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BIRD SONG STRUCTURE AND TRANSMISSION IN THE NEOTROPICS: TRENDS, METHODS AND FUTURE DIRECTIONS

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Resumen. – La estructura y transmisión del canto de las aves Neotropicales: Tendencias, métodos y preguntas para el futuro. – El canto juega un papel muy importante en la ecología, evolución y comportamiento de las aves, y es usado principalmente por los machos, para la atracción de las hembras y la defensa del territorio. Las señales vocales transmitidas a largas distancias, tales como el canto, están adaptadas para un hábitat particular y para ser transmitidas a las máximas distancias con un mínimo de distorsión. Desde los años 70 se han conducido estudios de hábitat relacionados con diferencias entre la estructura y transmisión del canto, pero ha existido un mayor enfoque hacia hábitat templados que hacia hábitat tropicales. Este articulo resume los diferentes métodos que pueden ser empleados con el fin de investigar la compleja relación entre el hábitat y el canto de las aves. Comienza con una discusión de la dicotomía entre "templado" y "tropical" y las razones por las cuales los cantos de las aves tropicales pueden ser diferentes de los cantos de las aves de regiones templadas. Después se introduce la hipótesis de la adaptación acústica y se resumen brevemente las tendencias más importantes reveladas por estudios de la estructura y transmisión del canto. Finalmente, se resumen los enfoques más importantes para estudiar la relación entre el hábitat, la estructura y la transmisión del canto: 1) estudios de la transmisión del sonido, que pueden investigar cómo el sonido se transmite a través del medio ambiente natural; 2) estudios que comparen las características del canto entre categorías del habitat; y 3) estudios focales de especies, con objeto de dilucidar la relación entre el hábitat, la estructura y la transmisión del canto en una o en algunas especies. Esta tercera categoría puede ser dividida en cuatro subcategorías de estudios: observaciones descriptivas, transmisión del canto, transmisión recíproca, y cantos emitidos artificialmente y su respectiva respuesta. Se resaltan los enfoques más comunes así como preferidos de cada tipo de estudio, y se sugieren futuras preguntas. La meta final de este trabajo es crear un recurso de ayuda en investigaciones Neotropicales futuras relacionadas con el hábitat, la estructura del canto y su transmisión.

Abstract. – Song plays a critically important role in the ecology, evolution, and behavior of birds, and is used principally for mate attraction and territory defense. Long-distance vocal signals, such as song, are often adapted to particular habitats in order to transmit over maximal distances with minimal distortion. Studies of habitat-related differences in song structure and transmission have been conducted since the 1970s, but there is a heavy focus on temperate rather than tropical habitats. In this paper, I summarize the numerous methods that can be used to investigate the complex relationship between habitat and song in birds. I begin with a discussion of the tropical-temperate dichotomy, and why tropical bird song might be different than temperate bird song. I then introduce the acoustic adaptation hypothesis and briefly summarize some major trends that have been revealed by studies of song structure and transmission. Finally, I outline the major approaches to studying the relationships between habitat, song structure, and song transmission: 1) sound transmission studies, which investigate how sound propagates through the natural environment; 2) surveys, which compare song characteristics between categories of habitats; and 3) focal species studies, which are aimed at elucidating the relationships between habitat, song structure and song transmission in one or a few species. This third category can be further split into four sub-categories of study: descriptive, song transmission, reciprocal transmission, and playback and response. I highlight the most common and preferred approaches of each type of study, and suggest future avenues of research. My ultimate goal is to create a resource to aid in future Neotropical research on habitat-related song structure and transmission. *Accepted 23 November 2007.*

Key words: Bird song, sound transmission, tropics, habitat, vegetation, acoustic adaptation hypothesis, animal communication, attenuation, degradation.

INTRODUCTION

Bird song plays an important role in territory defense and mate attraction (Catchpole & Slater 1995). 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 2002a) and hybridization prevention (reviewed in Slabbekoorn & Smith 2002a). 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). The study of the structure and transmission of bird song in relation to natural habitats was founded in the tropics, with pioneering research by Morton (1975) directly leading to work from Marten *et al.* (1977), Marten & Marler (1977), and Ryan & Brenowitz (1985). However, despite the fact that many studies have been conducted in both tropical and temperate regions, very few have compared the structure and transmission of bird song between the two habitats. 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 behavioral ecology, it would not be surprising to find that birds in the tropics exhibit different patterns of variation in song structures and different singing behaviors than temperate species. With our current knowledge, we cannot address this question, nor can we properly answer whether habitat might play a role in any song differences that are detected. Moreover, with tropical habitats continuing to disappear, it is important to gain information about the species living in these diminishing habitats before it is too late.

To encourage research on song structure and transmission in the tropics, I provide a summary and critical evaluation of the dominant methodologies used in previous studies, as well as a brief overview of some findings from these studies. I start by elaborating on differences between tropical and temperate habitats, and then briefly summarize some trends that have been elucidated thus far in the study of song structure and transmission. The majority of this review is dedicated to a detailed summary of the numerous and varied methodologies used to study song structure and transmission, outlining the major categories and sub-categories of research techniques. I touch on the multiple variations of each type of study in order to illustrate the kinds of questions that can be answered, with an emphasis on the most commonly used approaches. I end with a summary of the advantages of each method, as well as some recommendations for future avenues of research. My intent with this paper is to stimulate further research in this area, and provide a resource that researchers can use when formulating their own approaches to studying bird song in the tropics. My emphasis on Neotropical research is largely due to the greater number of studies that have been conducted in the New World tropics, but many of the recommendations for research should be applicable to research in the Old World tropics, and the temperate region as well.

TROPICAL VS 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. The tropical-temperate dichotomy is used in this review for illustration purposes, but it should be recognized that this oversimplification can exaggerate the differences between, and mask the variation within, tropical and temperate regions.

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 behavioral ecologies (Stutchbury & Morton 2001). Differences in breeding season and migratory behaviors, stemming primarily from climatic differences, influence other behaviors such as territoriality, mating system, and communication (Stutchbury & Morton 2001). With greater species diversity in the tropics, and approximately 80% of passerine species breeding in tropical regions, an incomplete knowledge of the biology of tropical species limits our understanding of avian biology in general. This fact has prompted Morton (1996) and Stutchbury & Morton (2001) to suggest that it might be more reasonable to consider the behavioral ecology of tropical birds as the standard, and temperate species as divergent. While many studies regarding the song 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 will contribute to our understanding of bird song, avian behavioral ecology, and the important associations between birds and their physical environments.

THEORY AND TRENDS IN SONG STRUCTURE AND TRANSMISSION

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 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

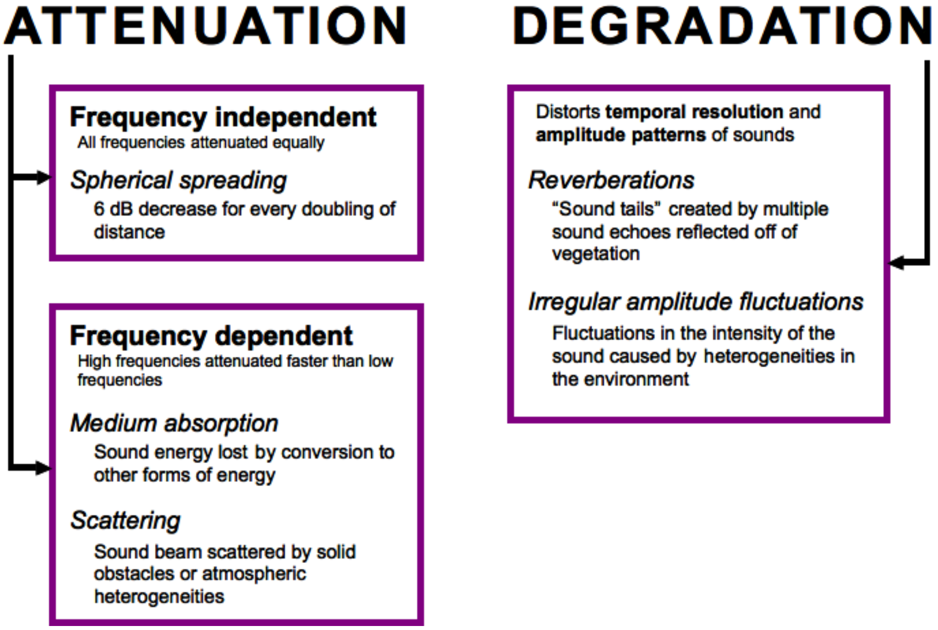

FIG. 1. Common terminology and concepts used to describe the acoustic distortion caused by transmission through the natural environment. Based on Wiley & Richards (1978), Bradbury & Vehrencamp (1998), and Slabbekoorn (2004).

(Wiley & Richards 1982). Excellent summaries of the forces affecting the transmission of sounds and bird song through the natural environment can be found in two main textbooks: Slabbekoorn (2004b) presents an easy-to-understand introduction, while Bradbury & Vehrencamp (1998) provide a more technical and detailed account. Wiley & Richards (1978, 1982) present additional summaries. Figure 1 provides a summary of the major terms used in the study of sound transmission, based on the concepts outlined in these reviews.

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. It suggests that evolution has favored 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, see Fig. 1) and degradation (temporal and structural distortion, see Fig. 1). 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 and less frequency-modulated in closed (i.e., forest) habitats than in open (i.e., grassland) habitats, because the songs of forest birds are generally subject to more reverberation and frequency-dependent attenuation than those of grassland 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 confirm 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 frequency variables were consistent with predictions of the acoustic adaptation hypothesis, but the single temporal variable was not (Boncoraglio & Saino 2007). Collectively, these and other studies have demonstrated some general relationships between habitat, song structure and sound transmission.

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 forest 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 forest and grassland 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 absense 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 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 faster trills (Handford & Lougheed 1991), a greater prevalence of side bands and buzzes (Wiley 1991), more notes, and broader bandwidths (Tubaro & Lijtmaer 2006). In contrast, forest species tend to have pure, tonal songs (Morton 1975) with fewer notes, longer notes, and longer intervals between notes (Badyaev & Leaf 1997, reviewed in Wiley & Richards

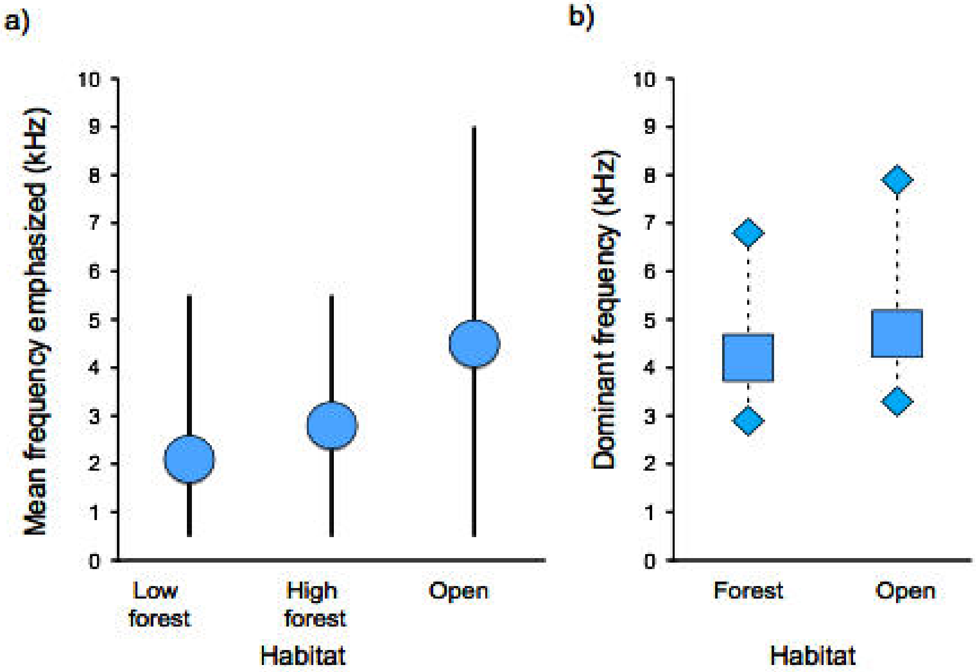

FIG. 2. a) Means and ranges of frequency emphasized (frequency where the most energy is concentrated) in Neotropical forest and grassland bird songs, as estimated from Figure 4 of Morton (1975). Original data are from 85 species between upper and lower level forest and 21 species in open grassland in Panama. b) Mean dominant frequencies (frequency of maximum amplitude) of songs from temperate forest and grassland birds, with mean minimal and maximal frequencies indicated by vertical bars. Original data were presented for 29 forest species and 18 grassland species in Figure 1 of Wiley (1991).

1982). This trend of slower trilled tonal songs in forest 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 1986a). 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 (Fig. 2). It is important to note that these studies (Morton 1975, Wiley 1991) did not use identical methods, and that Wiley (1991) focused on a subset (oscine passerines) of the kinds of birds that Morton (1975) included (oscine and suboscine passerines, as well as non-passerines). However, even with the awareness of these methodological differences, the frequency difference between tropical and temperate song seems to be very large for forest species. Tropical birds concentrate the energy of their songs into low frequencies (mean frequency emphasized is 2.1 kHz; Morton 1975), while temperate birds have a higher average dominant frequency (frequency of maximum amplitude is 4.2 kHz; Wiley 1991). Additionally, 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 vegetation. 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 further to mates or rival conspecifics. Additionally, there may be additional 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, katydids, 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). More research is needed to clarify these possible song differences between birds living in tropical and temperate habitats. This research should focus on open as well as closed tropical habitats, and should attempt to ascertain the reasons for any frequency and structural differences that may be discovered.

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 a long-distance signal; broadcasting it as far as possible with minimal attenuation and degradation so that receivers can detect and recognize it. 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 that intended receivers (neighbors or mates) are nearby, or that a degraded signal is adequate for its intended purpose (Aubin *et al.* 2004, Kroon & Westcott 2006). It could also be that some signals are designed to minimize variability in transmission quality rather than maximize distance traveled (Brown & Handford 1996, 2000,

TABLE 1. Factors that may influence the evolution of song structure.

Variables	Reasoning	References
Vegetation, physical environment	Bird song may be adapted to particular environments	Morton 1975, Rothstein & Fleischer 1987, Brown & Handford 2000
Body size	Larger birds may produce lower-pitched songs	Bowman 1979, Ryan & Brenowitz 1985, Bertelli & Tubaro 2002
Bill morphology	Beak size and shape influences temporal features of songs	Podos 2001, Seddon 2005, Ballentine 2006
Phylogeny	Phylogeny may constrain song evolution	Laiolo & Rolando 2003, Rheindt *et al.* 2004
Ambient noise	Ambient noise can select for higher or lower-pitched songs	Ryan & Brenowitz 1985, Slabbekoorn & Peet 2003
Perch height	Perch height will influence transmission	Nemeth *et al.* 2001, Mathevon *et al.* 2005
Territory size and population density	Territory size and population density will determine how far a signal must travel	Lemon *et al.* 1981, Calder 1990
Intended receiver	Close-range and long-range signals will experience different selective pressures	Wiley & Richards 1978, Aubin *et al.* 2004, Nemeth *et al.* 2006
Sympatry with related species	Songs may diverge to help prevent hybridization	Bowman 1979, Irwin 2000, Slabbekoorn & Smith 2002a
Sexual selection	Females (or males) may prefer certain song features, such as trills	Vallet & Kreutzer 1995, Ballentine *et al.* 2004

2003). Additionally, some amount of signal alteration can actually be useful to birds if it is advantageous to know how far away neighboring birds are, because degradation can act as a distance and location cue (Richards 1981, Morton 1982, Morton 1986).

Secondly, there are a number of factors that influence the evolution of song structure beyond the natural environment (see Table 1). 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 (Podos 2001, Ballentine 2006). Sexual selection can also influence song structure if female birds prefer specific features in male songs (Vallet & Kreutzer 1995, Ballentine *et al.* 2004). Additional factors include territory size, population density, and intended receivers (Lemon *et al.* 1981, Cosens & Falls 1984, Calder 1990, Nemeth *et al.* 2001, 2006). Acoustic signals therefore represent a compromise between multiple selective forces that can sometimes work in opposition.

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, so it is important to recognize and utilize the most common and accepted techniques.

METHODOLOGIES: SONG STRUCTURE AND TRANSMISSION

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. There is some overlap between these types of studies and often researchers will combine techniques in one multi-faceted study, but these general categories are useful for understanding the various approaches. For example, both focal species and sound transmission studies can involve broadcasting test sounds through the environment, but these studies differ in their objectives. Sound transmission studies are often focused on determining general principles of sound transmission while focal species studies are concerned with a particular species. For this reason, many sound transmission studies involve computer-generated sounds whereas focal species studies often use actual song recordings. Additionally, the line between surveys and focal species studies is sometimes blurred since surveys can include a small number of species and focal species studies can include more than one. The main difference is that surveys are used to understand overall trends between categories of habitats whereas focal species studies attempt to ascertain patterns in habitat-related song differences within particular species of interest.

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). Model sounds are compared to the transmitted sounds to ascertain the effects of attenuation and degradation. The same experimental setup can be used in multiple habitat types, and then attenuation, reverberation, and other sources of degradation can be measured in relation to various factors. The specific designs of sound transmission studies are dependent on the question being asked, and researchers can vary the sound stimuli, propagation distances, speaker and microphone heights, and habitat.

TABLE 2. Variables that researchers can control or measure when conducting survey studies.

Variables	Variation
Habitat	A few habitat categories (e.g., forest, edge, grassland) or one or more continuous habitat variable
Species	Oscine, suboscine, non-passerine
Size of study site	Large (continent, world), small (single study site)
Number of species	Variable (2-200)
Body size and bill morphology	Song frequency and temporal features can be affected by bill morphology and body size (see Table 1)
Phylogeny	Closely-related species may have similar songs

Sound stimuli can be bands of, or full-spectrum, random noise (e.g., Morton 1975, Marten & Marler 1977, Marten *et al.* 1977, Martens 1980, Ellinger & Hödl 2003, Nelson 2003), pure tones of constant or modulated frequency (e.g., Marten *et al.* 1977, Slabbekoorn *et al.* 2002), pulses of sound (e.g., Richards & Wiley 1980), computer-generated trills with slow or fast amplitude modulation (e.g., Brown & Handford 2000, Naguib 2003), or balloon bursts (e.g., Padgham 2004). Studies using random noise and pure tones of many frequencies allow for the creation of attenuation or propagation curves, demonstrating differences in frequency-dependent attenuation (e.g., Morton 1975); they represent the most basic way to assess differences in attenuation under various conditions. More specific questions require particular sets of stimuli. For example, Richards & Wiley (1980), working in temperate North Carolina, studied the effects of reverberation and irregular amplitude fluctuations by broadcasting pure tones and pulses of sound through grassland and forest habitats. Ellinger & Hödl (2003) conducted a pulse tone study to understand the effects of reverberation in a primary lowland rainforest in Venezuela. To investigate the potential differential effects of degradation on rapidly amplitude-modulated trills vs slow amplitude-modulated whistles, Brown & Handford (2000) broadcasted synthesized slow and fast amplitude-modulated sounds at a fixed height and distance through five habitats in Ontario, Canada. Naguib (2003) conducted a similar study in Germany with synthesized slow and fast trills; he added an extra dimension by using trills at multiple frequencies. Slabbekoorn *et al.* (2002) investigated the effect of frequency modulation on reverberation in a rainforest in Cameroon by using pure tones with varying degrees of frequency modulation.

Sound transmission studies typically use multiple distances, ranging from 5 m to 100 m. A set of recordings collected with microphones at 5, 10, 20, 40, 60, 80 m away from the speaker would be very typical (e.g., Richards & Wiley 1980), although some researchers use fewer distances, such as 20, 40, 80, and 120 m (e.g., Naguib 2003). Some researchers generate their model sound by re-recording their test sound at a close distance, such as 2.5 m (e.g., Marten *et al.* 1977). The optimal distances that should be used ultimately depend on the question being asked and the amplitude that the sounds are being broadcasted at, but using 4–6 distances from 5 m to 100 m, with a model sound recorded at 2.5 m or less may be the most favorable approach.

Researchers can vary the heights of speakers and of microphones, allowing for many permutations. Often, microphones and speakers are placed at the same height, for strictly horizontal propagation (e.g., Morton 1975, Richards & Wiley 1980, Brown & Handford 2000, Naguib 2003), and this is a reasonable approach if the subject under investigation strictly relates to the distance or height of the transmission. However, if a researcher is curious about the vertical structure of the habitat, such as stratification of vegetation, diagonal propagations help to create more useful comparisons (e.g., Nelson 2003). More research involving transmission between different layers would be relevant for Neotropical forests due to complex vegetation stratification.

Some studies are performed to simply understand how different sounds propagate (e.g., Richards & Wiley 1980, Nelson 2003, Ellinger & Hödl 2003), but researchers can also investigate how habitat structure influences sound propagation by conducting the same experiment in several habitats (e.g., Morton 1975, Marten & Marler 1977, Brown & Handford 2000, Padgham 2004). The simplest habitat categories are forest and open (e.g., Naguib 2003, Padgham 2004), followed by edge habitat (Morton 1975), and then by more fine scale categories of habitat such as coniferous, hemlock, or deciduous (Marten & Marler 1977). Marten *et al.* (1977) investigated forests of different ages ranging from edge to mature, while Slabbekoorn *et al.* (2007) compared urban and forested habitats. Habitat structure should be quantified with some vegetation measurements, such as those described in the "descriptive studies" section, below. One important area for future research will be the quantification of attenuation and degradation in different habitats within the tropics, such as cloud forest vs dry forest, or at different times of the year, rather than assuming that sound is affected in the same ways by all tropical habitats at all times of year.

Early sound transmission research in the 1970s and 1980s demonstrated the basic principles of attenuation and propagation in various habitats ranging from tropical to temperate, open to closed. However, many studies of sound transmission have been conducted with a specific biological question in mind. For example, Morton (1975), related his findings regarding sound transmission of different frequencies to a survey of birds in his study area, explaining that many birds in forest habitats have low-frequency songs because those songs propagate furthest in dense forests. Some focal species studies use findings from sound transmission studies to inform their conclusions on any differences in song that appear to be related to habitat. For example, Hunter & Krebs (1979) compared the songs of Great Tits (*Parus major*) across many European countries, and then used the results of sound and song transmission experiments to help explain the differences between localities and habitats.

The findings from these transmission studies form the basis for our understanding of sound transmission in different situations and habitats (see "Trends" section, above, or Wiley & Richards 1978, Wiley & Richards 1982, Catchpole & Slater 1995, and Slabbekoorn 2004b for reviews). However, our knowledge is far from complete. More studies in new habitat types, as well as replication of experiments in previously studied habitats, will help create a more thorough understanding of the multiple effects that habitat and vegetation structure can have on the attenuation and reverberation of different types of sounds. The vertical structure of many Neotropical forests is more complex than that of typical temperate forests (Richards 1952, Terborgh 1985), so it is relevant to compare sound propagation between the two regions to determine the selective pressures on birds to utilize certain frequencies or structural features in their songs. Sound transmission studies also present useful additions to focal species studies, since they establish a reference level of attenuation and degradation occurring in the habitats under study.

Survey studies. Sound transmission studies have revealed that signals experience differential attenuation and degradation dependent on the type of habitat they propagate through (see above). 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 habitat in which these species live. The specific methods used in survey studies are highly inconsistent because there are many variables that can be taken into account. 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 (see Table 2 for a summary).

Some surveys include a few closely-related species such as warblers (Lemon *et al.* 1981, Badyaev & Leaf 1997, Van Buskirk 1997), tinamous (Bertelli & Tubaro 2002), corvids (Laiolo & Rolando 2003), antbirds (Seddon 2005), or grosbeaks and saltators (Tubaro & Lijtmaer 2006), while some involve up to 177 diverse species (Morton 1975). Many studies focus on passerines (e.g., Sorjonen 1986a, Wiley 1991, Rheindt *et al.* 2004) while some have included non-passerines (Morton 1975, Ryan & Brenowitz 1985, Bertelli & Tubaro 2002, Blumstein & Turner 2005). The geographic scale of surveys ranges from small to large, such as Australia (Blumstein & Turner 2005), eastern North America (Wiley 1991), or worldwide (Laiolo & Rolando 2003). When selecting the number, distribution, and kinds of species to be compared, it is important to consider possible confounds. For example, oscine passerines learn their songs, perhaps allowing for faster evolutionary changes to song structure in response to habitat differences, so if non-learning suboscines or non-passerines are included in a survey, the number of species in each category should be balanced between habitats. This may be particularly relevant for studies comparing tropical and temperate birds, because suboscines are more numerous in the Neotropics than in any other region, which could bias survey results if not properly accounted for.

Many studies have investigated differences in bird song between the two large categories of open vs closed habitat (e.g., Laiolo & Rolando 2003, Rheindt *et al.* 2004, Saunders & Slotow 2004, Blumstein & Turner 2005). However, it is useful to include additional classes of habitat such as edge (Morton 1975, Ryan & Brenowitz 1985, Sorjonen 1986a, Bertelli & Tubaro 2002, Tubaro & Lijtmaer 2006), coniferous and deciduous forests (Wiley 1991, Badyaev & Leaf 1997), and marshland (Cosens & Falls 1984), or quantify multiple habitat variables (Van Buskirk 1997). Investigating habitat in terms of height or vegetation layer in forests can also be informative, but is rare in the literature (Lemon *et al.* 1981, Seddon 2005). Moving beyond broad classes of habitats towards an increasingly fine-scale and quantitative analysis of habitat measurement will be important in future studies

Body size relates to song frequency (Bowman 1979, Ryan & Brenowitz 1985), and bill morphology constrains the structural and temporal characteristics of song in some species (Podos 2001). Body size is commonly accounted for when assessing differences in bird song across categories of habitat (e.g., Wiley 1991, Badyaev & Leaf 1997, Bertelli & Tubaro 2002, Laiolo & Rolando 2003, Blumstein & Turner 2005), but bill morphology is less often examined (e.g., Laiolo & Rolando 2003, Seddon 2005). Body size is a particularly important covariate because it has been shown that birds living in open habitats tend to be smaller than those in closed habitats (Ryan & Brenowitz 1985, but see Sorjonen 1986a) and it may be that tropical and temperate birds are different sizes as well; body size should therefore be included in any survey study. The choice of body size measurement can vary between studies, since many traits can indicate body size, including weight or wing length. The approach that Handford & Lougheed (1991) used in their (focal) study of Rufous-collared Sparrows (*Zonotrichia capensis*), is one of the better techniques: they measured multiple body size traits and then employed principle component analysis to compress those measures into one single body size variable. Accounting for relatedness between species is also important, although there is still some debate about when it is appropriate to control for phylogenetic relationships (Rheindt *et al.* 2004). When phylogenies are well-constructed, a detailed phylogenetic analysis can be conducted (e.g., Van Buskirk 1997, Bertelli & Tubaro 2002, Laiolo & Rolando 2003, Rheindt *et al.* 2004). However, if phylogenetic relationships are less clear, species or genus pairs comprised of one species from each habitat type can be used to assess song differences (e.g., Smith & Yu 1992, Saunders & Slotow 2004, Blumstein &

TABLE 3. Measurements, of whole songs or of song components, that are often used in survey studies. Letters refer to references, below.

	Based on frequency characteristics	Based on temporal or structural characteristics
Based on whole songs or calls	Frequency range/bandwidth (a,b,f,g,h,i,j,l,m,n,o) Dominant/emphasized frequency (a,b,c,e,f,g,i,k,m,n,o) Maximum frequency (b,e,g,h,i,k,l,m,n,o) Minimum frequency (e,g,h,i,j,k,l,m,n,o) Number of syllables in a given frequency range (d) Number of syllables with bandwidth in a given range (d) Fundamental frequency (j) Carrying frequency and second carrying frequency (j) Variation in carrying frequency and in second carrying frequency (j) Energy splitting range (j) Average frequency (l) Maximum frequency of first, middle, or final note (n) First and second frequency change (n)	Duration of song, inter-note interval, silence preceding terminal syllable, inter-song pause, first note, middle note, and/or final note (b,d,f,g,h,j,l,m,n,o) Number of notes and/or syllables (d,g,h,l,m,n,o) Presence of harmonics, buzzes, and/or side bands (e,k) Maximum number of a single syllable type (b,d) Extent of frequency modulation (tones vs trills) (a) Measure of "grouping pattern" of syllables (b) Percentage of whistles vs modulated elements (d) Percentage of short, medium, and long elements (d) Number of fast trilled vs slow trilled syllables (d) Number of repeated syllable types (d) Number of elements/song/sec (d) Minimal period of trilled syllables (e) Occurrence of a rapidly repeated syllable (f) Proportion of notes adjacent an identical note (h) Ratio in amplitude from second to first peak (j) Pace/number of notes per second (n)
Based on individual notes or syllables	Bandwidth of note or pulsed unit (h,j,m) Frequency range/bandwidth of terminal syllable (b) Maximum and dominant/emphasized frequency of terminal syllable (b) Dominant/emphasized frequency of terminal syllable (b) Bandwidth of pulsed unit (j) Maximum, minimum, and dominant/emphasized frequency (m)	Duration of note or pulsed unit (g,h,j,l,m,o) Number of syllable and/or note types (b,h) Duration of terminal syllable (b) Rate of change of frequency in terminal syllable (b) Proportion of time from beginning to minimum frequency (h) Number of inflection points in slope of frequency modulation (h) Variation in duration of pulsed unit (j)

References: a) Morton 1975; b) Lemon *et al.* 1981; c) Ryan & Brenowitz 1985; d) Sorjonen 1986a; e) Wiley 1991; f) Smith & Yu 1992; g) Badyaev & Leaf 1997; h) Van Buskirk 1997; i) Bertelli & Tubaro 2002; j) Laiolo & Rolando 2003; k) Rheindt *et al.* 2004; l) Saunders & Slotow 2004; m) Blumstein & Turner 2005; n) Seddon 2005; o) Tubaro & Lijtmaer 2006.

Turner 2005), although this is less favorable. There are additional factors that can be taken into account when conducting a survey study, such as ambient noise (e.g., Ryan & Brenowitz 1985), territory size or population density (e.g., Cosens & Falls 1984), song community

TABLE 4. Statistical techniques that can be used in survey, descriptive, and transmission studies.

Statistical test	Survey studies	Descriptive	Sound, song & reciprocal transmission
Discriminant analysis	Lemon *et al.* 1981	Shy 1983, Anderson & Conner 1985, Sorjonen 1986b, Date & Lemon 1993, Nicholls & Goldizen 2006, Ruegg *et al.* 2006, Lijtmaer & Tubaro 2007	
Principle component analysis	Sorjonen 1986a, Badyaev & Leaf 1997, van Buskirk 1997, Seddon 2005, Tubaro & Lijtmaer 2006	Handford & Lougheed 1991, Tubaro & Segura 1994, Kopuchian *et al.* 2004	
Regression, correlation, GLM	Wiley 1991, Bertelli & Tubaro 2002, Laiolo & Rolando 2003, Rheindt *et al.* 2004	Hunter & Krebs 1979, Shy 1983, Handford & Lougheed 1991, Tubaro & Segura 1995, Slabbekoorn & Peet 2003	Marten *et al.* 1977, Richards & Wiley 1980, Nemeth *et al.* 2001
Mantel tests, matricies, cluster analysis	Sorjonen 1986a, van Buskirk 1997	Anderson & Conner 1985, Ruegg *et al.* 2006	
ANOVA, ANCOVA, MANOVA, Kruskal-Wallis	Cosens & Falls 1984, Ryan & Brenowitz 1985, Wiley 1991, Blumstein & Turner 2005, Ellinger & Hödl 2003, Seddon 2005, Tubaro & Lijtmaer 2006,	Anderson & Conner 1985, Williams & Slater 1993, Kopuchian *et al.* 2004, Nicholls & Goldizen 2006, Lijtmaer & Tubaro 2007	Wilczynski *et al.* 1989, Dabelsteen *et al.* 1993, Date & Lemon 1993, Brown & Handford 2000, 2003, Naguib 2003, Nelson 2003, Hansen *et al.* 2005, Leader *et al.* 2005, Kroon & Westcott 2006, Nemeth *et al.* 2006
t-test, Mann-Whitney, Wilcoxon signed-rank test	Cosens & Falls 1984, Blumstein & Turner 2005	Shy 1983, Waas 1988, Lijtmaer & Tubaro 2007	Cosens & Falls 1984, Mathevon *et al.* 1996
Contingency tables	Wiley 1991, Blumstein & Turner 2005		Cosens & Falls 1984

(Sorjonen 1986a), or other factors that might influence song evolution (Table 1 and 2) but these studies are less common than those accounting for body size and phylogeny. Attention to ambient noise is increasing in focal studies (below), and may be an important variable in future surveys as well. Territory size might be important when comparing tropical to temperate birds because there is some evidence that tropical birds hold larger territories (Terborgh *et al.* 1990). Researchers should include as many factors as possible to provide a comprehensive understanding of the possible influences on the frequency and structure of bird song in the various habitats.

Generally speaking, surveys "compare songs", but there are a number of different ways that this can be done. First, songs are acquired from focal recordings or from audio CD guides or other archives (e.g., Wiley 1991, Seddon 2005). Second, sound spectrograms are produced to visualize songs. In the past, sounds were visualized using Sonographs, instruments made by Kay Elemetrics (e.g., Lemon *et al.* 1981) but now numerous computer programs can be used to produce and measure sound spectrograms. Example programs include Canary or its successor Raven (Cornell Laboratory of Ornithology), Avisoft SASLab Pro Software (Raimund Specht, Berlin), SIGNAL (Engineering Design, Belmont, MA), and Syrinx PC (John Burt, www.syrinxpc.com). Third, researchers measure frequency and temporal characteristics of whole songs or individual notes from sound spectrograms of several songs for each species (see Table 3 for a comprehensive list). The number of measurements can range from three or four (e.g., Morton 1975, Bertelli & Tubaro 2002) to more than 15 (e.g., Lemon *et al.* 1981, Sorjonen 1986a, Seddon 2005). The best measurements are consistent with previous research, such as maximum, minimum and dominant frequency (frequency of maximum amplitude), bandwidth (difference between maximum and minimum frequency), song duration, number of notes, and an indication of how slow or fast the song elements are repeated, such as inter-note interval (i.e., spacing between successive notes), or number of fast and slow trilled syllables. While less common, measures such as the presence of harmonics, buzzes, or side bands, and the extent of frequency modulation are also important because they are predicted to vary with habitat. A variety of statistical approaches can be used to relate song characteristics to habitat and other variables such as body size or phylogeny (see Table 4 for statistical approaches). Regressions and ANOVAs, based on original measurements or on composite measures from principle component analysis, are both useful for comparing song characteristics across a number of habitat types. More specifically, ANCOVAs allow the inclusion of possible covariates such as body size, while regressions are more popular when assessing the influences of multiple variables such as phylogeny, body size, and bill length. Principle component analysis is useful when many song or vegetation measurements are taken, but it can prevent later pooling of results, such as in a meta-analysis (Boncoraglio & Saino 2007). It may therefore be advantageous to include an analysis where frequency variables are separate from temporal structural variables.

A few survey studies have been conducted in the Neotropics (e.g., Morton 1975, Seddon 2005) but the general applicability of the information provided by these studies may be limited. More surveys should be carried out in order to broaden our understanding of trends in bird song and to understand the relevance of the acoustic adaptation hypothesis to Neotropical birds. For example, a large-scale survey of hundreds of species across several countries should be conducted to confirm Morton's (1975) findings regarding Panamanian birds. Furthermore, an even larger study including tropical and temperate studies would be extremely useful in assessing the differences that may exist between tropical and temperate bird song. Attention should be paid to body size, phylogeny, and ambient noise or territory size, whenever possible.

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.

Dozens of species have been studied with the intent of discerning habitat-related differences in song structure, including tits (e.g., Hunter & Krebs 1979, McGregor & Krebs 1984, Doutrelant *et al.* 1999, Slabbekoorn & Peet 2003, Doutrelant & Lambrechts 2001), wrens (e.g., Naguib 1995, Mathevon *et al.* 1996, Holland *et al.* 1998, 2000), Old World warblers (e.g., Irwin 2000, Mathevon & Aubin 2001, Slabbekoorn *et al.* 2002, Balsby *et al.* 2003), bowerbirds (Kroon & Westcott 2006, Nicholls & Goldizen 2006), thrushes (Dabelsteen *et al.* 1993, Nemeth *et al.* 2006, Ruegg *et al.* 2006), sparrows (e.g., Wasserman 1979, Waas 1988, Handford & Lougheed 1991, Tubaro & Segura 1994, Lijtmaer & Tubaro 2007), and many others. Focal species studies can be split into four general categories: 1) Descriptive studies: researchers measure various frequency and temporal parameters of songs from birds living in different habitats and then compare these characteristics to see if conspecifics from various habitats sing different songs; 2) Song transmission studies: similar to sound transmission studies (above), these studies consist of broadcasting recordings of bird songs through different environments and comparing the transmission of these songs in various conditions or habitats; 3) Reciprocal transmission studies: bird songs recorded in more than one habitat are re-recorded in multiple habitats and transmission is compared; 4) Playback and response studies: songs recorded under different conditions are played to birds and behavioral responses are evaluated. Combining more than one of these approaches into one study is common and useful. It is often informative to include descriptive and transmission elements in one study (e.g., Date & Lemon 1993, Nemeth *et al.* 2001, Nicholls & Goldizen 2006) and some people also investigate the transmission of computer-generated sounds to compliment their focal species studies (e.g., Bowman 1979, Hunter & Krebs 1979, Cosens & Falls 1984, Slabbekoorn *et al.* 2002, Slabbekoorn & Smith 2002b, Nicholls & Goldizen 2006).

Descriptive studies. The methods used in descriptive focal species studies are very similar to those used for surveys; therefore much of the advice in the above section is relevant here. Birds' songs are recorded in multiple habitat types (see Budney & Grotke 1997 for a useful technical review of recording in tropical environments), measured with sound analysis software, and then compared between habitats. Like surveys, there are multiple characteristics of songs that can be measured (Table 3 summarizes measurements typically used in surveys) and these song characteristics can be related to multiple ecological variables. Habitat description involves an initial classification of habitats into categories such as open, closed, marshland, mixed, coniferous, or woodland forest, and rainforest. Beyond that, it is useful to take vegetation measurements such as the species, density and diameter of trees, as well as canopy height and some qualitative description of understory density and ground cover (e.g., Shy 1983, Williams & Slater 1993, Hylton & Godard 2001, Nicholls & Goldizen 2006). Climatic variables (Ellinger & Hödl 2003, Ruegg *et al.* 2006) ambient noise (e.g., Slabbekoorn & Peet 2003, Slabbekoorn & den Boer-Visser 2006), and vertical distribution of vegetation (e.g., Ellinger & Hödl 2003) are also informative. Measurements that help differentiate between the habitats are most useful, and therefore the specific parameters depend on the habitats being studied. Similarly, the structure of the songs determine the specific song parameters a researcher can measure, but a review of frequently used measurements ensures consistency with previous research. Commonly used frequency measurements include maximum and minimum frequency, dominant frequency (frequency of maximum amplitude), and bandwidth (different between maximum and minimum frequency) of the entire song or parts of songs (e.g., Handford & Lougheed 1991, Doutrelant & Lambrechts 2001, Nicholls & Goldizen 2006). The most common structural and temporal parameters are song duration, note number and duration, some measure of the speed of the song (e.g., cadence, duration of silence, inter-note interval; Williams & Slater 1993, Tubaro & Segura 1995, Doutrelant & Lambrechts 2001, Hylton & Godard 2001), and often a description of note structure (e.g., Hunter & Krebs 1979, Handford & Lougheed 1991, Irwin 2000, Naguib *et al.* 2001). Some researchers use automatic measurement procedures to divide songs into time frames of equal size and measure parameters from each time fame (e.g., Ruegg *et al.* 2006). Researchers should aim to measure as many song parameters as possible to describe the song frequency and structure. Focal species studies concentrate on only one or a few species, so it is possible to measure many variables in addition to habitat, allowing for a comprehensive evaluation of song structure in relation to habitat. These additional variables include body size (e.g., Hunter & Krebs 1979, Handford & Lougheed 1991, Doutrelant & Lambrechts 2001, Nicholls & Goldizen 2006), consideration of phylogeny and geographic distribution (e.g., Bowman 1979, Sorjonen 1986b), territory size or population density (Hunter & Krebs 1979, Irwin 2000), avian song community (e.g., Hunter & Krebs 1979), and ambient noise (Slabbekoorn & Smith 2002b, Slabbekoorn & Peet 2003). Many variables should be included whenever possible, because it may be the case that variation in song between two habitats is explained not by vegetation structure, but by other variables such as ambient noise (Dingle *et al.* unpubl.) The most common methods used to compare bird songs from different habitats are ANOVAs (based on original measurements or composite variables from principle components analysis), regressions, and discriminant analyses.

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; many points discussed in the above section are therefore relevant here. 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, and different habitats on the propagation of particular species' songs. Many experiments include several distances from 5 m to 200 m (e.g., Balsby *et al.* 2003) but some questions can be answered with only one distance (e.g., Hunter & Krebs 1979, Mathevon *et al.* 1996, Hansen *et al.* 2005). Typically, at least one distance is biologically relevant, such as territory diameter of the focal species (e.g., Mathevon *et al.* 2005). A much closer distance, ranging from 1 m to 10 m, is used to create the model recording (e.g., Cosens & Falls 1984, Holland *et al.* 1998, Nemeth *et al.* 2006). Because birds can perch at various heights when singing or listening to conspecifics, it is often informative to investigate the effects of perch height by including multiple speaker and microphone heights (e.g., Wilczynski *et al.* 1989, Dabelsteen *et al.* 1993, Balsby *et al.* 2003, Mathevon *et al.* 2005, Nemeth *et al.* 2006). If the goal is to assess differential propagation of bird song in various habitats, the experiment should be replicated in all habitats under consideration; replication within habitats is also desirable to ensure that results are representative. Analyses in song transmission studies compare measures of attenuation or degradation across song elements, distances, heights, and habitats. Cross-correlating model and observed songs using software such as SIGPRO (Pedersen 1998) is the most common method (e.g., Dabelsteen *et al.* 1993, Nemeth *et al.* 2006), although some alternative methods are also used (e.g., Hansen *et al.* 2005, Leader *et al.* 2005). Ultimately, the specific experimental design will depend on the question under investigation, but common approaches are desirable to ensure consistency with previous research. Statistical analyses are most often ANOVAs and regressions (see Table 4).

Reciprocal transmission studies. Reciprocal transmission experiments assess how bird songs from various habitats 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. Habitats, distances and perch heights are selected in the same way as song transmission studies. As examples, Gish & Morton (1981), Date & Lemon (1993), Kroon & Westcott (2006) and Nicholls & Goldizen (2006) looked at native and foreign song propagation in different habitats, while Nemeth *et al.* (2001) conducted a reciprocal transmission study with song posts of different heights instead of different habitats. The question of human influence can be investigated by including habitats with varying degrees of human impact (e.g., Leader *et al.* 2005). Statistical analysis in this type of experiment is the same as in song transmission studies (see Table 4).

Playback and response studies. Playback studies introduce a behavioral 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 (e.g., King *et al.* 1981, Doutrelant *et al.* 1999), altered in the frequency domain to simulate attenuation of higher frequencies (e.g., Brémond & Aubin 1990, Naguib 1995, Holland *et al.* 2000, Mathevon & Aubin 2001, Leader *et al.* 2005), or altered in the time domain to create or simulate reverberations (e.g., Naguib 1995, Naguib 1997, Mathevon & Aubin 2001, Slabbekoorn *et al.* 2002). Degraded songs can be created by re-recording at various distances (e.g., Doutrelant *et al.* 1999) or by artificially distorting them with computer software (e.g., Mathevon & Aubin 2001). In some cases, the stimulus itself remains the same and the environmental conditions change, such as in an investigation of the effect of ambient noise on birds' recognition of songs (e.g., Lengagne & Slater 2002). Playback studies are often conducted in the field, but questions of female response may be best carried out in a controlled laboratory setting (e.g., King *et al.* 1981). Responses can be measured in terms of territorial behaviors such as latency to response, shortest distance between focal bird and speaker, time spent within 5 m of the speaker, number of songs, and number of flight, or with copulatory assays (territorial displays: Fotheringham *et al.* 1997, Doutrelant *et al.* 1999, Westcott & Kroon 2002; copulatory assay: King *et al.* 1981). The strength of various responses is then compared between conditions to determine if birds react differently to the various stimuli. One important consideration in playback & response studies is whether the original songs used for stimuli are familiar or unfamiliar to the target birds (see Naguib 1996 and Morton 1998 for opposing viewpoints regarding the importance of familiarity). Playback and response tests are useful because they allow the birds' responses to inform any conclusions regarding whether degradation or differences in dialect (e.g., Leader *et al.* 2005) are behaviorally significant, rather than relying strictly on the statistical methods in the above studies. They provide a nice follow-up to descriptive studies (e.g., if songs in different habitats are found to be different, play the various songs back to birds in both habitats) and song or reciprocal transmission studies (e.g., play back songs re-recorded in the different habitats).

Focal species studies complement sound transmission and survey studies to enhance our understanding of the applicability of the acoustic adaptation hypothesis and how the structure and frequency of bird songs relate to habitat differences. Each focal species study contributes to our knowledge of avian communication in different habitats, but our sample of birds is still highly skewed towards the temperate region and we do not know if temperate patterns will be mirrored in the tropics. When we consider that there are many more species of tropical birds than temperate birds this discrepancy is even more conspicuous; more studies must be conducted on tropical birds if we are to understand environmental influences on communication in birds.

CONCLUSIONS AND FUTURE DIRECTIONS

The evidence for habitat-related differences in bird song structure and transmission is mixed, whether using large-scale surveys or intense investigations of one species. Some studies show clear relationships between habitats and bird song, whereas other studies show glaring contradictions. Reasons for these mixed results include inconsistent methodologies and the fact that multiple factors influence the evolution of song structure beyond the natural environment (see Table 1 and "Trends" section, above). One way we can help to improve the consistency of findings in future Neotropical work is to use comparable methods. This overview highlights a vast number of studies in order to summarize the numerous methods used to investigate transmission and bird song, with an emphasis on the most common and preferred methods. It also draws attention to some specific studies that should be conducted to advance our understanding of the structure and transmission of bird song in relation to the natural environment.

As a summary: 1) While many sound transmission studies have been previously conducted in temperate and tropical habitats, they continue to be useful additions to focal species studies because they establish a reference level of attenuation and degradation occurring in the habitats under study. 2) Survey studies are important for understanding large-scale patterns of habitat-related differences in bird song and the acoustic adaptation hypothesis. A survey including several hundred species across several countries would conclusively demonstrate patterns in the structure of bird song between forest and grassland habitats in tropical and temperate areas. On a smaller scale, surveys comparing tropical bird song to temperate bird song should be conducted to understand if the currently perceived differences in song from these two regions actually exist. All surveys should take body size and phylogeny into account; other variables such as ambient noise and territory size should be included when possible. 3) Focal species studies can provide further insight into the applicability of the acoustic adaptation hypothesis and the evolution of song structure. Within the four categories of focal species studies, transmission studies and playback studies may be more valuable than descriptive studies. While descriptive studies can demonstrate interesting differences in the song structure of one species between different habitat types, it is difficult to demonstrate that these song differences are related to their environment rather than genetics, social learning or other factors. Song transmission studies are useful because they help us understand how songs transmit, but the are only relevant to the acoustic adaptation hypothesis when they are repeated in more than one habitat. In contrast, reciprocal transmission studies are very informative because they test the transmission of songs from multiple habitats including the native habitats from which those songs were acquired. Reciprocal transmission studies are therefore important in understanding if differences in bird song between different habitats are actually related to the transmission of their songs in those habitats. The behavioral element introduced into studies of song transmission by playback and response experiments is valuable because it helps us understand whether differences in song transmission are biologically relevant and actually influence the behavior of birds. An ideal series of studies might include elements of sound transmission to understand the general patterns of sound modification by the environment, followed by focal species studies such as descriptive, song or reciprocal transmission, and playback and response. Using multiple approaches and including many variables in addition to habitat within one study will help create a more thorough picture of the structure of song in relation to transmission in different habitats.

In conclusion, large-scale survey studies will help to elucidate the influence of habitat on the structure and transmission of bird song in temperate and tropical habitats. Those focused on specific Neotropical species continue to increase the breadth and depth of our knowledge concerning the evolution of avian communication in the Neotropics. I hope Neotropical ornithologists will use this review as a reference when developing their own approaches, and use common and widely accepted measures and techniques. In doing this, findings from future studies will be comparable to each other and can be pooled to create a larger understanding of avian communication in the Neotropics. Much work remains to be done if we are to eliminate the discrepancy between the knowledge of tropical and temperate bird species. Moreover, there are conservation biology motivations for understanding current habitat-related patterns of song structure and transmission: If birds are adapted to communicate in their historical habitats, changes to ecosystems may have implications for avian communication. With increasing ill effects of anthropogenic activity in tropical environments, it is exceedingly important to understand how changes to natural environments may interfere with current communication patterns of Neotropical species.

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