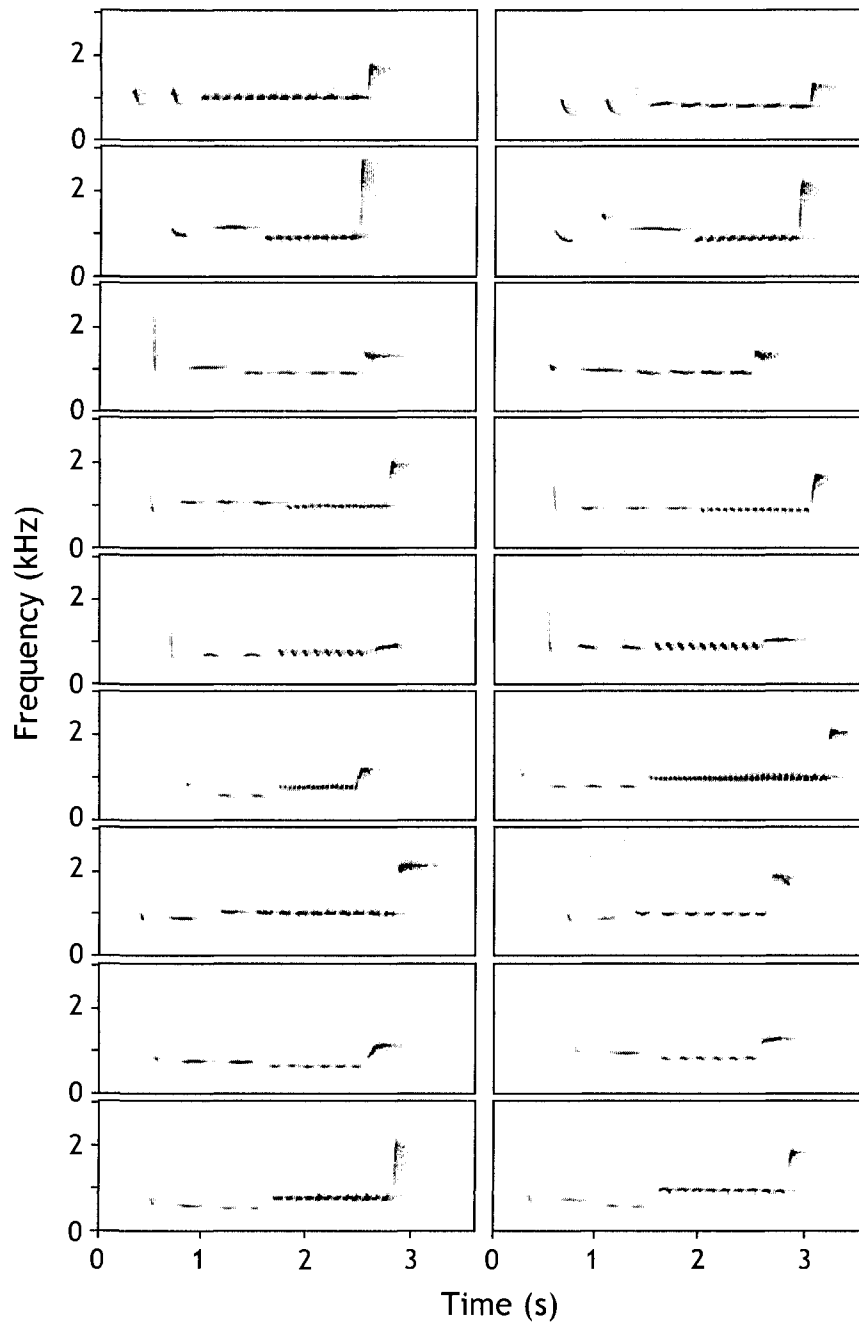
Figure 2. Spectrograms of two examples of each of the nine most common song classes in our population of Rufous-and-white Wrens. Songs are shown in pairs, with two examples of song class 1 at the top to song class 9 at the bottom. The pairs of songs were recorded from different males.
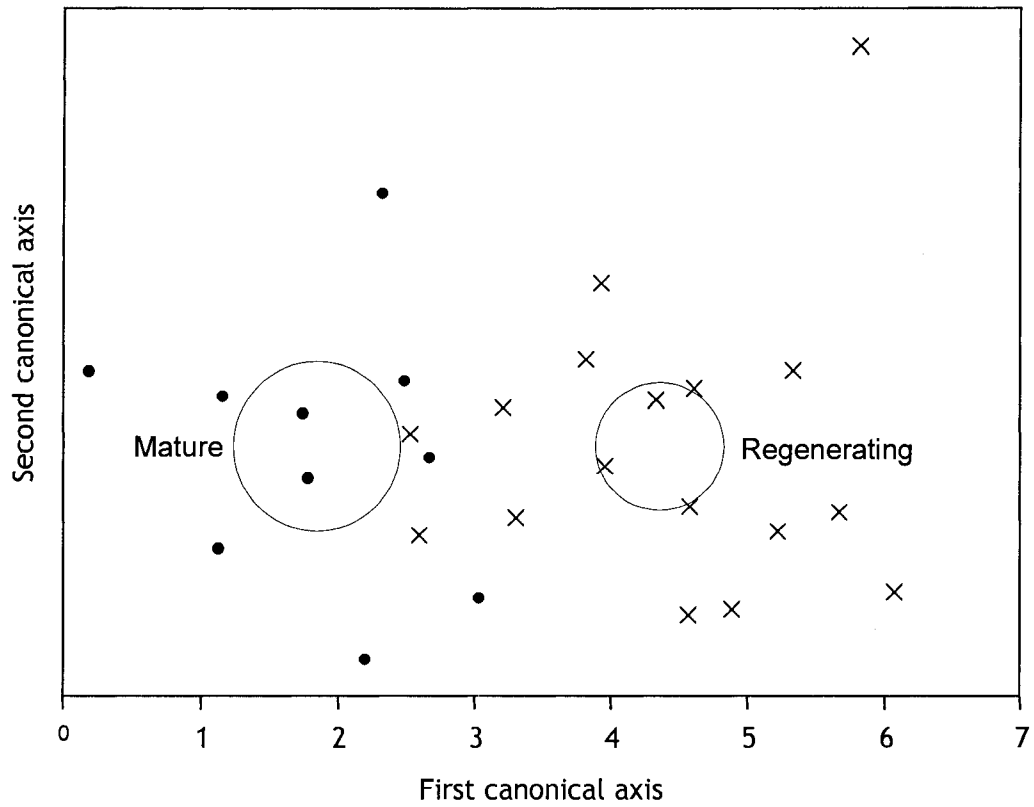
Figure 3. Scatterplot of the discriminant function resulting from the analysis of mature and regenerating forests. All 27 sampling points are shown. Ellipses show 95% confidence limits for the multivariate mean of each group.
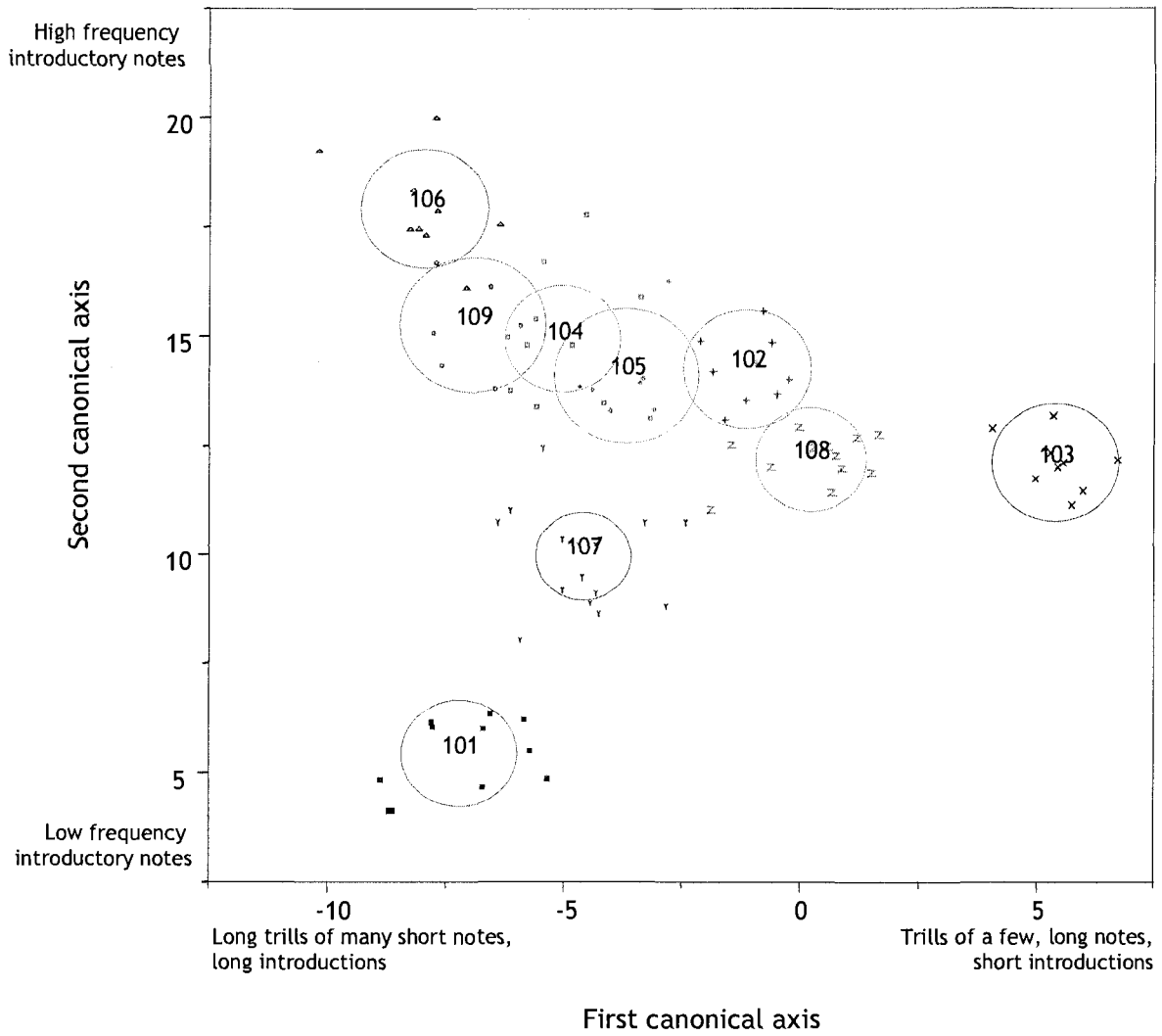
Figure 4. Scatterplot of the discriminant function resulting from the analysis of the most common nine song classes sung by Rufous-and-white Wrens in Sector Santa Rosa, Costa Rica. All 102 songs are shown. Ellipses show 95% confidence limits for the multivariate mean of each group, and numbers show an arbitrary number assigned to each song type class. See Table 3 for canonical details.

Chapter 4

Song perch height in Rufous-and-white Wrens:

Does behaviour enhance effective communication in a tropical forest?

Chapter Summary

Animal signals are distorted as they transmit through the environment. Many species have evolved strategies to minimize distortion of vocal signals; song structure can change over evolutionary time in a way that minimizes attenuation and degradation in a specific habitat, and signallers can modify their behaviour to do the same. We investigated signalling behaviour in rufous-and-white wrens, *Thyothorus rufalbus*, a Neotropical songbird in which both sexes sing, with a specific focus on perch height. Based on previous findings, including a detailed sound transmission study, we predicted that rufous-and-white wrens would choose elevated song perches in order to maximize the distance their songs travel, and that males and females would show different perch height choices. We observed pairs in 17 territories in a tropical forest in Costa Rica to determine the perch heights of birds when singing, producing non-song vocalizations, foraging, collecting nesting material, perched before and after flying, and engaging in other behaviours. We found that both activity and sex influenced perch height. Birds sang from a variety of heights, but the highest perches were used during singing. Birds minimized singing from within 1 m of the ground, whereas foraging occurred primarily on the ground, and engaged in all other activities at variable heights between the extremes used for singing and foraging. Males generally perched higher than females, which may reflect sex differences in communication strategies. The finding that rufous-and-white wrens vary their perch height with specific activities suggests that they modify their behaviour to enhance long-distance communication.

Introduction

Like all forms of animal communication, acoustic signals are distorted from their original

structure as they transmit through the natural environment from one individual to another (Wiley & Richards 1982; Bradbury & Vehrencamp 1998; Slabbekoorn 2004). Animals have evolved multiple strategies to ensure that their messages are heard by intended receivers (Arak & Eiriksson 1992; Mathevon et al. 2004). For example, the acoustic adaptation hypothesis proposes that animals' vocalizations change over time to become structured in a way that reduces attenuation (decrease in signal strength) and degradation (distortion of temporal and amplitude patterns) in their particular environment (Rothstein & Fleischer 1987; Brown & Handford 2000; reviewed in Boncoraglio & Saino 2007, Barker 2008). Evidence from broad multi-species surveys as well as various focal species studies have shown that habitat does appear to shape the structure of vocalizations in many instances (e.g. Shy 1983; Wiley 1991; Brown et al. 1995; Slabbekoorn & Smith 2002; Kopuchian et al. 2004), although there is also conflicting evidence (e.g. Lemon et al. 1981; Williams & Slater 1993; Daniel & Blumstein 1998; Hylton & Godard 2001; Bosch & De la Riva 2004).

Animals may also use behavioural techniques to overcome obstacles to long-distance communication by vocalizing from a location that enhances signal propagation. Sound transmission experiments have shown that some species can increase the propagation distance of their acoustic signals either by vocalizing from some distance above the ground (Waser & Brown 1986; Arak & Eiriksson 1992; Mathevon et al. 1996), or by vocalizing from within an open midstory rather than a foliated canopy of a forest (e.g. Blumenrath & Dabelsteen 2004). Such behaviours may be particularly important in light of habitat disturbance. If a species' vocalizations match its historical habitat but not a subsequently altered one, the animal's behaviour may adjust more quickly to habitat changes than signal structure can, enabling animals to continue to communicate at long distances despite having

vocalizations that are less matched to their habitat. Despite the potential communication benefits that signallers may derive from choosing perch heights that facilitate sound transmission, only a few studies have systematically explored perch height choice in free-living animals (e.g. Hunter 1980; Krams 2001).

We investigated perch height choice in rufous-and-white wrens, *Thryothorus rufalbus,* a Neotropical passerine bird in which males and females both sing solo songs and combine their songs to form duets. Duets in this species have been suggested to play a role in acoustic contact, joint territory defence, and mate guarding (Mennill & Vehrencamp 2005; Mennill 2006; Topp & Mennill 2008; Mennill & Vehrencamp in press). Rufous-and-white wrens are insectivores and are known to spend much time close to the forest floor; they feed primarily on the ground (Ahumada 2001) and they build their nests out of long strings of plant material and fungus which they collect from the ground or peel from tree trunks, thick branches, and vines. Performing songs from the ground level can pose communication difficulties because, in general, animal sounds produced from very close to the ground tend to experience more attenuation than those produced at greater heights. This is the result of destructive interference of reflections off the ground as well as greater attenuation through scattering if there is substantial vegetation at ground level (Wiley & Richards 1978; Martens 1980; Embleton 1996). In a recent song transmission study of rufous-and-white wrens (Chapter 2), we found that both sexes suffer from a substantial song transmission disadvantage when singing from a height of 1 m above the ground as compared to higher perches of 5 m or 7 m. Additionally, we found evidence that rufous-and-white wrens may maximize their ability to hear male songs by perching at 7 m, and female songs by perching at 1 m or 5 m (Chapter 2).

In the present study, we evaluate perch height choice by rufous-and-white wrens engaged in singing and non-song activities. Our goal was to examine whether rufous-and-white wrens systematically vary perch height to enhance the transmission distance of their songs or their ability to hear the songs of conspecific individuals. Based on the results of our song transmission study (Chapter 2), combined with previous findings showing that rufous-and-white wren territories are very large and that song is used in territorial defence (Mennill & Vehrencamp 2005; Menill & Vehrencamp in press), we predicted that rufous-and-white wrens would use elevated song posts to maximize their communication range. We also predicted that males and females would demonstrate different perch height choices, since previous studies have shown that the sexes exhibit some divergent singing behaviours arguing that songs may serve different functions for males and females (Mennill & Vehrencamp 2005; Mennill 2006; Topp & Mennill 2008; Mennill & Vehrencamp in press). Lastly, we predicted that activities other than singing would also influence perch height, given that they may involve particular resources (e.g. food, nesting material) which are present at specific heights.

Methods

Rufous-and-white wrens are resident Neotropical passerines ranging from Mexico to northern South America. Our study took place in Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°40'N, 85°30'W). Within this site, rufous-and-white wrens inhabit areas of mature humid forest as well as regenerating late successional forest. From 5 May to 13 August 2007, we conducted behavioural observations of rufous-and-white wrens in 17 territories. Birds were given unique combinations of three coloured bands and one

numbered metal band. All 17 males were individually marked, and 14 of 17 females were individually marked; the remaining females were easily distinguished on the basis of their location and individually-distinctive song repertoires (Mennill & Vehrencamp 2005).

We conducted behavioural observations between approximately 0500 and 0630 hours (CST) each morning by following birds around their territory for an extended time period. We recorded all vocalizations produced by both males and females during these observation sessions using digital recorders (Marantz PMD-660) and directional microphones (Sennheiser ME66/K6). During recording sessions, we estimated perch heights at any point when we knew a bird's location, and then dictated into the microphone the estimated height, the bird's identity, and its activity (see below). Heights were estimated to a precision of 1 m, and height markers around the study site acted as calibrators to aid with our height estimation. Like many wrens, rufous-and-white wrens are extremely difficult to observe because of their habit of skulking through thick underbrush (Brewer 2001). Consequently, our observation periods included extended periods of not being able to see the focal bird(s), punctuated by brief encounters where we could observe their behaviour. If we visually observed any individual for an extended period of time, we collected only one height observation per perch, and waited for birds to move to a new perch before we collected another height observation. Because females sing much less frequently than males and also seemed to be more secretive, we collected many more observations of males than females.

When transcribing the data collected during observation sessions, we divided the activities of the wrens into six categories: (1) singing; (2) producing non-song vocalizations (including species-typical harsh chattering calls and low pitched hooting calls); (3) foraging; (4) collecting nesting material; (5) flying between perches (in which case we measured the

perch that the bird flew from or to); and (6) other behaviours that were observed more rarely (including building the nest, feeding young, preening, or engaging in semi-aggressive chases). We analysed the observations for males and females (n = 575) in SPSS (SPSS Inc., Chicago, IL) using a mixed model factorial ANOVA with sex and activity (with six levels) as fixed factors and perch height as the dependent variable. Territory was included as a random factor to control for variability between pairs and habitat structure between territories; the mature forest in some territories was sometimes twice as tall as the regenerating forest in other territories. We conducted post-hoc tests using Tukey's HSD test. All values are reported as mean ± SE, median. All tests are two-tailed with a significance threshold of α = 0.05.

Results

We collected a total of 585 perch height observations of rufous-and-white wrens; 528 observations of 17 males, 47 observations of 10 females, and 10 observations of unidentified birds. Mixed model factorial ANOVA on the 575 birds for which sex was known showed a significant effect of activity ($F_{5,142}$ = 3.39, P = 0.006) on perch height (Fig. 1). Post-hoc comparisons revealed that birds perch significantly higher when they sing (4.83 ± 0.17 m, 4.00 m) than while foraging (0.70 ± 0.40 m, 0.03 m; P < 0.001), flying (2.39 ± 0.53 m, 1.00 m; P < 0.001), and engaging in other activities (2.83 ± 0.47 m, 2.00; P = 0.001), but not while engaged in non-song vocalizations (3.57 ± 0.45 m, 3.25 m; P = 0.087) or nest-material collection (4.18 ± 0.70 m, 3.00 m; P = 0.861; Fig. 1). The perches that birds foraged at were significantly lower than those used during non-song vocalizations (p = 0.004) and nest-material collection (P = 0.001), but not those during flying (P = 0.31) or other activities (P = 0.09; Fig. 1). There was substantial overlap in the heights of perches used during non-song

vocalizations, nest-material collecting, flying, and other activities. The biggest difference was between the heights of singing birds and the heights of foraging birds (Fig. 1). Rufous-and-white wrens used a broad range of perches during singing (0 to 15 m), although they appeared to minimize singing from perches below 1 m (Fig. 2a). Foraging birds, in contrast, were almost exclusively observed at 1 m or below (Fig. 2b). All other activities showed a range of heights, including heights below 1 m and up to 13 m (Fig. 2c).

Mixed model factorial ANOVA also showed a significant effect of sex on perch height (Fig. 3), such that males perched higher than females, on average (median for males: 3.50 m; females: 1.00 m; $F_{1,12} = 5.64$, $P = 0.04$). The interaction between activity and sex was also significant ($F_{5,7} = 5.45$, $P = 0.02$), indicating that the perch height difference between males and females was not consistent across all activities (Fig. 1).

Discussion

Rufous-and-white wrens sing from perches that range in height from on the ground to 15 m, although they appear to minimize singing from very close to the ground relative to how much time they spend near the ground participating in other activities. The highest perches were used by males during singing. Our analyses corroborate previous findings that foraging in this species occurs on or near the ground (Ahumada 2001). All other activities occurred at intermediate heights, with substantial overlap in the heights of perches used during different activities. Overall, males used higher perches than females, particularly during singing, foraging, and flying between perches.

Many bird species use elevated song posts (e.g. Harrison 1977; Götmark & Post 1996), even when foraging is suboptimal at those heights and energy and time are spent

flying to song posts (Greig-Smith 1983). There must therefore be some advantage gained in

using elevated song posts, and separating foraging from singing. One possibility is that

auditory and visual communication is enhanced by singing from particular perches (Hunter

1980; Beck & George 2000). Another is that perching higher may enable birds to better

detect or hide from predators, which may be particularly relevant if song attracts predators

(Hunter 1980; Beck & George 2000; Krams 2001). Lastly, it may be that birds use elevated

song posts to enhance their ability to see and hear conspecifics (Holland et al. 1998;

Mathevon et al. 2005; reviewed in Dabelsteen 2005).

Many song transmission experiments have demonstrated that excess attenuation of

songs can be reduced by singing from elevated songs posts (e.g. Dabelsteen et al. 1993;

Mathevon et al. 1996; Mathevon et al. 2005). Generally, singing from within 1 m of the

ground causes increased excess attenuation (Marten et al. 1977), which can be avoided by

choosing higher song posts. Our previous research showed that rufous-and-white wren songs

experienced less attenuation and were less distorted when sung from perch heights of 5 m

and 7 m than when sung from 1 m above the ground (Chapter 2). In this study, we found that

while Rufous-and-white wrens utilized a wide range of heights for singing, they sang very

few songs from within 1 m of the ground, which is consistent with our prediction that they

would choose elevated perch heights. Rufous-and-white wrens may use elevated song posts

to enable within- and extra-pair communication. One demonstrated function of duetting in

rufous-and-white wrens is the maintenance of acoustic contact between pair members

(Mennill & Vehrencamp in press). Since the average distance of separation between duetting

partners is 19.2 m and pairs have been measured performing duets from as far apart as 144.3

m (Mennill & Vehrencamp in press), avoiding singing from heights below 1 m may ensure

that their songs are heard by their breeding partners. Furthermore, playback studies have demonstrated that solo and duet songs function in territorial defence against conspecific rivals in this species (Mennill 2006). Since rufous-and-white wren territories are large, and the unoccupied space between territories is substantial (on average, more than 100 m; Mennill & Vehrencamp in press), there may be strong pressure to reduce excess attenuation of their songs to extend their communication range and be heard by neighbours.

Vegetation structure can vary between habitats and microhabitats. Birds may not be choosing specific heights to perch at, but may instead be choosing particular layers in the forest. For example, transmission experiments have shown that songs experience more attenuation when they are broadcasted from within a foliage layer (Martens 1980; Wilczynski et al. 1989; Blumenrath & Dabelsteen 2004). Some birds may also choose exposed perches to enable visual components of their advertisement displays (e.g. Beck & George 2000). Conversely, some birds sing within more foliated areas, perhaps to conceal them from predators (e.g. Hunter 1980; Parker & Tillin 2006). The forest structure at our study site is quite variable, so if rufous-and-white wrens use song posts based on foliage density at a small scale (either avoiding or preferring), we would expect a wide variety of perches used during singing, such as that shown in our study. This species is monomorphic and we only rarely observed a visual component (tail-wagging) during singing. Most activities, other than those which utilized a resource that was available at particular heights (such as gathering nest-building material), occurred at relatively low heights. Perhaps rufous-and-white wrens choose to perform most activities in the foliated understory because it offers concealment from predators. Indeed, wrens (family Troglodytidae) are notorious for both their secretive

behaviour and cryptic plumage colour (Brewer 2001), which may reflect a phylogenetic history of avoiding predation.

It has been suggested that elevated perches are even more effective as listening posts than song posts (e.g. Mathevon et al. 2005). The results of our previous song transmission experiment (Chapter 2) showed some evidence that rufous-and-white wrens show a slight receiver advantage of perching at 7 m when listening to male songs, or at 1 m or 5 m when listening to female songs. Males, who appear to have a more active role in territorial defence (Mennill 2006; Mennill & Vehrencamp in press), may then choose high song posts so that they can listen for and keep track of neighbours who may respond to their songs (Dabelsteen 2005). The benefit of elevated listening posts may also explain why males tend to perch higher than females. One proposed function of rufous-and-white wren duets is mate guarding, where males show significantly higher duet responsiveness to female songs during the female fertile period, presumably as a way of advertising her mated status and minimising partnership or paternity loss (Topp & Mennill 2008). Males may therefore use higher perches to ensure that they hear songs given by their females as well as any responses from nearby males. Females, in contrast, do not show mate guarding tendencies to the same degree as males. Because rufous-and-white wrens show joint territory defence against intruders, we might expect that males and females use similar perches when singing and duetting towards rival birds (or playback). This idea was not tested here but could be a future avenue of investigation in this species.

It could be suggested that differential levels of foliation at various levels in the forest may have led to a bias in our ability to observe birds at different heights, particularly if birds were difficult to observe when singing from low perches, or foraging at high perches. Our

experience, over four months of data collection for this study, taught us that we were capable of observing birds at various heights regardless of their activity. The distribution around the means for singing perch height (Fig. 2) indicates that we were capable of visualising birds across a variety of perch heights when they sang. We found that birds were most difficult to observe while foraging because they were silent at this time, yet we observed them foraging primarily on the ground, which is among the more visually-occluded levels of the forest at our study site. If birds were singing from the ground, we would likely be able to observe them better than if they were foraging, since their songs would make them easier to localize. Like Hunter (1980), we interpret our results as revealing a true pattern of perch height usage in rufous-and-white wrens.

In conclusion, rufous-and-white wrens sing from a variety of perch heights, but they occupy their highest perches when singing, they sing from significantly higher perches than their preferred foraging height, and they appear to minimize singing from perches low to the ground. We therefore conclude that rufous-and-white wrens modify their behaviour to enhance acoustic communication, in agreement with predictions made based on a detailed sound transmission study. Males may perch higher than females because they have a more active role in territory defence, because male and female songs have different functions, or because males are using high perches as listening posts to hear female songs and the responses of rival individuals in adjacent territories.

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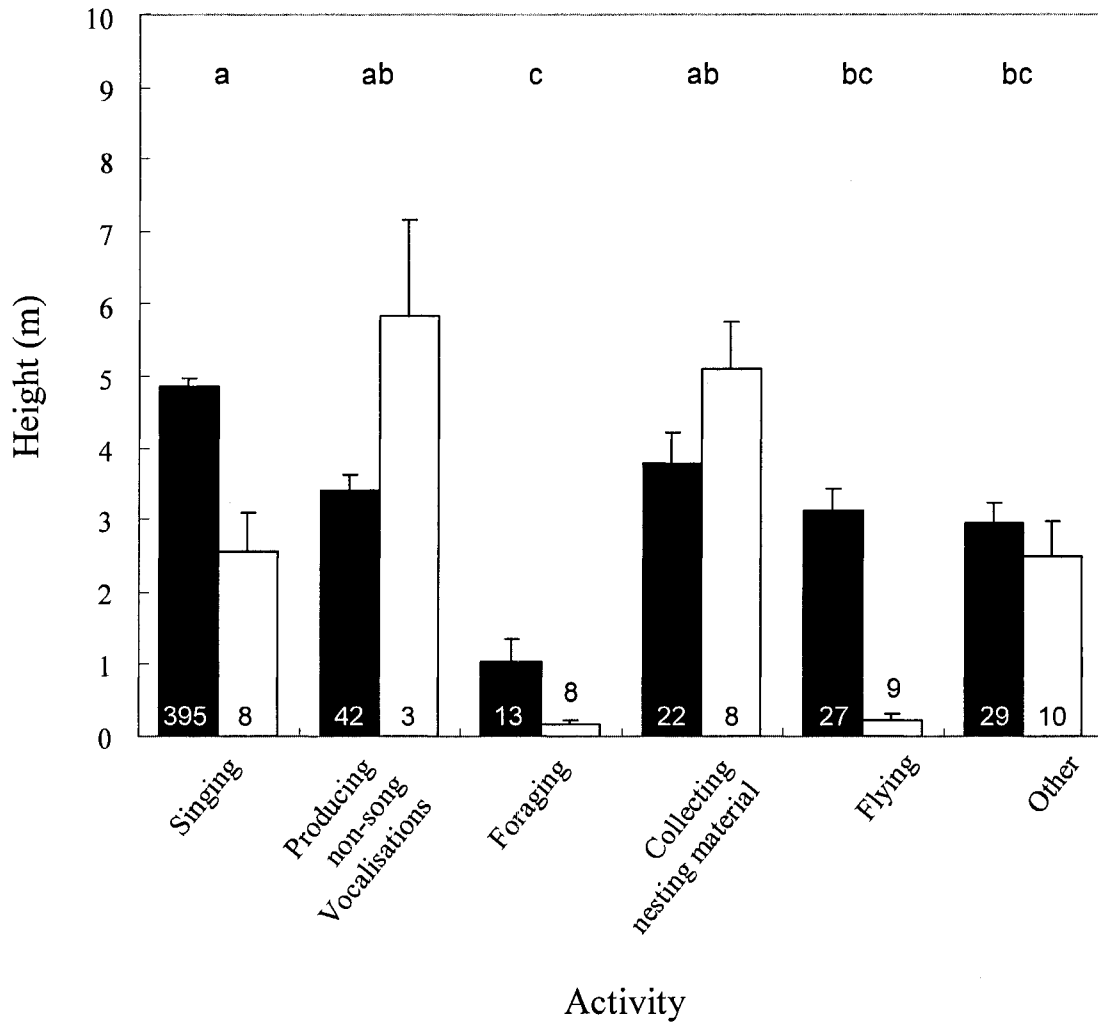
Figure 1. Average perch heights for rufous-and-white wrens when engaging in different activities, demonstrating the significant main effect of activity and the interaction between activity and sex. Males are shown in black bars and females in white bars. Error bars represent standard error; the number of observations is indicated on each bar. Letters above bars indicate multiple comparisons between activities (across sex); activities connected by the same letters are not significantly different at the $\alpha = 0.05$ level.
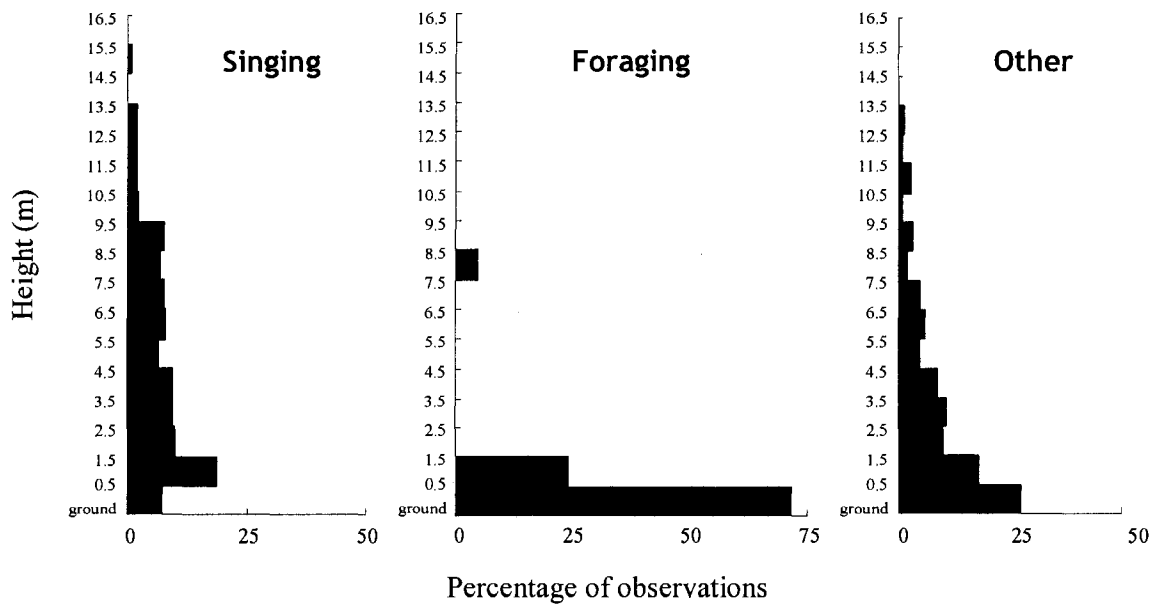
Figure 2. Distribution of perch heights for all 585 observations of rufous-and-white wrens during singing, foraging, and all other activities (i.e. producing non-song vocalizations, collecting nesting material, flying from one perch to another, and other less common activities).
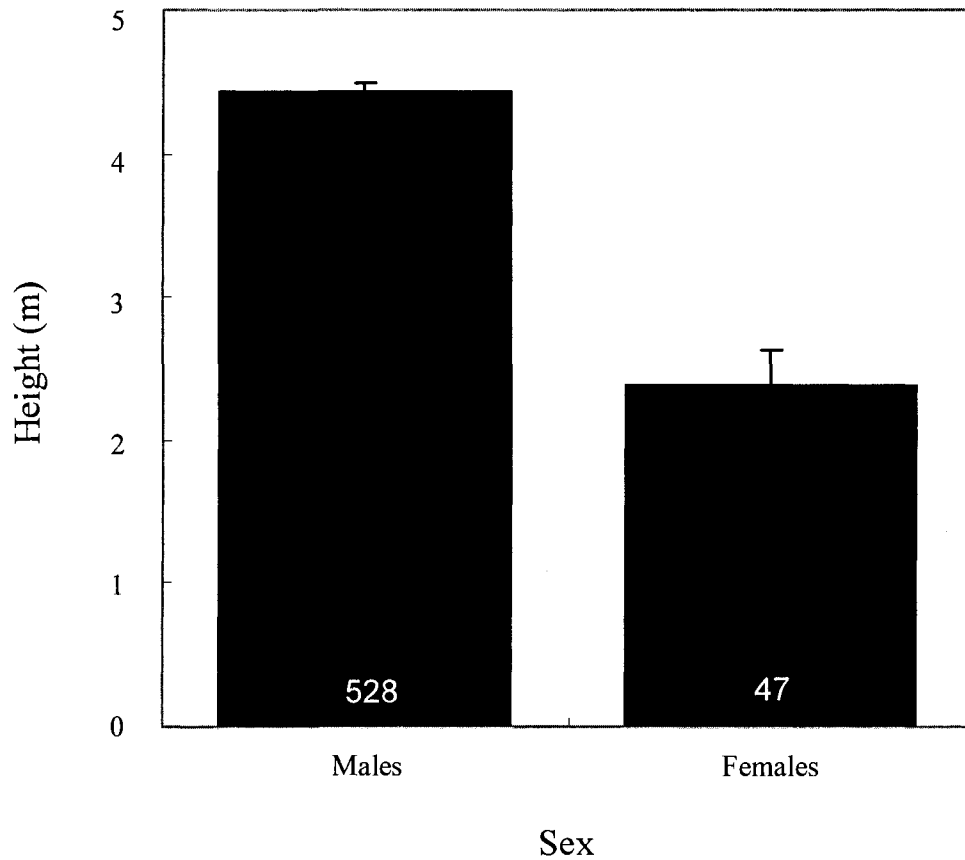
Figure 3. Average perch heights for male and female rufous-and-white wrens, showing the significant main effect of sex. Error bars represent standard error; number of observations is indicated on each bar. The variability between pair and habitat conditions was reduced through the inclusion of territory as a random factor.

Thesis Summary

The degradation of animal signals as they propagate over long distances can have implications for detection and recognition of those signals, and therefore communication between individuals. For vocal signals, the type and amount of degradation is affected by a number of factors such as habitat, signal structure, and signaller height. This thesis explores the transmission properties, song structure, habitat characteristics, and singing behaviour of Rufous-and-white Wrens (*Thryothorus rufalbus*) a Neotropical songbird in which both males and females sing.

In Chapter 2 I report the results of a sound transmission experiment designed to investigate the effects of distance, song post height, receiver perch height, sex of signaller, and microhabitat on song degradation in Rufous-and-white Wrens. Some of my findings are consistent with previous research. For example, song degradation increased regularly with distance between signaller and receiver. Also consistent with previous research, my experiment showed a significant influence of song post height on degradation; songs transmitted best when emitted from moderate heights (5 m and 7 m) than low heights (1 m), although the specific patterns varied with receiver distance, receiver height, and microhabitat. Some of my findings stand in contrast to previous research. For example, I found a subtle and inconsistent pattern regarding receiver height, whereas many previous studies found that receiver (i.e. microphone) height had a large influence on signal propagation. I also found inconsistent results regarding habitat, although it is clear that Rufous-and-white Wren songs were more degraded in an open field (i.e. foreign habitat) than in the forest (i.e. native habitat). The novel aspect of my transmission experiment was the comparison of male and female songs. Female songs were generally more degraded than male songs. My transmission

study contributes to a growing body of research on the propagation of animal vocalizations through the natural environment, and it provides new perspectives particularly in relation to a comparison of male and female song degradation.

The acoustic adaptation hypothesis proposes that animals' vocalizations will change over evolutionary time and become adapted to their habitats in a way that maximizes sound transmission by reducing attenuation and degradation. In Chapter 3 I investigated the relationship between song structure and habitat in Rufous-and-white Wrens, to asses whether the structure of their songs may be influenced by habitat characteristics. I found that the mature and regenerating sections of forest within Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica, show different vegetation structure. I also found that the classes of song types previously used for categorizing the songs of Rufous-and-white Wrens are readily distinguished using a multivariate discriminant analysis approach. Being able to include song class in my comparison of song structure and habitat was important because it helped control for variability in song structure. Such a technique would be especially valuable for revealing an effect of habitat in a repertoire-singing bird if one exists, and I encourage others to follow this approach. I did not find a strong effect of habitat on song structure; the only song feature that appeared to differ between mature and regenerating forests was the terminal syllable. It may be that Rufous-and-white Wren song structure is shaped by other factors such as sympatry with congeners or sexual selection, rather than habitat. It may also be that the forests were too structurally similar, or too geographically separated to allow habitat to separately and significantly influence songs in the two areas.

Based on the results of my transmission study and other previous research, I developed a set of predictions regarding the use of behaviour to overcome communication

challenges. Results from Chapter 2 suggested that Rufous-and-white Wrens should use perch heights of 5-7 m and avoid perches of 1 m if their songs are to transmit maximally. Since Rufous-and-white Wren territories are large and they use song in territorial defence, I predicted that they should use elevated song posts to maximize their communication range. Previous studies have shown that the sexes exhibit some divergent singing behaviours, so I predicted that males and females would demonstrate different perch height choices. Lastly, I predicted that activities other than singing would also influence perch height, given that they may involve particular resources (e.g. food, nesting material) which are present at specific heights. Field observations of Rufous-and-white Wrens supported all three of these predictions. Rufous-and-white Wren perch height choice is influenced by the activity; songs are performed from the greatest heights of up to 15 m, foraging occurs on the ground, and the wrens perform other activities, such as collecting nesting material and performing non-song vocalizations, at heights between those two extremes.

Birds have evolved multiple techniques to overcome communication challenges. Here I investigated the degradation of Rufous-and-white Wren song and examined two of the techniques used to overcome song degradation: song structure and perch height choice. Regarding the first technique, my song transmission study showed that Rufous-and-white Wren song was more degraded in non-native fields than in their native forest habitats, suggesting that to some degree their songs are structured to match their native habitats. However, further examination of song structure in a descriptive study did not reveal a strong relationship between song structure and habitat. Regarding the second technique, the song transmission study also showed that Rufous-and-white Wren song suffers a transmission disadvantage when sung from heights of 1 m, leading to predictions that these birds should

use elevated perch heights. Behavioural observations revealed that Rufous-and-white Wrens do indeed choose to sing from elevated perch heights and minimize singing from within 1 m of the ground. The song transmission study and the behavioural study also demonstrated sex differences in both song transmission and singing behaviour: female songs showed greater degradation than male, and males and females used different perch heights, with males choosing higher perches than females. Overall, I conclude that Rufous-and-white Wren songs are generally structured to transmit well in their forest habitats, but habitat-related differences in song structure that accumulate over evolutionary time may only become apparent over greater distances or between more different habitats. Instead of having songs that are specifically adapted for their microhabitats, Rufous-and-white Wrens use behavioural techniques to help communicate at long distances, by choosing elevated perch heights. Male songs transmit better than female songs, and males choose higher song perches than females, which may be related to particular sex roles and suggests that long-range communication is more important for males than for females.

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