

The Evolution of Communication in
a Complex Acoustic Environment

David A. Luther

A dissertation submitted to the faculty of the University of
North Carolina at Chapel Hill in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
Curriculum of Ecology

Chapel Hill
2008

Approved by:
Haven Wiley
Peter White
Joel Kingsolver
Rob Bierregaard
Martin Doyle

Abstract

DAVID A. LUTHER: The Evolution of Communication in a Complex Acoustic Environment
(Under the direction of Haven Wiley)

Animals use communicatory signals for species recognition, mate choice, and territory defense. In many cases, communication occurs in the presence of other species with similar signals, which can make it difficult to discriminate conspecific from heterospecific signals. To avoid interference from syntopic signals, species should partition communication space. I studied partitioning of acoustic space in the dawn chorus of birds in the Amazon basin, an example of communication in high levels of heterospecific background noise.

My research analyzed bird songs to determine whether the timing of signal transmission, the structure of signals, or both, serve to partition the acoustic space among different species. I used a combination of acoustic censuses and field experiments to investigate acoustic partitioning. With the censuses, I documented the times and places at which species sing, and I measured the features of each species' song to determine their locations in acoustic space. Playback experiments in the field enabled me to test predictions about partitioning of both acoustic signal space and acoustic perceptual space.

The analyses of the acoustic censuses revealed that songs of species that used the same forest stratum and sang during the same 30-min intervals had more dispersed signals than other species. The first experiment indicated that signalers and receivers coordinate the timing of production and reception of signals within the dawn chorus. The

second experiment revealed that, although the partitioning of acoustic signal space was disjunct, with gaps between nearest species' signals, the partitioning of acoustic perceptual space was saturated. Since signals are degraded as they travel through the environment, receivers must respond to degraded signals mixed with background noise. As a consequence, receivers should allow for more variation in signals than signalers include at the source.

The results of these censuses and experiments allowed me to examine the influence of background noise from heterospecific species on the evolution of acoustic communication. It is the first study to investigate acoustic perceptual space in a multi-species community. The results indicate that signalers and receivers have evolved distinct strategies to reduce errors in recognizing conspecific signals.

DEDICATION

I dedicate this work to my wife Amy whose love and support have sustained me through this process. I'd also like to dedicate this to my parents for giving me a passion for natural history. Finally I'd like to dedicate this research to the tropical forests of the world for inspiring my curiosity.

TABLE OF CONTENTS

LIST OF TABLES.....	vii
---------------------	-----

LIST OF FIGURES.....	viii
----------------------	------

Chapter

I. Sources of Background Noise and Animal Communication.....	1
Introduction.....	1
Sources of background noise.....	4
Signaler adaptations to background noise.....	10
Adaptations to environmental structure.....	15
References.....	19
II. The acoustic community and its influence on signal evolution: bird song in the neotropics.....	24
Introduction.....	25
Methods.....	27
Results.....	36
Discussion.....	38
References.....	47
III. Experimental evidence of temporal partitioning in the perception and production of songs in a neotropical dawn chorus.....	61
Introduction.....	62
Methods.....	66
Results.....	70

Discussion.....	71
References.....	75
IV. Acoustic signal space and perceptual space: A comparison in a complex neotropical avifauna.....	82
Introduction.....	83
Methods.....	85
Results.....	91
Discussion.....	94
References.....	99
V. Conclusion.....	111
APPENDIX A List of species in the acoustic community.....	116

LIST OF TABLES

Table

2.1 Principal component loadings for acoustic properties of avian songs.....	52
3.1 Principal component loadings for behavioral responses to playback experiments.....	79
4.1 Parameters of synthesized songs.....	102
4.2 Principal component loadings for behavioral responses to playback experiments.....	103
4.3 Comparison of models.....	104

LIST OF FIGURES

Figure

2.1 Spectrogram of <i>Piprites chloris</i> song.....	53
2.2 Songs of 83 species in two dimensional acoustic space.....	54
2.3 Dispersion of songs in acoustic space.....	55
2.4 Euclidean distance between songs of congeners and random species.....	56
2.5 Euclidean distance between songs of family members and random species..	57
2.6 Songs in the same and different stratum.....	58
2.7 Songs in the inner and outer quartiles of the community acoustic space.....	59
2.8 Vocal activity and distance from the center of acoustic space.....	60
3.1 Mean responses to playback treatments.....	80
3.2 Strength of response to playback treatments.....	81
4.1 Sonogram of synthesized songs.....	105
4.2 Mean responses to playback treatments.....	106
4.3 Strength of response to playback treatments.....	107
4.4 Mean species responses to different song morphs.....	108
4.5 Logistic regression of behavioral responses.....	109
4.6 Mean responses in signal and perceptual space.....	110

SOURCES OF BACKGROUND NOISE AND ANIMAL COMMUNICATION

ABSTRACT

Animals rely on long-range communication for species recognition, mate selection, and territorial defense, but background noise from the environment can constrain their communication. Background noise from both biotic and abiotic sources is ubiquitous. In general, noise from abiotic sources has energy mostly below 1 kHz while arthropods tend to produce sounds in the 4 – 10 kHz range. In contrast, most birds and mammals in forests have vocalizations with frequencies between 1 and 4 kHz. There are several ways that signalers could improve the efficiency of their signals to counteract the constraints of background noise. Signalers could make long-term and short-term signal adjustments to increase the detectability of their signals. These adjustments can include increases in contrast between signals and noise or increases in redundancy or intensity of signals. This study reviews the sources of background noise and their influence on animal communication in terrestrial environments.

INTRODUCTION

Animals rely on long-range communication for species recognition, mate selection, and territorial defense, but background noise from the environment can constrain their communication. A receiver often must detect a signal or discriminate between signals in the presence of irrelevant but similar energy in the environment (Bradbury &

Vehrencamp 1998; Brenowitz 1982; Ryan & Brenowitz 1985; Wollerman 1999). The maximum distance at which a receiver can separate a signal from noise limits the possibility of communication to a particular area around the signal. This area, in which a signal can be detected and discriminated by the receiver, is the active space of the signal (Brenowitz 1982).

Many of the factors that determine the active space of a signal have been well studied in the acoustic communication of birds. There have been comprehensive reviews of the physical influences on acoustic signal transmission, including attenuation with increasing distance from the signaler (Morton 1975; Naguib & Wiley 2001; Richards & Wiley 1980; Wiley & Richards 1982). It is clear that when a signal's amplitude is reduced to a level equal to the sensory threshold of the receiver, the maximum transmission distance has been reached (Klump 1996). However, the physical environment, amplitude of a signal, and sensory thresholds are not the only factors that influence the distance at which a signal can be detected. Background noise is another major determinant of the active space of a signal.

Background noise affects the active space of a signal because it influences both the detection and discrimination of a signal by the receiver (Wiley 1994; Wiley 2006; Wiley & Richards 1982). Detectability is a measure of a receiver's ability to separate a signal from background noise, whereas discriminability is the ability to separate two signals. Background noise is any energy in the environment that is irrelevant to the communication between a signaler and a particular receiver. Background noise is ubiquitous in natural environments from both biotic and abiotic sources. Sources of background noise include conspecific individuals, related heterospecific species, and other organisms, as well as physical features in the environment, such as wind and water.

The intensity and nature of background noise have important consequences for signal discrimination. For example, background noise that is loud, near the receiver, and similar to the signal creates greater problems than noise that is quiet, distant and dissimilar (Bradbury & Vehrencamp 1998).

To avoid the negative effects of acoustic interference, signalers should evolve signals that contrast with the background noise of their environment (Endler 1993; Miller 1982; Wiley 1994; Wiley 2006). Since the ability to communicate is limited by the distance over which a signal can be detected by a receiver, and background noise can constrain this distance, background noise has the potential to produce strong selection on the evolution of animal communication. Thus background noise is expected to impose selection on acoustic signals that could lead to evolutionary changes in the structure of signal features (Bradbury & Vehrencamp 1998; Brenowitz 1982; Klump 1996; Ryan & Brenowitz 1985; Wollerman 1999; Wollerman & Wiley 2002b).

To date there have been thorough reviews of signal transmission through different habitats (Wiley and Richards 1982) and detection of signals in noise (Klump 1996; Brumm and Slabberkoorn 2005), but there is still not a comprehensive review of the sources of background noise that effect acoustic communication. The aim of this study is to review the sources of background noise and their influence on animal communication in terrestrial environments.

SOURCES OF BACKGROUND NOISE

Physical environment

The physical environment provides many sources of background noise. Wind, rivers, and rain produce relatively continuous background energy over a wide band of frequencies. All of these sources generate relatively low frequency sound that can present a substantial source of interference with acoustic signals. Rivers and waterfalls usually produce constant sound with peak frequencies below 1 kHz (Brumm & Slabbekoorn 2005) but noise above 1 kHz can be substantial (Brumm & Slater 2006). Animals that vocalize near these sources of noise face the constant challenge of transmitting their signals in the presence of potentially high-amplitude noise.

Wind and air turbulence passing over vegetation are also major sources of background noise. Wind-generated noise is greatest at low frequencies. Generally the most intense frequencies are under 200 Hz, and wind does not usually contribute much noise at frequencies above 2 kHz (Ellinger & Hodl 2003). In general there is less wind in forests than over open grasslands. Consequently there are lower intensities of wind-generated noise within a forest and higher intensities over grasslands (Morton 1975; Ryan & Brenowitz 1985). Ellinger and Hodl (2003) measured background noise at 5 heights in a Venezuelan tropical rainforest and found that wind-generated noise was most pronounced in the midstory and canopy. Regardless of habitat-type, wind levels are usually lowest in the early morning and increase in the middle of the day and afternoon (Ellinger & Hodl 2003). Thus background noise from wind tends to increase during the course of the morning (Brenowitz 1982; Morton 1975; Ryan & Brenowitz 1985; Waser & Waser 1977).

Rain occurs regularly in all habitats, except deserts, and is another source of background noise that is likely to constrain acoustic communication. Lengagne and Slater (2002) studied the background noise caused by rain in a European broadleaf forest, during the winter, and found that rain produced noise with frequencies primarily between 0 and 5 kHz. These frequencies overlap the acoustic signals used by 94% of European bird species and most amphibian and mammal species as well. Thus rain provides a significant source of background noise that can interfere with the acoustic communication of most species of terrestrial vertebrates. On the other hand, rain is usually most prevalent during the middle of the day and during afternoons (Waser & Waser 1977; Wiley & Richards 1982), so communication at night and during the morning are less likely to be interfered with by rain.

Insect noise

The primary sources of continuous high-frequency noise in terrestrial habitats are insects. Major contributors include orthopterans and cicadas, which tend to produce signals with frequencies of 4 kHz or higher. Different habitats are likely to have different insect communities, which in turn have distinct assemblages of vocalizations.

To investigate the spectral differences in background noise between two adjacent habitats Slabbekoorn (2004) recorded background noise in rainforest and gallery forest surrounded by savanna in Cameroon. During hourly acoustic samples, 1.5 m above the ground, from 0700 – 1700 at 14 locations across the two habitats, gallery forest had noise levels that were about equal through out the frequency spectrum. One exception was a band of loud insect noise above 6.0 kHz, which was loudest at 7.0 kHz, and present most

of the day. In east African gallery forest, Waser and Brown (1986) found similar patterns of background noise, with insects producing sounds primarily between 6 kHz and 8 kHz.

In comparison, Slabbekoorn's (2004) rainforest sites had insect noise in the 4 – 8 kHz range with higher amplitudes than those found in the adjacent gallery forest. In addition, rainforest sites had 2 frequency bands dominated by insects. Large cicadas occupied the lower frequencies, between 3.0 kHz and 4.5 kHz, while noise from other insect species occupied the frequencies between 5 kHz and 7 kHz. In lowland rainforest of Venezuela Ellinger and Hodl (2003) measured background noise for 24 hour periods at 3 different sites during 5 different months. The insect chorus at these sites occupied frequencies between 3.15 kHz and 12.5 kHz, with the highest amplitudes between 5 and 7 kHz.

Researchers have also investigated insect noise at different heights in a forest. Ryan and Brenowitz (1985) recorded background noise in Panama both near the ground and 1.5 m above the ground for several minutes at 0600 h, 0700 h, and 0800 h. They determined that noise levels on the ground and at 1.5 m above the ground were indistinguishable. Ellinger and Hodl (2003) recorded background noise at 5 different heights between ground level and the canopy (0.45 m, 2.5 m, 5 m, 12.5 m, and 21 m) and found that insect noise tended to decrease with height but did not differ significantly with height. From these few studies it appears that insect noise is often equally loud at different heights in a forest.

There can be large amounts of variation in the amplitudes and frequencies of the background noise during different times of day (Ellinger and Hodl 2003). Ellinger and Hodl (2003) found that insects reached their highest intensities during dusk between 1830 and 2000 h at frequencies between 3.15 kHz and 12.5 kHz. Cicadas also had a synchronized chorus just before the avian dawn chorus at sunrise and again later in the

morning, also described by Young (1981). Canopy insects in a Bornean lowland rainforest also produced an intense insect dusk chorus (Reide 1998). In addition Reide observed that the dusk chorus between 1800 h and 1900 h was temporally organized with cicadas (Cicadae) calling during the first 30 min and crickets (Grylloidea) and frogs (Anura) vocalizing during the second 30 min. While the dusk chorus of insects and frogs seemed to be temporally synchronized, diurnal and nocturnal species exhibited less precise temporal synchronization. Slaberkooorn (2004) observed that large cicadas called primarily between 0900 and 1200 in the morning and again just before dusk. He also noted that other diurnal insects at rainforest sites started calling early in the morning and that the frequency of the noise increased throughout the morning until it leveled off at midday. Ellinger and Hodl (2003) observed that during the night there was a continuous level of noise from insects in the frequencies between 5 – 6.3 kHz. In addition crickets produced short peaks of low intensity at 3.15 kHz during dawn and dusk.

Although so far we have limited information about the hourly and daily patterns of insect noise, we have even less information about seasonal variation. Studies in Ecuador and Cameroon have anecdotally described greater background noise from insects in the wet season as opposed to the dry season (De la Torre & Snowdon 2002; Slabbekoorn 2004), but details of the differences were not provided.

From the few studies thus far on background noise generated by insects there seem to be consistent spectral profiles across similar habitats. These patterns suggest consistency in noise characteristics related to habitat type, which can cautiously be applied at broad scales across continents. However it is difficult to compare studies because each sampled on different schedules. So far researchers have only scratched the surface in describing

hourly, daily, and seasonal variation in background noise from insects, and future studies are sure to find interesting results.

Heterospecific and conspecific acoustic signals

One result of communicating in the presence of background noise from another species can be acoustic interference, in which similar heterospecific signals reduce the detectability and discriminability of both species' signals. Furthermore many animals communicate in situations, such as frog choruses and avian dawn choruses, that make it especially difficult to discriminate conspecific from similar heterospecific signals (Bremond 1978; Brumm & Slabbekoorn 2005; Gerhardt & Huber 2002; Pfennig 2000; Wiley 1994; Wollerman & Wiley 2002b). In addition to the problem of detecting a conspecific signal among sounds of different species, some species, such as birds that breed in colonies, also face the challenge of detecting individual signals in the presence of a multitude of conspecific signals (Jouventin & Aubin 2002; Jouventin et al. 1999). Thus background noise from heterospecific species and conspecific individuals can present problems for the correct detection and discrimination of signals.

In temperate habitats many species have denser populations than those in species-rich tropical habitats. As a consequence acoustic interference from conspecific signals might be greater in temperate communities than in tropical communities. Since songs of the same species share the same spectral features, they can be especially effective at causing acoustic interference. As a result many species exhibit a variety of tactics such as chorusing and call alternation, to avoid acoustic interference from conspecific individuals. In contrast, tropical communities are dominated by acoustic competition

between species other than those of interest to a particular receiver. A consequence might be more stereotyped signals of birds in tropical forests.

Receivers face different problems of signal detection and discrimination in the presence of continuous background noise as compared to episodic noise. For example, the avian dawn chorus consists of brief discontinuous events of high intensity. The majority of diurnal avian species vocalize during the avian dawn chorus, which makes it an excellent example acoustic communication in the presence of high levels of heterospecific background noise. It usually begins 15 to 30 minutes before sunrise and continues for 2 to 3 hours after sunrise. During the dawn chorus, species differ in the timing of their singing (Allard 1930; Allen 1913), and in the tropics many species only vocalize at specific times in the morning. For example, many species of tinamou (Tinamidae), puffbird (Bucconidae), and woodcreeper (Dendrocolaptidae) only sing at or before sunrise, while other species begin their vocal activity later in the morning (Blake 1992; Parker 1991). One potential explanation for these differences in singing times is the avoidance of acoustic interference from spectrally similar signals.

Summary

In summary abiotic sources of noise produce background noise predominantly at low frequencies. Rivers provide a relatively constant source of noise whereas noise from wind and rain are generally greatest at certain times of day. In general, noise from wind and vegetation increases around midday and can remain high during the afternoon and dusk (Ellinger & Hodl 2003; Henwood & Fabrick 1979).

In general, noise from abiotic sources has energy mostly below 1 kHz while arthropods tend to produce sounds in the 4 – 10 kHz range. Consequently there is a

relatively quiet window between 1 and 4 kHz in many terrestrial environments. This window could explain why many birds and mammals in forests have vocalizations with frequencies between 1 and 4 kHz (Morton 1975; Ryan and Brenowitz 1985; Waser and Waser 1977). Ellinger and Hodl (2003) found 3 periods of relatively intense background noise in the course of a day: the dawn chorus of birds, air turbulence at midday, and the dusk and night chorus of Orthoptera and Cicadidae.

Insects that call persistently during dusk and the first half of the night produce nearly constant sound. In contrast, the dawn chorus of birds consists of sporadic sounds. Previous studies suggest that dawn choruses in primates (Waser and Brown 1986), cicadas (Young 1981), and birds (Brenowitz 1982; Henwood and Frabrick 1979) might take advantage of lower background noise from other sources at dawn. Other hypotheses for the timing of the avian dawn chorus include optimal conditions for sound transmission, poor feeding conditions (Catchpole & Slater 1995; Kacelnik & Krebs 1983).

SIGNALER ADAPTATIONS TO BACKGROUND NOISE

There are several ways that signalers could improve the efficiency of their signals to counteract the constraints of background noise. Signalers could make long-term and short-term signal adjustments to increase the detectability of their signals. These adjustments can include increases in contrast between signals and noise, or increases in redundancy or intensity of signals. A signal's contrast with background noise could be increased by spatial or temporal separation of signal and noise or by modification of the features of a signal. For instance, greater redundancy in the structure of a signal could

improve detection and discrimination by receivers. An increase in signal amplitude could usually increase contrast with background noise (Wiley 2006).

Contrast

To increase the contrast between a signal and background noise, signalers can adjust the frequency of a signal, their spatial location, or the time of signal transmission (Klump 1996; Brumm and Slabbekoorn 2005). An increase in the contrast with background noise is especially important when signals share the same frequency range (Bremond 1978; Lohr et al. 2003). For example animals that live in particularly noisy environments, such as those near rushing rivers and waterfalls, have acoustic signals in frequency ranges that reduce masking interference from the background noise. Dubois and Martens (1984) found that frogs and birds living near waterfalls and torrents produced high-pitched vocalizations in narrow frequency bands that contrast with the background noise of the rushing water. These adjustments increase the active space of a species' signal thus opportunities for correct detection and discrimination of their signals.

Slabbekoorn and Smith (2002) investigated environmental features, such as insect noise, that could influence song divergence in the Little Greenbul, *Andropadus virens*, in two adjacent habitats. In rainforest this species sings notes of relatively low frequency whereas in ecotone habitat, it uses relatively high-frequency notes. In rainforest, the frequencies of higher-pitched notes were presumably masked by high levels of background noise from insects, but these same frequencies were not masked in the ecotone. There was an association between the Little Greenbul's use of low frequency notes and the consistently low noise levels in the same frequency range in rainforest.

They concluded that background noise in different spectra in the two habitats most likely led to song divergence in the little greenbul in each habitat.

Heterospecific signals, another common source of background noise, also have the potential to disrupt intraspecific communication (Schwartz & Wells 1983; Wollerman & Wiley 2002a). Since signals can interfere with each other, features of signal structure that differ distinctly from those of other species should have advantages for conspecific recognition (Emlen 1972; Falls 1963; Marler 1960; Nelson 1988; Nelson & Marler 1990). Since species-specific signals are important for species recognition and mate choice, species should partition acoustic space to avoid acoustic interference from syntopic signals. Theory predicts that the competition for acoustic space should result in signal divergence, which would increase signal distinctiveness and opportunities for correct signal discrimination (Marler 1960; Miller 1982). To date there has been no direct evidence of signal partitioning of the spectral features of signals.

Because sound intensity attenuates with increased distance from the source signalers can reduce interference from background noise by moving away from its source. Spatial separation can result in a spatial release from acoustic interference and in an improved signal-to-noise ratio for the receiver (Klump 1996). If two syntopic species have similar vocalizations, spatial separation could reduce confusion. If separation is large enough, one species could be competitively excluded from the community. If species separate spatially, receivers in effect have an extra recognition cue to correctly identify conspecific signals. Therefore vertical separation could facilitate coexistence through the avoidance of direct competition.

Noise in the natural environment is rarely continuous (Klump 1996). By adjusting the timing of signal transmission to take advantage of gaps in noise, signalers can increase

the contrast of their signals with background noise and reduce or avoid acoustic interference from heterospecific signals (Ficken et al. 1974; Greenfield 1988; Narins 1992; Popp et al. 1985). A few studies have provided evidence that birds actively avoid acoustic interference by short-term temporal changes in delivery of songs, over seconds and minutes (Cody & Brown 1969; Ficken et al. 1974; Popp et al. 1985).

There is some evidence to suggest that singing by birds is affected by other species in their habitat. Cody and Brown (1969) studied the Wrentit, *Chamaea fasciata*, and Bewick's Wren, *Thryomanes bewickii*, two abundant species in chaparral habitat in California, and found that birds adjusted their diurnal rhythm of song production to avoid singing at the same time. Ficken et al. (1974) confirmed this observation in 2 forest species, the Red-Eyed Vireo, *Vireo olivaceus*, and Least Flycatcher, *Empidonax minimus*. The flycatchers avoided starting songs while red-eyed vireos were singing, then sang between red-eyed vireo songs. Popp et al. (1985) studied 4 forest species and found that they also avoided starting songs while other species were singing and confirmed this observation with playback experiments with Ovenbirds, *Seiurus aurocapillus*. The ovenbirds adjusted their singing pattern by singing immediately after the playback song ended and thus avoided overlap with other species' songs. This phenomenon has also been studied among conspecific individuals. Wasserman (1977) demonstrated that male White-Throated Sparrows, *Zonotrichia albicollis*, did not start songs when other male White-Throated Sparrows were singing. Instead they waited to sing until the other males were quiet. In further playbacks ovenbirds also waited until neighboring individuals of the same species were quiet before they started singing (Ficken 1985).

A larger temporal shift has been documented for the katydid *Neoconocephalus spiza*, which alters the time of calling from nocturnal to diurnal in the presence of acoustic

interference from other species (Greenfield 1988). In a study of calling by Tawny Owls, *Strix aluco*, during rain, Lengagne and Slater (2002) found the active space was reduced from 118 ha during dry weather to 1.7 ha during rain, a 69-fold decrease. Presumably as a result, tawny owls did not call during nights with heavy rain.

Signal redundancy

Redundancy is a common feature of animal signals. Signal detection theory predicts that increased redundancy can increase information transfer in the presence of noise (Wiley 1994). Potash (1972) tested this prediction by exposing Japanese Quails, *Coturnix japonica*, to increased levels of noise in the laboratory. He found that these quail increased the number of syllables with increased noise levels. Increased signal redundancy in the presence of background noise has also been demonstrated in King Penguins, *Aptenodytes patagonica*, (Jouventin et al. 1999) and Chaffinches, *Fringilla coelebs*, (Brumm and Slater 2006) in the field. In each case signalers extended the length of signals in the presence of environmental noise.

Amplitude

Signalers face the challenge of broadcasting signals so that they are heard above background noise. Regulating vocal amplitude, by increasing sound intensity when background noise is high and decreasing it when background noise is low, can increase the efficiency of acoustic signals. This process, known as the Lombard effect, has been reported to occur across taxa from humans and monkeys (Lombard 1911; Sinnott et al. 1975) to birds and frogs (Lopez et al. 1988; Pytte et al. 2003). The Lombard effect would serve to maintain a signal-to-noise ratio favorable for signal perception. Most of these

studies have documented this phenomenon in relation to background noise in the laboratory, but recently it has also been documented in natural conditions. Brumm (2004) found that male Nightingales (*Luscinia megarhynchos*) in noisier territories with more traffic noise sang louder songs than birds at less noisy locations. Males adjusted the amplitude of their songs depending on the amplitude of the background noise.

ACOUSTIC ADAPTATIONS TO ENVIRONMENTAL STRUCTURE

Acoustic signals used for long-range communication are adapted to optimize their transmission distance under the environmental pressures that act on sound transmission in their native habitat (Morton 1975). As a consequence species and populations that live in habitats with different acoustic properties should exhibit predictable differences in their song structures. Important factors that drive song structure adaptations are signal attenuation and degradation during sound transmission. Attenuation refers to a decrease in a signal's amplitude, which is caused in part by sound absorption and scattering by air and vegetation. Signal degradation refers to changes in spectral and temporal characteristics that affect the signal between the time that the sender transmits the signal and the receiver receives the signal.

Naguib and Wiley (2001) reviewed 7 processes that alter the structure of signals during propagation: the ground effect (within 1 meter of the ground), spherical attenuation, attenuation by atmospheric absorption, attenuation by scattering of directional sounds, accumulation of reverberation from objects near the path of transmission, accumulation of irregular amplitude fluctuations from non-stationary turbulence in the atmosphere, and diffraction of sound by temperature and other velocity gradients in the environment. Together all 7 effects create 4 kinds of changes in signals as

they travel from signaler to receiver: overall attenuation, frequency-dependent attenuation, reverberation, and fluctuation in amplitude. Frequency-dependent attenuation occurs when higher frequencies attenuate faster than lower frequencies. The physics of frequency-dependent attenuation suggest that for communication more than a meter above the ground, low frequencies, minimize attenuation regardless of habitat structure.

Reverberations result from sound scattered by reflective surfaces such as foliage, tree limbs and trunks and they are strongly associated with closed habitats (Wiley and Richards 1982). Reverberations blur the distinction between notes separated by short intervals, since the interval becomes filled with echoes that obscure rapid amplitude modulation. Amplitude modulations result from refraction as sound passes through pockets of air of differing temperature and velocity. They are associated with open habitats, which are less sheltered from wind and temperature changes than closed habitats. Since reverberations have stronger effects in forests and amplitude fluctuations have stronger effects in open areas, such as grasslands, we expect song structure to diverge in these different habitats.

Song structure adapts to local habitat structure in both frequency and temporal patterning (Morton 1975; Ryan and Brenowitz 1985). For example, songs with short notes and few notes repeated at long intervals are less affected by reverberations in forests. In fact, forest birds have songs with shorter notes, fewer frequency modulations, and longer intervals between notes compared with birds in open habitats (Wiley 1991). Songs in dense forests have especially low frequencies, a narrow frequency range, and simpler notes. Conversely, songs in open habitats such as grasslands are characterized by

relatively high frequencies, wider frequency ranges, complex notes, and short inter-note intervals compared with songs in forests.

Acoustic adaptation to different habitats can lead to song divergence and reproductive isolation between populations in different habitats. Patten et al. (2004) studied two subspecies of Song Sparrow, *Melospiza melodia*, in adjacent but structurally different riparian habitats. They found that habitat structure was a good predictor of song structure. Songs in more open habitat had higher frequencies and more rapidly repeated notes than songs produced in denser riparian vegetation. Playback experiments with females from each habitat revealed that females preferred songs from their same habitat. Analysis of genetic variation in microsatellite loci confirmed that there was little gene flow between the two subspecies.

Acoustic adaptation to habitats can also apply to variation within major habitats. Sound attenuation and reverberations are greatest in the densely vegetated understory and canopy as opposed to the relatively open midstory (Marten & Marler 1977). Reverberations are reduced at frequencies between 2 and 5 kHz in the relatively cluttered understory and canopy (Marten et al 1977, Ellinger and Hodl 2003). Since there are notable differences in how sound travels through different forest strata, we can predict that acoustic signals should optimize song transmission in these strata. Nemeth et al. (2001) tested this prediction in 5 sympatric species of antbirds that sing from different perch heights in a neotropical forest. They found that each species' song propagated with fewer reverberations and less excessive attenuation in the strata in which they normally sang compared to other strata. Similarly Seddon (2005) found that antbird species in different strata had song structures suited for the strata in which they sing. After

correcting for body size, bill morphology, and phylogenetic relatedness, Seddon (2005) found that antbirds in densely vegetated strata produced lower-pitched songs than species in the more open midstory.

In summary song features correlate with differences in habitat acoustics. Songs are selected for traits that increase the active space of a signal in a species' habitat. The selection on species' signals to match the transmission characteristics of their physical environment leads to convergence among sympatric species. The different effects of reverberations and amplitude modulations from the physical environment primarily affect the timing and complexity of notes. These differences can lead to divergent song structures in different habitats. If selection on song is strong enough it can lead to assortative mating between habitats and potentially affect gene flow between populations in different habitats. Differences in adaptation to environmental acoustics could lead to speciation.

REFERENCES

- Allard, H. A. 1930 The first morning song of some birds of Washington, D.C.: its relation to light. *American Naturalist* **64**, 436-469.
- Allen, F. H. 1913 More notes on the morning awakening. *Auk* **30**, 229-235.
- Blake, J. 1992 Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *Condor* **94**, 265-275.
- Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*: Sunderland, Mass. : Sinauer Associates.
- Bremond, J. C. 1978 Acoustic competition between the song of the wren (*Troglodytes troglodytes*) and the songs of other species. *Behaviour* **65**, 89-98.
- Brenowitz, E. A. 1982 The active space of red-winged blackbird song. *Journal of Comparative Physiology* **147**, 511 - 522.
- Brumm, H. 2004 The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* **73**, 434-440.
- Brumm, H. & Slabbekoorn, H. 2005 Acoustic communication in noise. In *Advances in the Study of Behavior*, pp. 151-209.
- Brumm, H. & Slater, P. J. B. 2006 Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology* **60**, 475-481.
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Cody, M. L. & Brown, J. H. 1969 Song asynchrony in neighboring bird species. *Nature* **222**, 778-780.
- De la Torre, S. & Snowdon, C. T. 2002 Environmental correlates of vocal communication of wild pygmy marmosets, *Cebus pygmaea*. *Animal Behaviour* **63**, 847-856.
- Dubois, A. & Martens, J. 1984 A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *Journal fur Ornithologie* **125**, 455-463.
- Ellinger, N. & Hodl, W. 2003 Habitat acoustics of a neotropical lowland rainforest. *Bioacoustics* **13**, 297-321.

- Emlen, S. T. 1972 An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* **41**, 130-171.
- Endler, J. A. 1993 The color of light in forests and its implications. *Ecological Monographs* **63**, 1-27.
- Falls, J. B. 1963 Properties of bird song eliciting response from territorial males. In *Proceedings of the International Ornithological Congress*, vol. 13, pp. 259-271.
- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974 Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* **183**, 762 - 763.
- Gerhardt, H. C. & Huber, F. 2002 *Acoustic communication in insects and anurans : common problems and diverse solutions*: Chicago : University of Chicago Press.
- Greenfield, M. D. 1988 Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* **36**, 684-695.
- Henwood, K. & Fabrick, A. 1979 A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *American Naturalist* **114**, 260-274.
- Jouventin, P. & Aubin, T. 2002 Acoustic systems are adapted to breeding ecologies: Individual recognition in nesting penguins. *Animal Behaviour* **64**, 747-757.
- Jouventin, P., Aubin, T. & Lengagne, T. 1999 Finding a parent in a king penguin colony: The acoustic system of individual recognition. *Animal Behaviour* **57**, 1175-1183.
- Kacelnik, A. & Krebs, J. R. 1983 The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* **83**, 287-309.
- Klump, G. M. 1996 Bird communication in the noisy world. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 321 - 338. Ithaca, NY: Cornell University Press.
- Lengagne, T. & Slater, P. J. B. 2002 The effects of rain on acoustic communication: Tawny owls have good reason for calling less in wet weather. *Proceedings of the Royal Society Biological Sciences Series B* **269**, 2121-2125.
- Lohr, B., Wright, T. F. & Dooling, R. J. 2003 Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour* **65**, 763 - 777.
- Lombard, E. 1911 Le signe de l'elevation de la voix. *Annales de Maladies de L'oreille et du Larynx* **37**, 101-119.

- Lopez, P. T., Narins, P. M., Lewis, E. R. & Moore, S. W. 1988 Acoustically induced modification in the white-lipped frog, *Leptodactylus albilabris*. *Animal Behaviour* **36**, 1295-1308.
- Marler, P. 1960 Bird songs and mate selection. In *Animal sounds and communication*, vol. 7 (ed. W. E. Lanyon & W. N. Tavolga), pp. 348-367. Washington D.C.: American Institute of Biological Sciences.
- Marten, K. & Marler, P. 1977 Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology* **2**, 271-290.
- Miller, E. H. 1982 Character and variance shift in acoustic signals of birds. In *Acoustic communication in birds*, vol. 1 (ed. D. E. Kroodsma & E. H. Miller), pp. 253-295. New York: Academic Press.
- Morton, E. S. 1975 Ecological sources of selection on avian sounds. *American Naturalist* **109**, 17-34.
- Naguib, M. & Wiley, R. H. 2001 Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour* **62**, 825-837.
- Narins, P. M. 1992 Evolution of anuran chorus behavior neural and behavioral constraints. *American Naturalist* **139**, S90-S104.
- Nelson, D. A. 1988 Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* **106**, 158-182.
- Nelson, D. A. & Marler, P. 1990 The perception of bird song and an ecological concept of signal space. In *Comparative perception, Vol. 2, Complex signals*, vol. 2 (ed. W. C. a. B. Stebbins, M.A.), pp. 443-78. New York: Wiley.
- Nemeth, E., Winkler, H. & Dabelsteen, T. 2001 Differential degradation of antbird songs in a Neotropical rainforest: Adaptation to perch height? *Journal of the Acoustical Society of America* **110**, 3263-3274.
- Parker, T. A. 1991 On the use of tape recorders in avifaunal surveys. *Auk* **108**, 443-444.
- Patten, M. A., Rotenberry, J. T. & Zuk, M. 2004 Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. *Evolution* **58**, 2144-2155.
- Pfennig, K. S. 2000 Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology* **11**, 220-227.
- Popp, J. W., Ficken, R. W. & Reinartz, J. A. 1985 Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk* **102**, 744-748.

- Potash, L. M. 1972 A signal detection problem and possible solution in Japanese quail *Coturnix japonica*. *Animal Behaviour* **20**, 192-195.
- Pytte, C. L., Rusch, K. M. & Ficken, M. S. 2003 Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*. *Animal Behaviour* **66**, 703-710.
- Richards, D. G. & Wiley, R. H. 1980 Reverberations and amplitude fluctuations in the propagation of sound in a forest - implications for animal communication. *American Naturalist* **115**, 381-399.
- Ryan, M. J. & Brenowitz, E. A. 1985 The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* **126**, 87-100.
- Schwartz, J. J. & Wells, K. D. 1983 An experimental study of acoustic interference between 2 species of neotropical tree frogs. *Animal Behaviour* **31**, 181-190.
- Seddon, N. 2005 Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* **59**, 200-215.
- Sinnott, J. M., Stebbins, W. C. a. B., M.A. & Moody, D. B. 1975 Regulation of voice amplitude by the monkey. *Journal of the Acoustical Society of America* **58**, 412-414.
- Slabbekoorn, H. 2004 Habitat-dependent ambient noise: Consistent spectral profiles in two African forest types. *Journal of the Acoustical Society of America* **116**, 3727-3733.
- Slabbekoorn, H. & Smith, T. B. 2002 Habitat-dependent song divergence in the little greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution* **56**, 1849-1858.
- Waser, P. M. & Brown, C. H. 1986 Habitat acoustics and primate communication. *American Journal of Primatology* **10**, 135-154.
- Waser, P. M. & Waser, M. S. 1977 Experimental studies of primate vocalization specializations for long-distance propagation. *Z. Tierpsychol* **43**, 239-263.
- Wasserman, F. E. 1977 Intraspecific acoustical interference in the white-throated sparrow *Zonotrichia albicollis*. *Animal Behaviour* **25**, 949-952.
- Wiley, R. H. 1991 Associations of song properties with habitats for territorial oscine birds of eastern North-America. *American Naturalist* **138**, 973-993.
- Wiley, R. H. 1994 Errors, exaggeration, and deception in animal communication. In *Behavioral mechanisms in evolutionary ecology* (ed. L. A. Real), pp. 157-189. Chicago: University of Chicago Press.

- Wiley, R. H. 2006 Signal detection and animal communication. *Advances in the Study of Behavior* **36**, 217-247.
- Wiley, R. H. & Richards, D. G. 1982 Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 131-181. New York & London: Academic Press.
- Wollerman, L. 1999 Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal Behaviour* **57**, 529-536.
- Wollerman, L. & Wiley, R. H. 2002a Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour* **63**, 15-22.
- Wollerman, L. & Wiley, R. H. 2002b Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* **52**, 465-473.
- Young, A. M. 1981 Temporal selection for communicatory optimization: the dawn-dusk chorus as an adaptation in tropical cicadas. *American Naturalist* **117**, 826-829.

THE ACOUSTIC COMMUNITY AND ITS INFLUENCE ON SIGNAL EVOLUTION: BIRD SONG IN THE NEOTROPICS

ABSTRACT

Animals use species-specific communicatory signals for species recognition, mate choice, and territory defense. In many cases, communication occurs in the presence of other species with similar signals, which can make it difficult to discriminate conspecific from heterospecific signals. Because heterospecific signals have the potential to disrupt intraspecific communication, species should partition acoustic space to avoid acoustic interference. To investigate acoustic partitioning in an environment with high levels of heterospecific background noise I studied the dawn chorus of birds in the tropics.

To characterize the acoustic community I replicated acoustic censuses during 2 hrs of the dawn chorus at both small (100 m) and medium (1 km) spatial scales and at short-term (1 hr), medium-term (2 day), and long-term (seasonal) temporal scales. I detected 82 sedentary species of birds that sang consistently throughout the censuses. 11 features from each species' song were measured and analyzed to quantify the acoustic space occupied by each species in the community. The Euclidean distances between species' songs in acoustic space were used to examine the dispersion of species' songs, the dispersion of phylogenetically related species, and the degree of crowding in the center of occupied acoustic space in comparison to the periphery. Songs of species that were in the same stratum and sang during the same 30-min intervals had the most dispersed signals.

Songs near the center of the acoustic space were more crowded than songs near the periphery. Species near the center also sang more frequently than species farther from the center. Songs of congeners and family members were not more dispersed than songs of random species. This study is a first attempt to characterize dispersion of birds' songs in a complex acoustic community and to investigate some spatial, temporal, and phylogenetic factors that influence the evolution of divergent songs.

INTRODUCTION

Species-specific signals convey important information to conspecifics that enable them to recognize each other, to make appropriate mate choice decisions, and to settle territorial disputes (Bradbury & Vehrencamp 1998). Acoustic interference from background noise should decrease the efficacy of intraspecific communication by affecting the detectability and discriminability of conspecific signals (Endler 1992). Detectability is a receiver's ability to separate a signal from background noise, whereas discriminability is the ability to separate two signals. Background noise, from both biotic and abiotic sources, is ubiquitous in natural environments. In addition, many animals communicate in aggregations, such as frog choruses and avian dawn choruses, that make it especially difficult to discriminate conspecific from similar heterospecific signals (Bremond 1978; Brumm & Slabbekoorn 2005; Gerhardt & Huber 2002; Pfennig 2000; Wiley 1994; Wollerman & Wiley 2002b). To avoid the negative effects of acoustic interference, signalers should evolve signals that contrast with the background noise of their environment (Endler 1993; Miller 1982; Wiley 1994; Wiley 2006).

Heterospecific signals are a common source of background noise (Schwartz & Wells 1983; Wollerman & Wiley 2002a). Heterospecific signals with similar features have the

greatest chance of interfering with each other and creating receiver errors. Such errors include responses to signals from different species, which could lead individuals to respond to inappropriate rivals or mates, or lack of responses to appropriate signals, which could result in additional time and risks in finding a mate or confronting a rival (Wiley 1994). Features of signal structure that differ distinctly from those of other species should have advantages for conspecific recognition (Emlen 1972; Falls 1963; Marler 1960; Nelson 1988; Nelson & Marler 1990). Thus signals might diverge in multidimensional acoustic space as defined by acoustic features, such as dominant frequency duration, number of notes, and other features that characterize the structure of a signal (Marler 1960, Miller 1982).

Nelson and Marler (1990) studied the acoustic space of a community of birds in New York and found that songs with similar song features were in close proximity in acoustic space. They also noted that the center of the community's acoustic space seemed to have more species in close proximity than the periphery. The species with songs in the center required more cues to identify conspecific songs than species with songs on the periphery of the acoustic space (Nelson and Marler 1990).

Because heterospecific signals have the potential to disrupt intraspecific communication, species should partition acoustic space to avoid acoustic interference from syntopic signals. Therefore the competition for acoustic space should result in divergence of signals (Marler 1960; Miller 1982). In addition, closely related species might be even more likely to interfere with each other's communication than less related species would. Despite the widespread occurrence of sympatric sister species, evidence for song divergence is scarce (Irwin & Price 1999).

Dawn choruses of birds in the tropics provide an example of communication in the presence of high levels of heterospecific background noise. The combination of high species diversity and a narrow window of time in which the majority of species sing increases opportunities for acoustic competition and limits possibilities for song divergence. In addition, many Amazonian forest species live in conditions with dim light and dense foliage, which obscure lines of sight. Consequently, they usually rely on acoustic signals for long-range communication. Beyond the basic species-specificity of their songs, we know little about how these songs are distributed in acoustic space and perceived in noisy acoustic environments.

In this study, I examine (1) the dispersion of species' songs in acoustic space, (2) the dispersion of phylogenetically related species in comparison to other pairs of species, (3) the dispersion of songs from the same location compared to different locations, and (4) the degree of crowding in the center of occupied acoustic space in comparison to the periphery. Overdispersed signals would indicate that selection for unambiguous species recognition has promoted coevolution of song features to improve intraspecific communication.

METHODS

Study location and acoustic censuses

This study included acoustic censuses during both the wet season (February and March) and the dry season (June and July) in 2004 at the Rio Cristalino Private Natural Heritage Reserve, 40 km north-east of the town of Alta Floresta, Mato Grosso, Brazil (9° 41' S, 55° 54' W). The Reserve is uncut lowland tropical moist forest (see Zimmer et al.

1997). The censuses were conducted at three sites, separated by 500 m to 1 km, in terra firma habitat. Each site included two points 100 m apart, and each census consisted of continuous simultaneous tape-recordings at both points. Censuses at all 3 sites were conducted three times during the wet season and four times during the dry season of 2004. Each census began 30 min before sunrise and continued for one hr. After a pause, recording resumed at 0700 and again at 0800 for 30 min (total time recorded during each census = 2 hr). The recordings were made with Sony TC D5 Pro II and Marantz PMD 222 tape recorders and Shure 33-1070D omnidirectional microphones placed 2 ± 0.1 m above ground. In this sampling design, recordings were replicated at both small (100 m) and medium (1 km) spatial scales and at short-term (1 hr), medium-term (2 day), and long-term (seasonal) temporal scales.

Acoustic community

The acoustic censuses detected songs from 137 species. This total does not include species only recorded while flying past the census points, such as parrots, hummingbirds, and nighthawks. The analyses included only species that sang during at least 1% of the total censused minutes (52 of the 5276 min of total time, a total of 82 species). Other species presumably sang too rarely to influence the acoustic community. In the majority of species males sang more often than females. Also females' songs were similar to the males and usually sung antiphonally with their mates. An exception to this pattern was the Buff-throated Woodcreeper, *Xiphorhynchus guttatus*, males and females of which had markedly different vocalizations and did not usually coordinate their songs. The analyses consequently included the complex vocalizations of both male and female *X. guttatus* as

if they were two species for a total of 83 different song patterns. For the mean mass of each species, I followed Terborgh et al. (1990) and Dunning (1993).

Acoustic analysis

In order to obtain examples of each species' songs that were as clean as possible for analyses of their acoustic features, examples were recorded with a Sennheiser ME66-K3U directional microphone and a Sony TC-D5 Pro II tape recorder in 2004 and a Marantz PMD660 digital recorder in 2006. For species detected on the acoustic censuses, but not recorded with the directional microphone, I analyzed the examples from the censuses. The tape recordings were digitized (16-bit accuracy, 22.05 kHz sampling rate, WAV format) with WildSpectra2 (version 050415, <http://www.unc.edu/~rhwiley/wildspectra.html>). One song from each of three different individuals (or when necessary from an individual at the same location but different seasons or years) was analyzed with Wildspectra1 (version 051027) (sampling rate of 22.05 kHz, frequency resolution 172 Hz, temporal resolution 5.8ms). Using the SongSignature feature of Wildspectra1, the following measures were obtained from each song (time, in milliseconds, and frequency, in Hz) (Fig. 1): (1) lowest dominant frequency, (2) highest dominant frequency, (3) overall dominant frequency, (4) song bandwidth (highest dominant frequency minus the lowest dominant frequency), (5) total number of notes, (6) song duration, (7) song rate (total number of notes divided by song duration), (8) change in song rate (ratios of the rates in each third of a song (Isler et al. 1998)), (9) complexity of the first note (the bandwidth of the note divided by the duration of the note, in turn divided by the number of inflections in the note), (10) complexity of

the last note, (11) complexity of the average note averaged (measurements from three successive notes in the first, middle, and last third of each song). The number of inflections in a note was determined from spectrograms by eye. To verify the measurements obtained with the SongSignature function of WildSpectral1, a subset of songs was also measured with traditional point-and-click methods.

Principal components analysis

Some of the acoustic features of songs were correlated with each other. To generate independent variables for the axes of acoustic space, I subjected the original acoustic features of songs to principal component analysis (PCA). Since this analysis requires variables with values for all individuals, when songs included only one note the measurements of the first note were also included as measurements for the average and last note. For songs with only two notes, the measurements of the notes were averaged to create the average measure. To normalize the total number of notes in a song I used a square-root transformation. PCA of the correlation matrix for the mean acoustic features of the 83 song patterns yielded 4 principal components (PCs) with eigenvalues greater than 1, which together explained 82 % of the variation (Table 1). PC1, explaining 40% of the variation, was positively correlated with frequency and note complexity variables. PC2 explaining 19% of the variation, was positively correlated with the number of notes and the change in rate of a song. PC3 explaining 14% of the variation, was positively correlated with duration and negatively correlated with the rate of a song. PC4 explaining 10% of the variation, was positively correlated with the number of notes and rate of a song and negatively correlated with note complexity. These 4 PCs were the axes of acoustic space within which I located each of the 83 song patterns.

Quantifying acoustic space and nearest-neighbor distance

To measure the separation of different species' songs in acoustic space, I calculated the Euclidean distance between species' songs in this four-dimensional acoustic space. The nearest-neighbor distance (NND) for each species was the distance to the closest neighbor in this acoustic space (Fig. 2). Because PCA normalizes the resultant PCs, it eliminates differences in scale that result from different units of measurement. The normalized PCs might not reflect the emphases that the different species of birds place on acoustic features during perception of sounds, but, in the absence of any information about how the various species might weight these features, there was no biological justification for a different measure of distance.

To determine whether the acoustic community was clustered, random, or overdispersed in acoustic space, I used the Clark and Evans' (1954) R as a measure of dispersion in K dimensions. The test compares observed NNDs in a population, R_a , to that in a randomly distributed population, R_e , of the same density, thus $R = R_a/R_e$. If $R = 1.0$, the distribution is random. Scores approaching 0 indicate increasingly clumped distributions, and those above 1.0 indicate increasingly uniform distributions. I followed Clark and Evans (1979) to calculate the expected NND in 4 dimensions, $r_e = 0.60813/\rho^{1/4}$, and the standard error of the mean distance to the nearest-neighbor, $r_{\sigma} = 0.55326/\rho^{1/4}$, in a randomly distributed population of density ρ . To calculate the observed density, I calculated the volume of the total acoustic space ($\pi^2/2 * r^4$ for a 4-dimensional hypersphere). The radius was the Euclidean distance from the 4-dimensional centroid of the acoustic community to the location of the species farthest from the

centroid. Outliers were not removed so the hypersphere in effect incorporated a buffer strip around the occupied volume, as recommended by Donnelly (1978).

Preliminary examination of the distribution of the song patterns in acoustic space revealed that species near the center were more clustered than those near the periphery. This pattern resulted in NND scores that were extremely clustered overall. Consequently I calculated the centroid of the acoustic community and then selected the inner quartile of species in the acoustic community for the final NND analyses. Species in the inner quartile of the acoustic community are presumably most likely to create acoustic interference for each other (Nelson & Marler 1990).

Acoustic community at multiple temporal scales

To investigate how acoustic partitioning might be expressed, NNDs were calculated for multiple spatio-temporal scales: 1) all species from all census points across all days and seasons, 2) species at one point during one morning, and 3) species within a one half hour period at one point. To see if there were differences in dispersion between species that sang early and late in the morning I investigated species that sang during 30-min periods at 2 different times, starting at approximately sunrise (0600) and at 0800. An index of community similarity (Jaccard's Index) between the four 30-min periods of the acoustic censuses revealed that these two time periods had a similarity value of 0.24, lower than those between the other 30-min periods. A one-way Analysis of Variance (ANOVA) compared the song activity of each species during each of the four 30-min periods of the acoustic censuses.

The 30-min temporal scale was further subdivided to investigate interactions of species that sang in the same stratum and species that were phylogenetically related. I

focused on the midlevel stratum, which had more species than the other strata. Likewise I focused on the suborder Tyranni (suboscines), which had more species than the other orders or suborders. I used suborder to group related species because the quantitative phylogenetic relationships between many of the species in Amazonia are still unknown. For all temporal scales, except all species across all days and seasons, all nearest-neighbor values were calculated and then averaged for an overall R dispersion value at each spatio-temporal scale.

To investigate whether or not smaller temporal scales had greater song dispersion than larger temporal scales, I compared R for species detected during the same 30-min period at one point to species detected at a point throughout the morning. To ensure independent samples, I randomly divided the different days of the acoustic censuses into 2 groups, each consisting of 20 point-days. The first group was used for the species during 30-min at a point and the second for all of the species at a point throughout a morning. A one-way ANOVA compared the R dispersion values of these 2 temporal scales.

Phylogenetic distance, singing strata, and acoustic space

To compare the similarity between songs of closely and more distantly related species I used ANOVA to compare species' NNDs and Euclidean distances between congeners & the Euclidean distance to randomly selected species from the community. For genera that included more than 2 species I randomly selected 2 for this analysis. In a one-way ANOVA, the categories of species (nearest-neighbor, congener, and random species) were the predictor variables, while Euclidean distance was the response variable. These methods were also used to compare the distance between songs of family members to the

distances between nearest-neighbors, family members, and random species. In this analysis pairs of species in the same family always excluded congeners. In the analysis by genera, an assessment of the residuals showed one genus (*Xiphorynchus*) as an outlier (greater than 2 standard deviations from the mean). This genus was removed before the final analysis, although this adjustment did not affect the statistical significance of the results.

I also compared the distance between songs of species in the same stratum of the forest to the distance between songs of species in different strata. Based on observations at Rio Cristalino as well as published information (del Hoyo 2002; Remsen 2003; Ridgely & Tudor 1994; Zimmer & Isler 2003), I categorized each species as singing primarily in one of the following strata: on the ground (within 0.1 m of the ground); understory (0.1 m to 4 m above ground); midlevel (4 m – 15 m above ground); subcanopy (15 m – 30 m), and canopy (30 m above ground - top of trees). For each species I calculated the Euclidean distance to the nearest-neighbor in the same stratum and the nearest-neighbor in a different stratum. A one-way ANOVA included stratum (same and different) as the predictor variable and NND as the response variable. In an assessment of the residuals one species (*Glyphorynchus spirurus*) was an outlier (greater than 2 standard deviations from the mean). This species was removed before the final analysis, although once again the removal of this outlier did not affect the statistical significance of the results.

Comparison of the center and periphery of the acoustic community

To measure changes in NND with distance from the center of the acoustic space, species were separated into the inner quartile and the outer quartile based on their Euclidean distance from the centroid of the acoustic community. A one-way ANOVA compared NNDs of species on the periphery and near the center of the acoustic space. In an assessment of the residuals, one point in the outer quartile was an outlier and was removed before the final analysis, although the removal of this outlier did not affect the statistical significance of the results.

To investigate if species near the center of acoustic space sing more frequently than species in the periphery of acoustic space, I compared each species' Euclidean distance from the centroid of the acoustic community with its mean amount of singing during the dawn chorus. The amount of singing in a morning was calculated for each species on each acoustic census and divided by the number of days and points at which it sang, for an average amount of singing per morning for each species. In general only one individual per species was recorded at each census point, but occasionally the census point was on the boundary of 2 individuals of a species so in some cases there might be 2 individuals per point. This analysis included the 50% of the species closest to the centroid. The species farther from the centroid might not be subject to as much competition for acoustic space as those near the center of the acoustic community. A linear regression explored the relationship between the distance from the center and amount of singing.

RESULTS

Acoustic community at multiple spatio-temporal scales

Of the 137 species that sang during at least one acoustic census, 82 sang during more than 1% of the total time (Appendix A). These species included 51 suboscines (Order Passeriformes; Suborder Tyranni), 7 oscines (Order Passeriformes; Suborder Passeres), and 24 non-passerines (Orders Tinamiformes; Galliformes; Columbiformes; Strigiformes; Caprimulgiformes; Trogoniformes; Coraciiformes; Piciformes). Similar numbers of species were detected during the wet and dry seasons, 81 and 73 respectively. The average number of species detected at each spatio-temporal scale revealed a nested structure with larger scales having more species and smaller scales having fewer species. For example the average number of species detected at any one site across all sampling days was 73, during one season 59, during one week 52, and during one day 41. Meanwhile the average number of species detected at a point per season, per week, and per day were, 52, 43, and 38, respectively. The average number of species detected at any one point in the 30 min starting at sunrise was 19 and the 30 min starting at 0800 was 16 species. ANOVAs revealed that 47 out of 82 species preferentially sang in certain 30-min periods of the dawn chorus. After a Bonferroni correction for multiple tests, only 18 species sang preferentially in certain 30 min periods.

At all spatio-temporal scales species were randomly distributed in acoustic space. For the largest spatio-temporal scale, all species across all days, R was close to 1 ($R = 1.01$, $z = 0.01$, $p = 0.99$). At single points during one morning, R varied from 0.83 – 1.22 with an average value of 1.04 ($z = 0.75$, $p = 0.45$). Species that sang together in the same 30-min period, starting at sunrise, had greater dispersion than larger temporal scales, such as the whole morning, but were still not more uniformly distributed than expected by chance (R

= 1.19, $z = 0.21$, $p = 0.84$). There was only a slight difference between the 30 min period starting at sunrise and the 30-min period starting at 0800 ($R = 1.20$, $z = 0.21$, $p = 0.84$). Species that sang in the same 30-min period as well as in the same stratum showed even more dispersion ($R = 1.28$, $z = 0.3$, $p = 0.76$). Phylogenetically related species singing in the same 30-min period showed the greatest dispersion ($R = 1.32$, $z = 0.35$, $p = 0.73$). In an ANOVA of dispersion among species singing in the same 30-min period, at sunrise, and species singing at any one point during one morning, the 30-min period was more dispersed than all of the species at the point (Fig. 3) ($F(1,38) = 4.61$, $p = 0.038$).

Phylogenetic distance, singing strata, and acoustic space

The acoustic censuses detected 11 genera with more than one species. In 9 of these genera congeners were not nearest-neighbors in acoustic space. The two exceptions were nearest-neighbors in acoustic space were *Columba* and *Trogon*. The mean within-genera Euclidean distance between species was 2.31 while the mean NND for all species was 0.81 ($F(1,20) = 16.57$, $p = 0.0006$). There was no significant difference between the within-genera Euclidean distance and the Euclidean distance to a randomly chosen species (Fig. 4).

The acoustic censuses detected 13 families with more than one species. Euclidean distances to the nearest family member were much greater than NNDs, 2.89 and 0.87, respectively ($F(1,24) = 28.78$, $p < 0.0001$). There was no significant difference between the within-family Euclidean distance and the Euclidean distance to a randomly chosen species (Fig. 5).

82 species were grouped into the 5 strata (14 ground, 11 understory, 37 midlevel, 10 subcanopy, and 10 canopy species). Species had mean NND within strata of 1.41 and mean NND between strata of 1.03 (Fig. 6) ($F(1,164) = 13.18, p < 0.0004$).

Comparison of center and periphery of the acoustic community

The quartile closest to the centroid consisted of 20 species (12 suboscines, 5 oscines, and 3 nonpasserines) with an average mass of 71.4 grams. The species in the quartile farthest from the centroid consisted of 21 species (14 suboscines, 1 oscine, and 6 nonpasserines) with an average mass of 60.8 grams. The mean NND of species near the center and near the periphery of acoustic space was 0.67 and 1.44, respectively (Fig. 7). ANOVA revealed that species closer to the centroid of the acoustic community had smaller NND than species near the periphery ($F(1,39) = 20.29, p < 0.0001$). There were 40 species in the 50% closest to the centroid. There was a strong relationship between distance from the centroid of acoustic space and a species' mean amount of singing during the dawn chorus (Fig. 8) ($R^2 = 0.12, m = -3.73, p = 0.027$).

DISCUSSION

In this study I examined the effects of acoustic competition on song structure and singing in a community of birds in Amazonia. The results suggest that the songs of species that interact acoustically are under selection from acoustic competition to evolve song features and behaviors that minimize acoustic interference. This conclusion is especially true for closely related species as well as species that sing in the same stratum. In addition species that share the same stratum and sing in the same 30 min interval

showed greater dispersion in acoustic space than did species from different strata and those that sing at different times in the morning. Thus problems of communication seem to be associated with relatively small-scale temporal and spatial interactions between immediate acoustic neighbors, rather than with the whole avian community. These results suggest that the need to recognize conspecific signals against background noise composed of similar heterospecific signals can lead to the divergence of song features in birds.

Species in the center of the community acoustic space have closer nearest-neighbors than species on the periphery of the community acoustic space. Because the center is more crowded than the periphery, central species have a greater chance of acoustic interference from heterospecific signals. In addition centrally located species sang more frequently than species further from the center, perhaps to compensate for their crowding in acoustic space.

Acoustic community at multiple spatio-temporal scales

Few studies have shown community-wide character displacement (Dayan & Simberloff 2005; Dayan et al. 1990), but a number of studies support the hypothesis that close competitors coevolve to increase their differences (Dayan & Simberloff 1998; Dayan & Simberloff 2005). The present study is the first to show that bird song can also coevolve as a result of interspecific competition. Previous studies of acoustic competition have documented avoidance of interspecific overlap in the timing of signal transmission in birds (Cody & Brown 1969; Ficken et al. 1974), frogs (Littlejohn 1959; Schwartz & Wells 1984) and insects (Greenfield 1988), but documenting differences in acoustic

signal features has been more difficult. Results from studies that have investigated temporal (Sueur 2002), spectral (Chek et al. 2003; Hodl 1977; Littlejohn 1959) or spatial (Chek et al. 2003; Drewry & Rand 1983; Duellman & Pyles 1983) acoustic dispersion have found differences in syntopic species' signals but have not conclusively supported acoustic competition as the cause of signal divergence. Most of these studies described the differences in acoustic signal features, spatial separation of signalers, and timing of signaling among species living in the same community but did not conduct statistical community-wide comparisons of signal dispersion. In neotropical frog communities Check et al. (2003) used null models to test for overdispersion among species-specific acoustic signals and found evidence for overdispersion of signals in 3 out of 11 communities, but after correcting for multiple tests none of the communities was statistically significant for overdispersion. However their study showed that the communities with the highest diversity also exhibited the most dispersion in acoustic space.

Despite multiple studies and predictions that species in the same community should divide the acoustic space to improve signal detection and discrimination, there has been no previous conclusive evidence of signal partitioning. One reason might be that acoustic space has multiple axes, including song features, the timing of signaling, and the spatial location of signalers, which together create a large combination of parameters among which acoustic space could be divided among community members. Some species' signals might diverge along one axis while others diverge along a different axis. If both species have similar dominant frequencies they could further divide the acoustic space, with species A singing early in the morning and species B singing late in the morning, to

avoid signal confusion (see Chapter 3). Thus it can be difficult to determine which axes should reflect signal divergence.

This study investigated acoustic partitioning along multiple acoustic axes. Despite the analysis of multiple song features and temporal scales, it did not document an overdispersed pattern of signals in acoustic space overall. The distribution of species in acoustic space was clustered with many species in the center and fewer species dispersed around the periphery (see discussion below). This distribution could be a result of commonalities in the mechanisms of sound production across the majority of the species in the community. Most species were medium-sized insectivorous birds with more or less similar bill shapes, which are both important factors to the types of song features that a bird can produce (Podos 1996; Ryan & Brenowitz 1985). In addition, bird songs are adapted to optimize their transmission distance under the environmental pressures that act on sound transmission in their native habitats (Morton 1975; Wiley & Richards 1982; Marten & Marler 1977; Naguib & Wiley 2001). Since all of the species in this study live in the same habitat there should be convergence among the features of their songs.

Despite the aforementioned limitations that could make it difficult to observe acoustic partitioning, this study did find that signals of species that sang in the same 30-min intervals and in the same stratum had significantly greater signal dispersion than species in the community that did not sing at the same place and time. Therefore spatial and temporal cues, as well as song features, could all be important axes in determining the dispersion of signals in acoustic space. The results from this study provide evidence for effects of acoustic competition at small temporal scales leading to coevolution of signals

among syntopic species. Thus, species with similar signals that interact most frequently should have the greatest need for signal divergence.

When different species with similar signals interact, selection should favor divergence of these signals to minimize interference as well as to reduce the risk of interspecific hybridization (Coyne & Orr 2004), a process called reproductive character displacement (Servedio & Noor 2003). Knowledge of the conditions that facilitate this divergence can aid our understanding of the role of competition in adaptive radiation (Schluter 2000) and the role of selection in creating reproductive isolation and speciation (Gerhardt & Huber 2002).

If reproductive character displacement leads to mating behaviors that diverge between conspecific populations, individuals might fail to recognize signals of conspecifics from different populations. Pfennig and Ryan (2006) used artificial neural networks to determine whether or not signals and signal reception would diverge in 2 different populations that were exposed to different types of background noise. In their models, signals and signal recognition diverged as a result of increased contrast to the background noise in each population. Their study provides evidence that background noise can be a source of signal divergence in different populations. If mating behaviors diverge between conspecific populations, individuals could fail to accept conspecifics from the alternative populations as mates. As a result these conspecific populations might become reproductively isolated and ultimately undergo speciation. Thus reproductive character displacement could potentially initiate speciation (Hoskin et al. 2005; Howard 1993).

Phylogenetic distance, singing strata, and acoustic space

In this study I found that the songs of syntopic species in the same genus or family have songs that are less similar than many species that are not closely related. In fact the distance between songs of species in the same genus was almost equal to the distance to random species' songs. Signal divergence among closely related syntopic species is thought to reduce potential mating errors and provide reinforcement for recently separated species (Hobel & Gerhardt 2003). However, this study provided no evidence that recognition of signals from congeners face greater consequences than from the signals of distantly related species. Possibly congeners are using other discriminatory cues, such as the time of day when signals are broadcast (see Chapter 3), or the strata from which a signal is broadcast, or visual cues to avoid mating errors.

While the overall result of this study showed that songs of congeners and family members were not nearest-neighbors, there were 2 genera, *Trogon* and *Columba*, for which acoustic nearest-neighbors were in the same genus. In both cases the species were in the same stratum and the similarity of their signals could result from convergence of songs for heterospecific recognition. Convergence of signals in sympatry (de Kort et al. 2002) could be a result of interspecific territoriality and should favor a recognition of heterospecific competitors for the defense of resources (Cody 1969). In such cases species might use cues other than song, such as visual cues, to avoid mating errors.

Songs of species in the same stratum are thought to converge on similar song characteristics as a result of adaptations to their signaling environment (Marten & Marler 1977; Nemeth et al. 2001; Seddon 2005; Wiley 1991; Wiley & Richards 1982; Naguib & Wiley). However the results of this study indicate that species in the same stratum do not

have acoustic nearest-neighbors in the same stratum, presumably in order to avoid acoustic interference. Spatial separation, such as singing from different stratum, should provide receivers with an additional cue for correct conspecific recognition (Klump 1996). Therefore we should consider the importance of species recognition and acoustic competition as well as effects from habitat structure when considering the evolution of acoustic signals for long-range communication.

Comparison of center and periphery of the acoustic community

Species in the center of acoustic space face different communication problems than species on the periphery (Nelson & Marler 1990). Nelson and Marler (1990) conducted discriminant function analyses of centrally and peripherally located species in a community acoustic space with 13 syntopic species. The central species, field sparrow *Spizella pusilla*, required 7 song variables for 98% correct classification while the peripheral species, chipping sparrow *Spizella passerina*, required only 3 song variables for 97% correct classification. Thus the centrally located species required more information for accurate song recognition and presumably had greater difficulty identifying conspecific signals because of the close proximity of many acoustic neighbors with similar song features. In the present study I compared the separation between species' signals at different locations, central and peripheral, in an acoustic community. The results indicated that the central species have closer acoustic neighbors than the peripheral species in tropical forests, just as Nelson and Marler (1990) found in the simpler communities of temperate fields.

Signal detection theory predicts that rare species should be on the periphery of acoustic space while common species should be closer to the center (Wiley 2006). Since rare species are more likely to respond erroneously to heterospecific signals, they might adapt their signals to be farther from the crowded center of acoustic space (Wollerman & Wiley 2002b). However birds are not the only source of biotic noise in the forest. Even though frogs and insects tend to produce sounds at higher frequencies than most species of birds, species of all taxa that produce noise at the same location share a common acoustic space. Birds that are on the periphery of the avian community acoustic space could be near the center of the frog or insect community acoustic space. Future studies should consider acoustic space across multiple taxa for a more complete picture of acoustic communities.

Individuals can compensate for the challenges of interference from background noise by adjusting their signaling behavior. These adjustments could include an increase in signal amplitude, contrast from background noise, or the rate of signal repetition (Brumm & Slabbekoorn 2005). In speciose acoustic communities, like those in Amazonia, the center of the acoustic space might be so crowded that species' signals have already adjusted to produce maximal contrast with the signals of acoustic neighbors (see Chap 4).

Another means of increasing correct signal detection and discrimination could be to increase the repetition rate of signals. In fact, signal detection theory predicts that increased redundancy can increase information transfer in the presence of noise (Wiley 1994). Brumm and Slater (2006) found that chaffinches, *Fringilla coelebs*, near streams, a source of background noise, increased the rate of signal repetition compared with chaffinches located farther from streams. In addition, Lengagne et al. (1999) found that

king penguins, *Aptenodytes patagonica*, increase the number of syllables in the presence of noise. These studies coupled with the results of the present study reveal that at least some species faced with increased levels of background noise sing more frequently than species with less background noise. Increased signal repetition could be a common behavior to overcome acoustic interference from background noise, but this possibility needs to be confirmed in more species. Alternatively these results might be explained by species near the centroid of acoustic space having denser populations than species further from the center of the acoustic community. Further investigation will be required to tease apart these two potential explanations of these results.

In conclusion, this study suggests that signals used by birds for acoustic communication in Amazonian forests are under selection to diverge from similar heterospecific signals. Signal divergence appeared only between species that interact acoustically at small spatio-temporal scales. This study also confirmed previous reports that the center of the acoustic community is more crowded than the periphery.

Acknowledgements

I would like to thank Haven Wiley for help in all aspects of this project. I would like to thank Maria Alice dos Santos Silva and Mario Cohn-Haft who helped with Brazilian research visas, and John Luther, Amy Upgren, Brad Davis, Vitoria da Riva Carvalho, and the staff of the Rio Cristalino RPPN for assistance in the field. I would like to thank Mario Cohn-Haft, Andrew Whitaker, Kevin Zimmer, and Alex Lees for help with initial species identification of mysterious vocalizations from my acoustic censuses. I also thank the Mellon Foundation, Explorer's Club, International and Latin American Studies at UNC, and the UNC Graduate School for funding this research project.

REFERENCES

- Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*: Sunderland, Mass. : Sinauer Associates.
- Bremond, J. C. 1978 Acoustic competition between the song of the wren (*Troglodytes troglodytes*) and the songs of other species. *Behaviour* **65**, 89-98.
- Brumm, H. & Slabbekoorn, H. 2005 Acoustic communication in noise. *Advances in the Study of Behavior* **35**, 151-209.
- Brumm, H. & Slater, P. J. B. 2006 Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology* **60**, 475-481.
- Chek, A. A., Bogart, J. P. & Loughheed, S. C. 2003 Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecology Letters* **6**, 235-247.
- Clark, P. J. & Evans, C. S. 1954 Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**, 445-453.
- Clark, P. J. & Evans, F. C. 1979 Generalization of a nearest neighbor measure of dispersion for use in K dimensions. *Ecology* **60**, 316-317.
- Cody, M. L. 1969 Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *The Condor* **71**, 222-239.
- Cody, M. L. & Brown, J. H. 1969 Song asynchrony in neighboring bird species. *Nature* **222**, 778-780.
- Coyne, J. A. & Orr, H. A. 2004 *Speciation*. Sunderland, MA: Sinauer.
- Dayan, T. & Simberloff, D. 1998 Size patterns among competitors: Ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* **28**, 99-124.
- Dayan, T. & Simberloff, D. 2005 Ecological and community-wide character displacement: the next generation. *Ecology Letters* **8**, 875-894.
- Dayan, T., Simberloff, D. & Tchernov, E. 1990 Feline canines community-wide character displacement among the small cats of Israel. *American Naturalist* **136**, 39-60.
- de Kort, S. R., den Hartog, P. M. & ten Cate, C. 2002 Diverge or merge? The effect of sympatric occurrence on the territorial vocalizations of the vinaceous dove *Streptopelia vinacea* and the ring-necked dove *S. capicola*. *Journal of Avian Biology* **33**, 150-158.

- del Hoyo, J. 2002 *Jacamars to Woodpeckers*. Handbook of the birds of the world. Barcelona: Lynx Editions.
- Donnelly, K. 1978 Simulations to determine the variance and edge-effect of total nearest neighbor distance. In *Simulation methods in archeology* (ed. I. Hodder), pp. 91-95. London, England: Cambridge University Press.
- Drewry, G. E. & Rand, A. S. 1983 Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* **1983**, 941-953.
- Duellman, W. E. & Pyles, R. A. 1983 Acoustic resource partitioning in anuran communities. *Copeia* **1983**, 639-649.
- Dunning, J. B., Jr. 1993 *CRC handbook of avian body masses*. Boca Raton, FL: CRC Press.
- Emlen, S. T. 1972 An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* **41**, 130-171.
- Endler, J. A. 1992 Signals, signal conditions, and the direction of evolution. *American Naturalist* **139**, S125-S153.
- Endler, J. A. 1993 The color of light in forests and its implications. *Ecological Monographs* **63**, 1-27.
- Falls, J. B. 1963 Properties of bird song eliciting response from territorial males. In *Proceedings of the International Ornithological Congress*, vol. 13, pp. 259-271.
- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974 Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* **183**, 762 - 763.
- Gerhardt, H. C. & Huber, F. 2002 *Acoustic communication in insects and anurans: common problems and diverse solutions*: Chicago : University of Chicago Press.
- Greenfield, M. D. 1988 Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* **36**, 684-695.
- Hobel, G. & Gerhardt, H. C. 2003 Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* **57**, 894-904.
- Hodl, W. 1977 Call differences and calling site segregation in anuran species from central Amazonian floating meadows. *Oecologia* **28**, 351-363.
- Hoskin, C. J., Higgin, M., McDonald, K. R. & Moritz, C. 2005 Reinforcement drives rapid allopatric speciation. *Nature* **437**, 1353-1356.

- Howard, D. J. 1993 Reinforcement: origin, dynamics and fate of an evolutionary hypothesis. In *Hybrid zones and the evolutionary process* (ed. R. G. Harrison), pp. 46-69. New York, NY: Oxford University Press.
- Irwin, D. E. & Price, T. 1999 Sexual imprinting, learning and speciation. *Heredity* **82**, 347-354.
- Isler, M. L., Isler, P. R. & Whitney, B. M. 1998 Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *The Auk* **115**, 557-590.
- Klump, G. M. 1996 Bird communication in the noisy world. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 321 - 338. Ithaca, NY: Cornell University Press.
- Lengagne, T., Jouventin, P. & Aubin, T. 1999 Finding one's mate in a king penguin colony: efficiency of acoustic communication. *Behavior Genetics* **136**, 833-846.
- Littlejohn, M. J. 1959 Call differentiation in a complex of seven species of *Crinia* (Anura, Leptodactylidae). *Evolution* **13**, 452-468.
- Marler, P. 1960 Bird songs and mate selection. In *Animal sounds and communication*, vol. 7 (ed. W. E. Lanyon & W. N. Tavolga), pp. 348-367. Washington D.C.: American Institute of Biological Sciences.
- Marten, K. & Marler, P. 1977 Sound transmission and its significance for animal vocalization. *Behavioral Ecology and Sociobiology* **2**, 271-290.
- McGarigal, K., Cushman, S. & Stafford, S. 2000 *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- Miller, E. H. 1982 Character and variance shift in acoustic signals of birds. In *Acoustic communication in birds*, vol. 1 (ed. D. E. Kroodsma & E. H. Miller), pp. 253-295. New York: Academic Press.
- Morton, E. S. 1975 Ecological sources of selection on avian sounds. *American Naturalist* **109**, 17-34.
- Nelson, D. A. 1988 Feature weighting in species song recognition by the field sparrow *Spizella pusilla*. *Behaviour* **106**, 158-182.
- Nelson, D. A. & Marler, P. 1990 The perception of bird song and an ecological concept of signal space. In *Comparative perception, Vol. 2, Complex signals*, vol. 2 (ed. W. C. Stebbins & M. A. Berkley), pp. 443-78. New York: Wiley.
- Nemeth, E., Winkler, H. & Dabelsteen, T. 2001 Differential degradation of antbird songs in a Neotropical rainforest: Adaptation to perch height? *Journal of the Acoustical Society of America* **110**, 3263-3274.

- Pfennig, K. S. 2000 Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology* **11**, 220-227.
- Pfennig, K. S. & Ryan, M. J. 2006 Reproductive character displacement generates reproductive isolation among conspecific populations: an artificial neural network study. *Proceedings of the Royal Society B* **273**, 1361-1368.
- Podos, J. 1996 Motor constraints on vocal development in a songbird. *Animal Behaviour* **51**, 1061-1070.
- Remsen, J. V. 2003 Furnariidae (ovenbirds). In *Handbook of the birds of the world*, vol. 8 (ed. J. del Hoyo, A. Elliott & D. Christie), pp. 162-357. Barcelona: Lynx Editions.
- Ridgely, R. S. & Tudor, G. 1994 *The birds of South America*. Oxford, England: Oxford University Press.
- Ryan, M. J. & Brenowitz, E. A. 1985 The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* **126**, 87-100.
- Schluter, D. 2000 *The Ecology of adaptive radiation*: Oxford University Press.
- Schwartz, J. J. & Wells, K. D. 1983 An Experimental Study of Acoustic Interference between 2 Species of Neotropical Tree Frogs. *Animal Behaviour* **31**, 181-190.
- Schwartz, J. J. & Wells, K. D. 1984 Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behavioral Ecology and Sociobiology* **14**, 211-224.
- Seddon, N. 2005 Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* **59**, 200-215.
- Servedio, M. R. & Noor, M. A. F. 2003 The role of reinforcement in speciation: Theory and data. *Annual Review of Ecology Evolution and Systematics* **34**, 339-364.
- Sueur, J. 2002 Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera : Cicadomorpha : Cicadidae). *Biological Journal of the Linnean Society* **75**, 379-394.
- Terborgh, J., Robinson, S. K. & Parker, T. A. I. 1990 Structure and organization of an Amazonian forest bird community. *Ecological Monographs* **60**, 213-238.
- Wiley, R. H. 1991 Associations of song properties with habitats for territorial oscine birds of eastern North-America. *American Naturalist* **138**, 973-993.
- Wiley, R. H. 1994 Errors, exaggeration, and deception in animal communication. In *Behavioral mechanisms in evolutionary ecology* (ed. L. A. Real), pp. 157-189. Chicago: University of Chicago Press.

- Wiley, R. H. 2006 Signal detection and animal communication. *Advances in the Study of Behavior* **36**, 217-247.
- Wiley, R. H. & Richards, D. G. 1982 Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 131-181. New York & London: Academic Press.
- Wollerman, L. & Wiley, R. H. 2002a Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour* **63**, 15-22.
- Wollerman, L. & Wiley, R. H. 2002b Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* **52**, 465-473.
- Zimmer, K. J. & Isler, M. L. 2003 *Family Thamnophilidae (typical antbirds)*. Handbook of the birds of the world Vol. 8. Barcelona: Lynx Editions.
- Zimmer, K. J., Parker, T. A., Isler, M. L. & Isler, P. R. 1997 Survey of a southern amazonian avifauna: the Alta Floresta region, Mato Grosso, Brazil. *Ornithological Monographs* **48**, 887-918.

Table 1. Loadings for the first five principal components derived from measurements of the acoustic properties of avian songs.

	PC1	PC2	PC3	PC4
Eigenvalue	4.84	2.24	1.63	1.15
Percent	40.34	18.71	13.62	9.58
Lowest dominant frequency (Hz)	0.36	-0.28	0.06	0.26
Highest dominant frequency (Hz)	0.39	-0.29	0.19	0.13
Song bandwidth (Hz)	0.31	-0.22	0.3	-0.07
Number of notes	0.18	0.45	0.08	0.43
Total duration (ms)	0.01	0.23	0.57	-0.11
Rate of song (notes / ms)	0.15	0.29	-0.37	0.59
Change in rate first and second portion of the song	0.19	0.36	0.34	-0.12
Change in rate second and third portion of the song	0.12	0.42	0.23	-0.04
Dominant frequency of song (Hz)	0.38	-0.29	0.11	0.19
First note complexity (bandwidth / duration / slopes)	0.34	0.17	-0.28	-0.34
Last note complexity (bandwidth / duration / slopes)	0.35	0.11	-0.27	-0.22
Average note complexity (bandwidth / duration / slopes)	0.36	0.12	-0.27	-0.38

Bold identifies variables than make an important contribution to the component (loading >0.3, (see McGarigal et al. 2000))

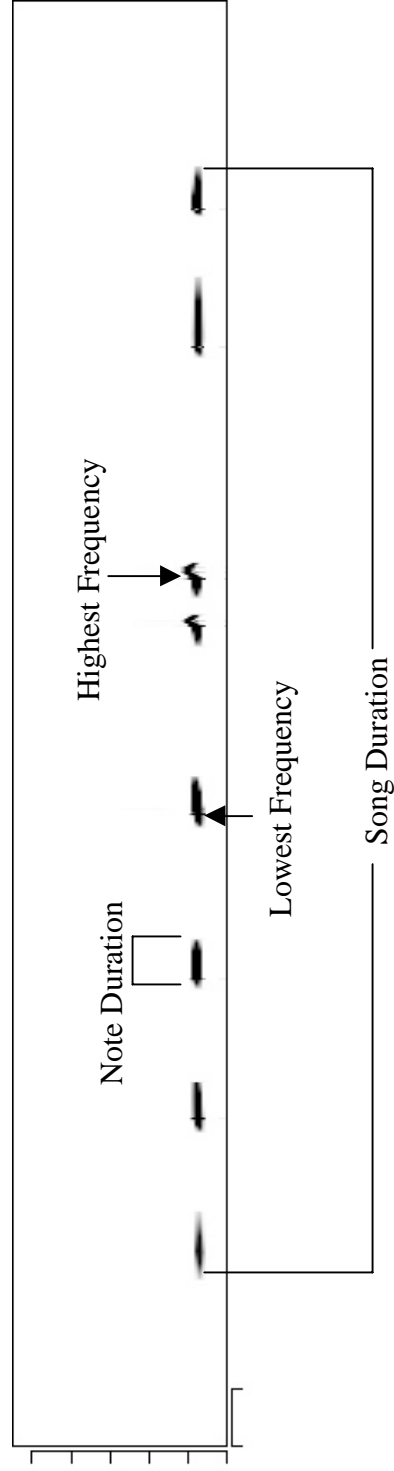


Figure 1. Spectrogram of a song of a Wing-barred Piprites *Piprites chloris*. The x-axis is time (ms) and the y-axis is frequency (Hz). See the text for a description of the song features.

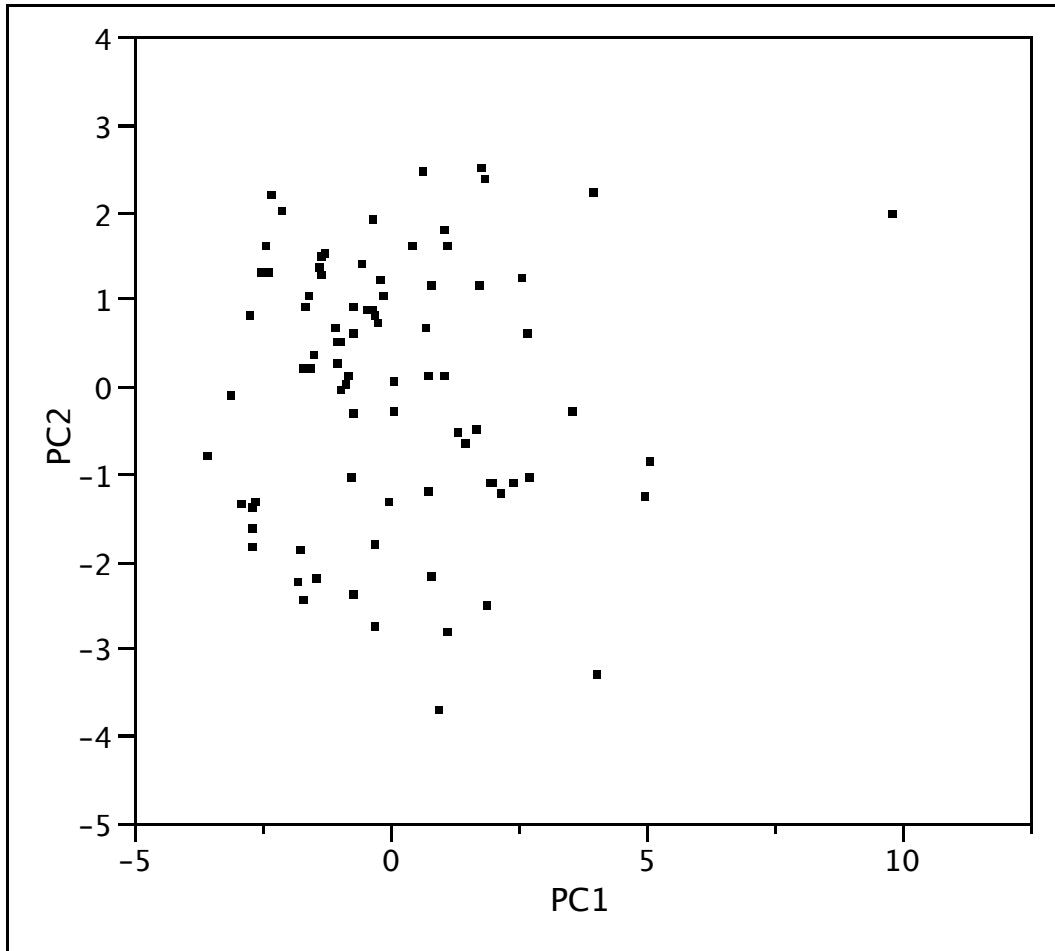


Figure 2. Songs of 83 species in a two-dimensional acoustic space defined by the first two principal components (PC). See Appendix A for a list of species corresponding to each point in the plot.

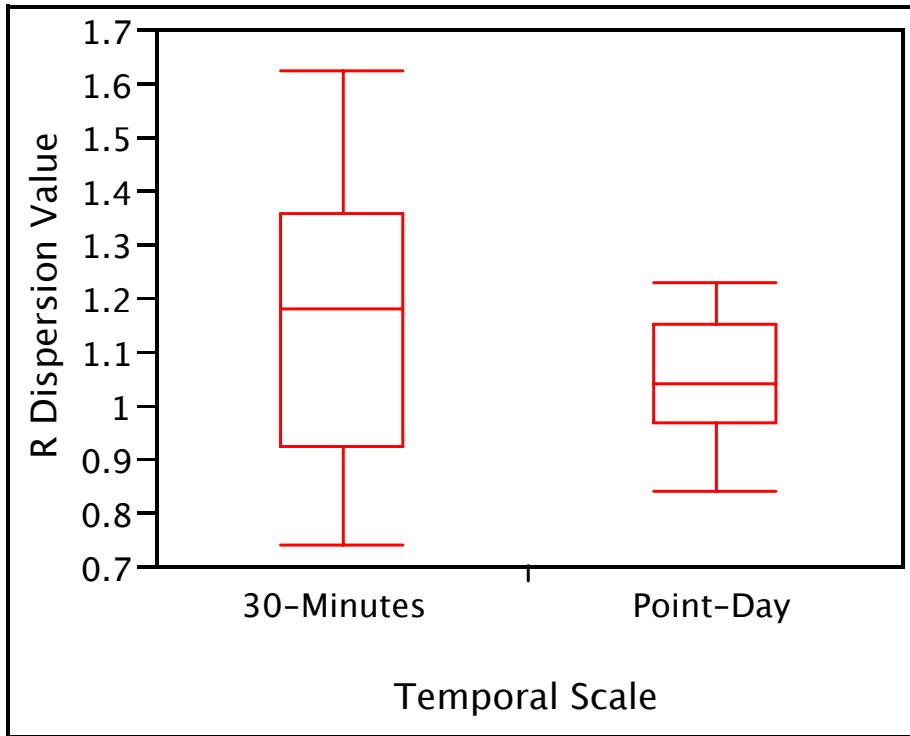


Figure 3. Dispersion in acoustic space (R) for birds that sang together at the same place during the same 30 min period and birds that sang together at the same point over the course of a morning. The central line represents the median, the lower and upper boundaries of the boxes represent 25th and 75th percentiles, respectively, and the lower and upper bars show the 10th and 90th percentiles, respectively.

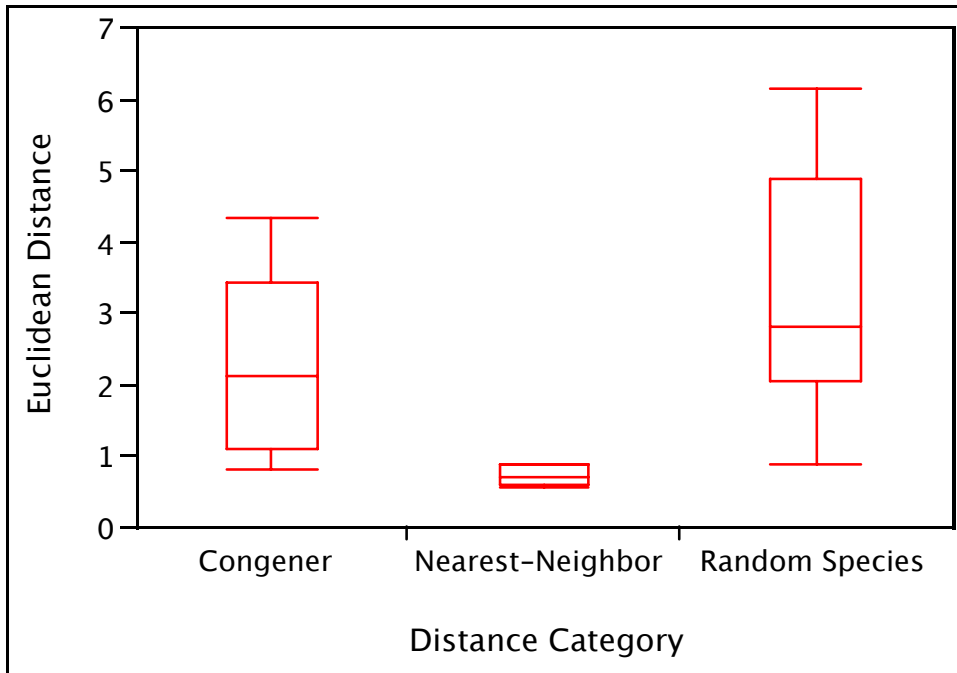


Figure 4. Euclidean distances between songs of congeners, nearest-neighbors, and unrelated species chosen at random in acoustic space.

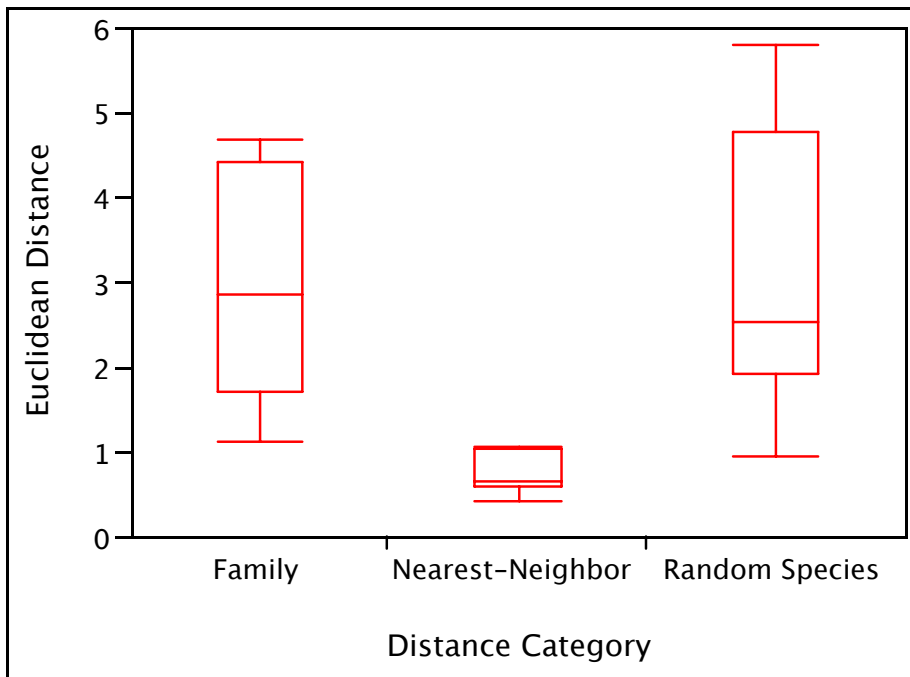


Figure 5. Euclidean distances between songs of family members, nearest-neighbors, and unrelated species chosen at random in acoustic space.

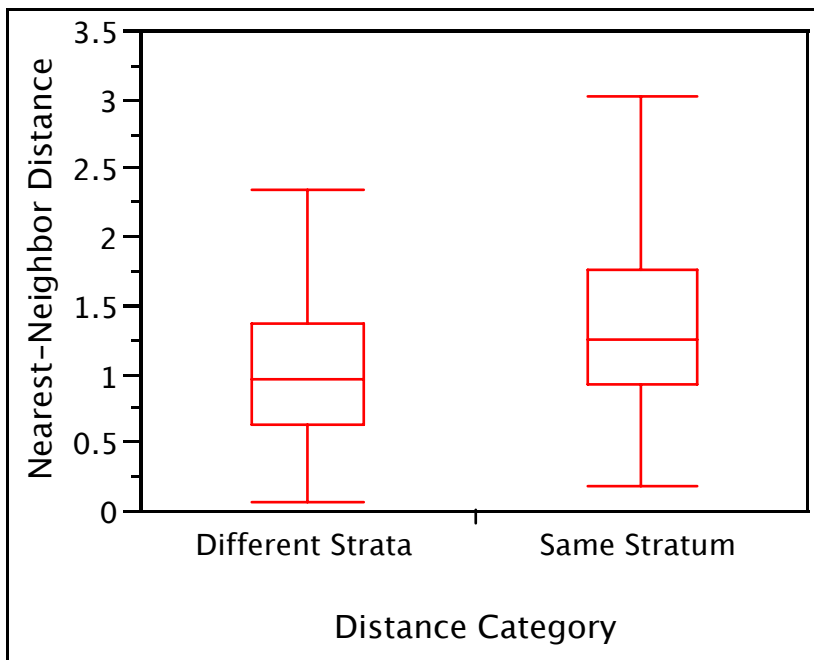


Figure 6. Nearest-neighbor distances between songs of species in the same stratum and species in different strata.

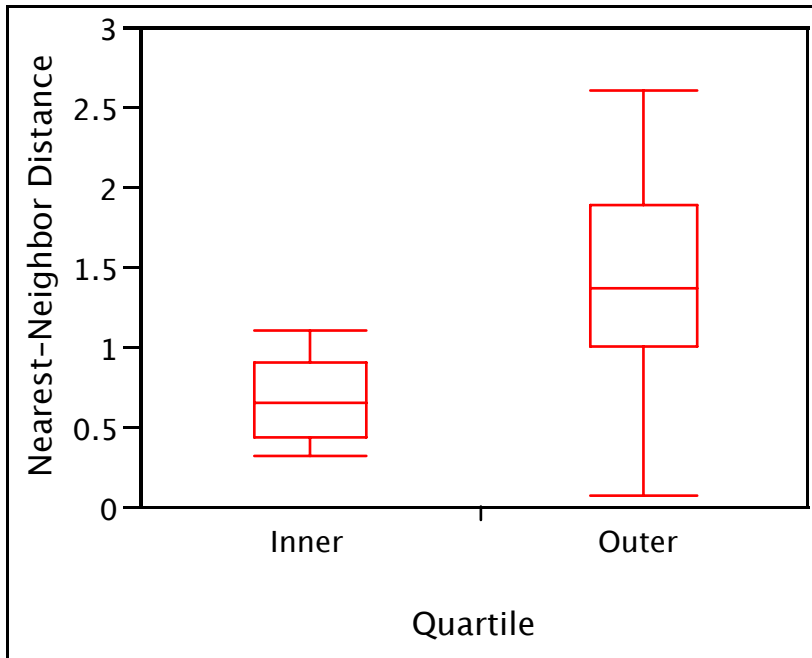


Figure 7. Nearest-neighbor distances between songs of species in the inner and outer quartiles of the community acoustic space.

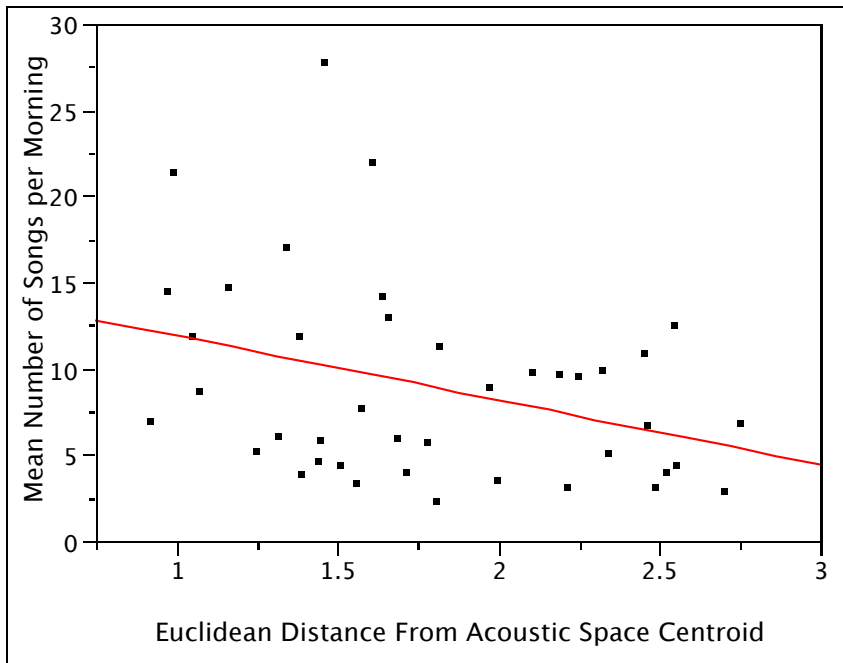


Figure 8. Relationship between a species' mean number of songs in a morning and a species' Euclidean distance from the centroid of the community acoustic space.

**EXPERIMENTAL EVIDENCE OF TEMPORAL PARTITIONING IN THE
PERCEPTION AND PRODUCTION OF SONGS IN A
NEOTROPICAL DAWN CHORUS**

ABSTRACT

The efficacy of most communication relies on the detection of species-specific signals against background noise. By interfering with the detection and discrimination of conspecific signals, background noise can interfere with intraspecific communication. Some species are known to alter the short-term timing of vocalizations to avoid acoustic interference from similar heterospecific signals, but the hypothesis that syntopic species might listen as well as vocalize at different times in order to reduce interference has never been tested experimentally. This study examined this hypothesis of temporal acoustic perceptual partitioning by using playback experiments to test the responsiveness of territorial birds to conspecific songs at typical and atypical times of singing during the dawn chorus. The study focused on four neotropical avian species in the acoustically complex environment of an Amazonian rainforest, two species that primarily sing early and two that primarily sing late in the dawn chorus. Each of the four species responded more strongly to playbacks at its' own typical time of vocalization. The results support the hypothesis that syntopic species of birds temporally partition the dawn chorus both in production and perception in a way that would reduce heterospecific interference in communication.

INTRODUCTION

Animals rely on long-range communication for mate selection, territorial defense, and species recognition, but background noise from the environment constrains interactions between signalers and receivers. A receiver often must detect a signal or discriminate between signals in the presence of much irrelevant but similar energy in the environment (Bradbury & Vehrencamp 1998; Brenowitz 1982; Klump 1996; Ryan & Brenowitz 1985; Wollerman 1999; Wollerman & Wiley 2002b). Since the ability to communicate is limited by the distance over which a signal can be detected by a receiver, and background noise can constrain the distance over which a signal might be detected, background noise can produce strong selection on the evolution of animal communication.

Background noise is ubiquitous in natural environments. Furthermore, many animals communicate in situations, such as frog choruses and avian dawn choruses, that make it especially difficult to discriminate conspecific from similar heterospecific signals (Bremond 1978; Brumm & Slabbekoom 2005; Gerhardt & Huber 2002; Pfennig 2000; Wiley 1994; Wollerman & Wiley 2002b). Background noise can come from conspecific individuals, related heterospecific species, and other organisms, as well as physical features in the environment, such as wind and water. One result of communicating in the presence of background noise from other species can be acoustic interference, in which heterospecific signals are similar enough that they reduce the detectability and discriminability of both signals. Detectability is a measure of a receiver's ability to separate a signal from background noise, whereas discriminability is the ability to separate two signals. To increase the detectability and discriminability of a signal and to reduce interference from irrelevant signals, signalers should increase the contrast between

their signals and the background energy in their environment (Endler 1993; Wiley 1994; Wiley 2006).

To increase the contrast between a signal and background noise, signalers can adjust the amplitude, frequency, or timing of their signals (Klump 1996; Brumm and Slabbekoorn 2005). Increasing the contrast with background noise is especially important when signals share the same frequency range (Bremond 1978; Lohr et al. 2003). Consequently, birds can shift the frequency ranges of their songs to increase the contrast with background noise (Patricelli & Blickley 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006).

Noise in the natural environment is rarely continuous (Klump 1996) and by adjusting the timing of signal transmission, to take advantage of gaps in noise, signalers can increase the contrast of their signals with background noise and reduce or avoid acoustic interference from heterospecific signals (Ficken et al. 1974; Greenfield 1988; Narins 1992; Popp et al. 1985). A few studies have provided evidence that birds actively avoid acoustic interference by short-term temporal changes in delivery of songs, over seconds and minutes (Cody & Brown 1969; Ficken et al. 1974; Popp et al. 1985). A larger temporal shift has been documented in the katydid *Neoconocephalus spiza*, which alters the timing of signal transmission from nocturnal to diurnal in the presence of acoustic interference from other species (Greenfield 1988). These examples illustrate an ability to alter the timing of signal transmission to reduce the effects of acoustic interference and to improve signal detectability.

Most studies of acoustic interference have focused on the interactions of a few species, but the problem of acoustic interference can be extended to a larger community in which acoustic partitioning could minimize overlap among similar signals from

multiple syntopic species (Chek et al. 2003; Drewry & Rand 1983; Hodl 1977; Littlejohn 1959; Sueur 2002). For example, syntopic species could partition acoustic space temporally, spatially, or structurally to avoid acoustic interference. Partitioning acoustic space on one or more of these axes could reduce interference and increase contrast with background noise from other species to improve intraspecific communication.

Partitioning the timing of signal transmission to avoid acoustic interference will only be effective if the receivers also shift when they are listening for a signal (Wiley 1994). If signal adjustments are not matched by receiver adjustments the signal will not be detected and communication will fail. The present study investigates perceptual partitioning of acoustic space, in which species in the same community adjust not only the timing of signal transmission to reduce interference from heterospecific signals but also the timing of listening for conspecific signals.

A receiver's performance can be affected by its expectations and attention. It can also be improved through the minimization of signal uncertainty. Any information that a receiver knows about a signal before it occurs, including the interval of time or location in which it might occur, will reduce uncertainty about the signal and help signal detection and discrimination (Wiley 2006). Thus, a signal that is restricted to a predictable interval of time will be more easily detected than a signal that might occur at any time. Since receivers most reliably detect signals when they expect them (Wiley 1994), they might reduce errors by lowering their thresholds for responses during blocks of time in which they are expecting a signal and raising their thresholds when signals are not expected. These shifts would result in receivers that appear to shift their attention to intervals of time when signals are expected. For example, in the avian dawn chorus, some species

might listen most attentively during the 30 minutes just before sunrise, while others listen during the 30 minutes after sunrise.

The avian dawn chorus provides an example of communication in the presence of high levels of heterospecific and conspecific background noise (Wiley 1994), especially in the tropics. In this study, I will refer to the dawn chorus as the 30 minutes before sunrise as well as the 2 to 3 hours after sunrise, a time during which the majority of neotropical birds vocalize. During the dawn chorus, species differ in the timing of their singing (Allard 1930; Allen 1913; Staicer et al. 1996). Many species in the neotropics only sing at specific times in the morning. For example, many species of tinamou (Tinamidae), puffbird (Bucconidae), and woodcreeper (Dendrocolaptidae) only sing at or before sunrise, while other species begin their vocal activity later in the morning (Blake 1992; Parker 1991). Acoustic censuses of the neotropical dawn chorus reveal a large amount of species turnover in vocal activity during the morning (see Chapter 2). One potential explanation for the difference in singing times is the avoidance of acoustic interference from spectrally similar signals. Heterospecific acoustic interference could lead to problems in signal detection and increase pressures for signal specialization and divergence (Miller 1982). To reduce acoustic interference and increase chances of correct signal detection and discrimination, species might sing in different blocks of time during the dawn chorus. Thus the selection to reduce acoustic interference from background noise would lead to the temporal partitioning of acoustic space.

This study investigates the occurrence of temporal acoustic partitioning as well as the correspondence of acoustic perception and production in temporal partitioning among syntopic species in a neotropical dawn chorus. I tested the responsiveness of receivers to conspecific songs at typical and atypical times for species-specific vocalizations during

the dawn chorus. Testing responsiveness at different times in the dawn chorus can demonstrate whether species listen for conspecific songs during blocks of time when they are most likely to occur. If partitioning does occur, species should have stronger responses to signals transmitted during their typical time for signaling and weaker responses during atypical times for signaling.

METHODS

Location and study species

All experiments took place at the Rio Cristalino Private Natural Heritage Preserve (RPPN), located 40 km north-east of the town of Alta Floresta in the state of Mato Grosso, Brazil (9° 41' S, 55° 54' W). Most of the site is lowland tropical moist forest (Zimmer et al. 1997). In 2004 I collected standardized and replicated recordings between 0530 and 0830 in terra firma habitat at Rio Cristalino. From these censuses I determined that many species sing primarily at distinct times in the dawn chorus. Of the 106 species regularly detected during the acoustic censuses, 34 species sang primarily in one 30 min or 1 hr block of time (see Chapter 2). Species that sang primarily during distinct times in the dawn chorus, either early or late, were selected for playback experiments.

Playback experiments on 15 individuals of 2 species that typically sang early, 8 White-browed Antbirds *Myrmoborus leucophrys* and 7 Warbling Antbirds *Hypocnemis cantator striata* were conducted in May and June 2006. In September and October 2006 this research continued with 8 individuals of 2 species that typically sang late, 6 Chestnut-backed Antshrikes *Thamnophilus palliatus palliatus* and 2 Black-faced Anthrushes *Formicarius analis*. I could not conduct all trials in May and June because the 2 late-singing species were only sporadically vocally active. In September and

October they were singing regularly. As a result all 4 species were tested during months when they were vocally active. All 4 species are territorial and non-migratory. Territories of individuals were delimited by following the movements of singing birds and marking the locations of counter-singing individuals with flagging. I successfully completed playbacks to 23 individuals of 4 species. On 4 occasions I attempted to conduct playback experiments but could not locate the individual. Each of these incidents took place during the species' atypical time of singing.

Preparation of songs for playback

Exemplars for playback were prepared from different individuals in the Rio Cristalino RPPN. In May and September 2006 songs were recorded with a Marantz PMD660 digital recorder (44 kHz digitizing rate, 16-bit accuracy WAV format) and a Sennheiser ME67 ultradirectional microphone from distances of 4 - 10 m. They were normalized to maximal amplitude with Wildspectra1 v.051027, www.unc.edu/~rwhiley. From acoustic censuses I calculated that the average number of songs per minute for *M. leucophrys*, *H. cantator*, *T. palliatus*, and *F. analis* was 3.1, 4.3, 3.8, and 3.7, respectively. I produced one-minute tracks with 4 songs per individual, which is close to the natural rate of singing for all 4 species. For each playback I randomly chose a track of a male recorded at least 3 territories away (> 500 m).

Procedures for playback

Each individual received two treatments, one early and one late in the morning. Early playbacks were conducted within 1 hour of sunrise, while late playbacks were conducted between 2 and 3 hours after sunrise. The playback speaker, a RadioShack mini amplifier

speaker (9V), was set near the center of a subject's territory, 1 m above the ground (except for playbacks to *F. analis*, for which the speaker was placed 30 cm above the ground) and connected with a 5 m lead to a Panasonic portable CD player SL S361C. After the speaker was in place, a playback song was selected at random (by rolling a die), subject to the constraints of the experimental design. Playback trials began when the subject had been silent for at least 5 minutes. Each trial lasted 26 minutes (5 min before playback, 1 min of playback, and 20 min afterwards). Both playbacks to an individual were conducted within 5 m of the same location near the center of its territory. Treatments were separated by at least 48 hours to minimize habituation and each subject received the treatments in random order. Territorial neighbors of the same species were not tested on the same day. A subject never received songs recorded from the same individual twice. All playbacks were adjusted to a peak sound pressure level (SPL) close to that of natural songs (81dB at 1 m, Realistic digital sound level meter, C weighting, fast response).

Responses of subjects

During the periods before, during, and after each playback I recorded (1) time from the start of playback to the first visible flight toward the speaker (approach latency in min), (2) closest distance to the speaker (in m), (3) maximum song perch height (in m), (4) time spent less than 5 m from the speaker (in min), (5) time from the start of playback to the first song (song latency in min), (6) total number of minutes singing, (7) number of songs, (8) number of call notes, (9) number of duets, (10) number of flights within 1 m of the speaker. Low values for (1), (2), and (5) and high values for (3), (4), (6-10) indicated strong responses to playback.

Analysis

Since many of the behavioral responses were correlated I used a Principal Components Analysis to reduce the measures of response to a smaller number of independent variables. This analysis extracted 4 principal components (PC) with eigenvalues greater than 1. Together they explained 75% of the variation (Table 1).

To test for differences in behavioral responses between typical and atypical times for singing by each species, I conducted a nested analysis of variance (ANOVA) of PC1 of the behavioral responses, with species nested within their typical times for singing, early or late, and typical times for singing crossed with times of playback, early or late. In an assessment of the residuals one point was an outlier, greater than 2 standard deviations from the mean. This point was removed before the final analysis, although the removal of this outlier did not affect the statistical significance of the results in this case. All statistical tests were calculated with JMP 5.1.

RESULTS

All species had stronger responses to songs played during their typical times of singing than to songs played during atypical times. The strong responses included shorter approach latency, shorter song latency, and closer approaches, as well as a greater number of songs, calls, duets, number of minutes singing, number of flights past the speaker, time spent closer to the speaker, and higher perch heights (Figure 1). While each species exhibited the majority of these responses, the expressions of responses differed among species. For example, *H. cantator* responded strongly at the typical time of playbacks with a greater number of duets, *M. leucophrys* responded with shorter song latency, and *F. analis* responded with shorter approach latency. In general, individuals from each species responded to both typical and atypical timing of playback treatments but responses at the atypical time of singing were less intense and less immediate.

ANOVA of the first PC scores revealed that both early- and late-singing species had stronger responses to songs played during their typical times of singing ($F = 17.67$, $p < 0.001$) (Figure 2). One species, *H. cantator*, an early-singing species, had a stronger response to both early and late playbacks than did other species ($F = 5.94$, $p = 0.02$). Individual species nested within singing category, early- or late- singing species, showed no statistical difference in their responses to early and late playback treatments ($F = 1.196$, $p = 0.31$), indicating that one species was not responsible for the observed differences in responses to playback treatments.

DISCUSSION

Species had stronger responses to songs played at their typical time of singing than at atypical times. Species exhibited large differences in the number of songs, the amount of time singing, and the amount of time close to the speaker. The strong preference for responses to intraspecific song during specific blocks of time during the dawn chorus coincides with the observation that these species preferentially sing in these same blocks of time. These results confirm temporal acoustic partitioning in perception as well as production of signals.

Signaling and listening during restricted times could also be related to a species' daily activity patterns. One hypothesis is that morning song occurs when light levels are insufficient for foraging, yet are adequate for social communication (Kacelnik 1979; Leopold & Eynon 1961). A recent study by Berg et al. (2006) on the ecological determinants of a neotropical dawn chorus found that foraging height and eye-size predict the species-specific sequence of singing in neotropical passerines. Their results suggest that ambient light levels determine the initiation of daily vocal communication. Birds that forage higher begin singing earlier than birds that forage at lower heights, and birds with bigger eyes sing before birds with smaller eyes.

This finding does not apply to the singing behavior of the four species in the present study, because the late-singing *T. palliatus*, which inhabits the midcanopy and subcanopy, sang later than *H. cantator* and *M. leucophrys*, which inhabit dense understory. The late-singing species *F. analis*, a ground dwelling species, conforms to the pattern reported by Berg et al. (2006). I did not take eye-size measurements of these species, but the late-singing species sang so late in the morning, 1 to 2 hours after sunrise,

that ambient light levels should not be a factor in the timing of their singing. The results of the present study do not necessarily contradict the results of Berg et al. (2006) for the period around dawn, but they do indicate that factors other than ambient light level and foraging height can determine the timing of a species' morning vocalizations, in some cases.

Previous studies have documented avoidance of short-term interspecific acoustic interference in birds (Cody and Brown 1969; Ficken et al. 1974), frogs (Littlejohn 1959; Schwartz & Wells 1984), and insects (Greenfield 1988), but documenting acoustic partitioning at large scales has been more difficult. Results from studies that have investigated the possibility of temporal (Sueur 2002), spectral (Littlejohn 1959; Hodl 1977; Check et al. 2003), and spatial (Chek et al. 2003; Drewry & Rand 1983; Duellman & Pyles 1983) acoustic partitioning have documented differences in syntopic signals and signaling behavior but have not conclusively supported partitioning to avoid heterospecific interference of communication. To date no studies appear to have tested perceptual acoustic partitioning with playback experiments. The results of this study demonstrate that acoustic partitioning does occur. They also suggest that experimentation based on prior information about the acoustic community could be a productive means for future investigations of acoustic partitioning.

For acoustic partitioning to occur, both signalers and receivers must coordinate their behavior. A shift in the timing of signal transmission to a specific time would also require a coordinated shift by the receiver to obtain a match in production and perception. If the receiver has a broad pattern of attention initially, such as listening all morning, rather than a more focused pattern, such as listening primarily for one hour, then this variant receiver and a variant signaler might both realize immediate advantages to shifting the

time of signaling (Wiley 1994). Since signalers and receivers can take advantage of gaps in the background noise to increase signal-to-noise ratios, a shift in the time of signaling should exploit these gaps to increase communication efficiency (Cody and Brown 1969; Ficken et al. 1974). Receivers should only respond when they recognize a correct signal, thus signalers should signal at times when they expect receivers to be listening, to increase their chances of a response. If receivers only pay attention at specific times, to reduce their chance of responding to similar heterospecific signals broadcast at other times in the morning, then the signalers should restrict their signals to times when receivers are listening (for a review of models of signal and receiver communication models see Endler & Basolo 1998). Communication that minimizes acoustic interference should increase correct detections of conspecific and rejections of heterospecific signals as well as reduce the number of erroneous responses to heterospecific signals and missed detections of conspecific signals (Wiley 1994; Wollerman & Wiley 2002a).

While the results of the present study indicate temporally selective listening and singing, they do not conclusively demonstrate acoustic interference as the source of the selectivity. To confirm this point, future studies should identify the syntopic signals that have similar acoustic features but do not necessarily occur at the same times. These similar, syntopic, but not synchronous, signals could be included as a playback treatment (mixed with a species' own songs) to determine their effects on receiver errors. Future studies should also investigate additional species to test the breadth of temporal acoustic partitioning throughout communities.

In summary, this study addressed the correspondence of song production and perception by tropical avian species singing in the dawn chorus. Of the two plausible explanations for these results, acoustic partitioning, as a result of acoustic competition,

and differences in diel activity rhythms, the latter is not supported by the results of the present study. Instead the results are consistent with the hypothesis of temporal acoustic partitioning.

Acknowledgements

I would like to thank Haven Wiley for help in all aspects of this project. I would like to thank Maria Alice dos Santos Silva and Mario Cohn-Haft who helped with Brazilian research visas, and John Luther, Amy Upgren, Vitoria da Riva Carvalho, and the staff of the Rio Cristalino RPPN for assistance in the field. I also thank the Mellon Foundation, Explorer's Club, International and Latin American Studies at UNC, and the UNC Graduate School for funding this research project.

REFERENCES

- Allard, H. A. 1930 The first morning song of some birds of Washington, D.C.: its relation to light. *American Naturalist* **64**, 436-469.
- Allen, F. H. 1913 More notes on the morning awakening. *Auk* **30**, 229-235.
- Berg, K. S., Brumfield, R. T. & Apanius, V. 2006 Phylogenetic and ecological determinants of the neotropical dawn chorus. *Proceedings of the Royal Society Biological Sciences Series B* **273**, 999-1005.
- Blake, J. 1992 Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *Condor* **94**, 265-275.
- Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*: Sunderland, Mass. : Sinauer Associates.
- Bremond, J. C. 1978 Acoustic competition between the song of the wren (Troglodytes troglodytes) and the songs of other species. *Behaviour* **65**, 89-98.
- Brenowitz, E. A. 1982 The active space of red-winged blackbird song. *Journal of Comparative Physiology* **147**, 511 - 522.
- Brumm, H. & Slabbekoom, H. 2005 Acoustic communication in noise. *Advances in the study of behavior* **35**, 151-209.
- Chek, A. A., Bogart, J. P. & Loughheed, S. C. 2003 Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecology Letters* **6**, 235-247.
- Cody, M. L. & Brown, J. H. 1969 Song asynchrony in neighboring bird species. *Nature* **222**, 778-780.
- Drewry, G. E. & Rand, A. S. 1983 Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* **1983**, 941-953.
- Duellman, W. E. & Pyles, R. A. 1983 Acoustic resource partitioning in anuran communities. *Copeia* **1983**, 639-649.
- Endler, J. A. 1993 Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **340**, 215-225.
- Endler, J. A. & Basolo, A. L. 1998 Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution* **13**, 415-420.
- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974 Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* **183**, 762 - 763.

- Gerhardt, H. C. & Huber, F. 2002 *Acoustic communication in insects and anurans : common problems and diverse solutions*. Chicago : University of Chicago Press.
- Greenfield, M. D. 1988 Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* **36**, 684-695.
- Hodl, W. 1977 Call differences and calling site segregation in anuran species from central amazonian floating meadows. *Oecologia* **28**, 351-363.
- Kacelnik, A. 1979 The foraging efficiency of great tits (*Parus major*) in relation to light intensity. *Animal Behaviour* **27**, 237-241.
- Klump, G. M. 1996 Bird communication in the noisy world. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 321 - 338. Ithaca, NY: Cornell University Press.
- Leopold, A. & Eynon, A. 1961 Avian daybreak and evening song in relation to time and light intensity. *Condor* **63**, 269-293.
- Littlejohn, M. J. 1959 Call differentiation in a complex of seven species of *Crinia* (Anura, Leptodactylidae). *Evolution* **13**, 452-468.
- Lohr, B., Wright, T. F. & Dooling, R. J. 2003 Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour* **65**, 763 - 777.
- McGarigal, K., Cushman, S. & Stafford, S. 2000 *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- Miller, E. H. 1982 Character and variance shift in acoustic signals of birds. In *Acoustic communication in birds*, vol. 1 (ed. D. E. Kroodsma & E. H. Miller), pp. 253-295. New York: Academic Press.
- Narins, P. M. 1992 Evolution of anuran chorus behavior neural and behavioral constraints. *American Naturalist* **139**, S90-S104.
- Parker, T. A. 1991 On the use of tape recorders in avifaunal surveys. *Auk* **108**, 443-444.
- Patricelli, G. L. & Blickley, J. L. 2006 Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* **123**, 639-649.
- Pfennig, K. S. 2000 Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology* **11**, 220-227.
- Popp, J. W., Ficken, R. W. & Reinartz, J. A. 1985 Short-term temporal avoidance of interspecific acoustic interference among forest birds. *Auk* **102**, 744-748.

- Ryan, M. J. & Brenowitz, E. A. 1985 The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* **126**, 87-100.
- Schwartz, J. J. & Wells, K. D. 1984 Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behavioral Ecology and Sociobiology* **14**, 211-224.
- Slabbekoorn, H. & Peet, M. 2003 Ecology: Birds sing at a higher pitch in urban noise - Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* **424**, 267-267.
- Staicer, C. A., Spector, D. A. & Horn, A. G. 1996 The dawn chorus and other diel patterns in acoustic signaling. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 426-453. Ithaca, NY: Cornell University Press.
- Sueur, J. 2002 Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera : Cicadomorpha : Cicadidae). *Biological Journal of the Linnean Society* **75**, 379-394.
- Wiley, R. H. 1994 Errors, exaggeration, and deception in animal communication. In *Behavioral mechanisms in evolutionary ecology* (ed. L. A. Real), pp. 157-189. Chicago: University of Chicago Press.
- Wiley, R. H. 2006 Signal detection and animal communication. *Advances in the study of behavior* **36**, 217-247.
- Wollerman, L. 1999 Acoustic interference limits call detection in a neotropical frog *Hyla ebreccata*. *Animal Behaviour* **57**, 529 - 536.
- Wollerman, L. & Wiley, R. H. 2002a Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour* **63**, 15-22.
- Wollerman, L. & Wiley, R. H. 2002b Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* **52**, 465-473.
- Wood, W. E. & Yezerinac, S. M. 2006 Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* **123**, 650-659.

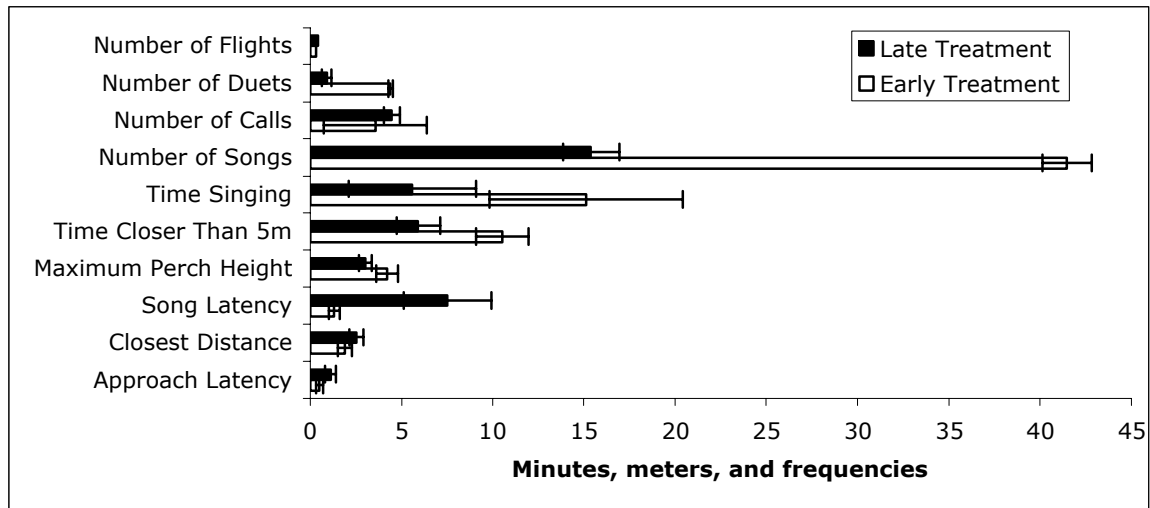
Zimmer, K. J., Parker, T. A., Isler, M. L. & Isler, P. R. 1997 Survey of a southern amazonian avifauna: the Alta Floresta region, Mato Grosso, Brazil. *Ornithological Monographs* **48**, 887-918.

TABLE 1. Factor loadings for the first four principal components derived from behavioral responses to playback experiments (see Fig 1).

	PC1	PC2	PC3	PC4
Eigenvalue	3.62	1.69	1.20	1.01
Percent of Variation Explained	36.16	16.91	12.03	10.09
Latency of Response (min)	-0.38	0.23	0.20	0.14
Closest Distance to Speaker (m)	-0.39	0.37	0.07	0.17
Maximum Perch Height (m)	0.03	0.37	0.62	0.18
Time Spent Less Than 5 m (min)	0.42	-0.11	0.01	-0.27
Song Latency (min)	-0.32	-0.21	0.04	-0.40
Number of Minutes Singing Response (min)	0.43	0.36	-0.04	0.10
Number of Songs	0.43	0.33	-0.13	0.07
Number of Calls	0.09	-0.48	0.34	0.18
Number of Duets	0.14	0.08	0.58	-0.60
Number of Flybys	0.17	-0.38	0.32	0.52

Bold denotes variables with factor loading greater than 0.3 (McGarigal et al. 2000).

(A)



(B)

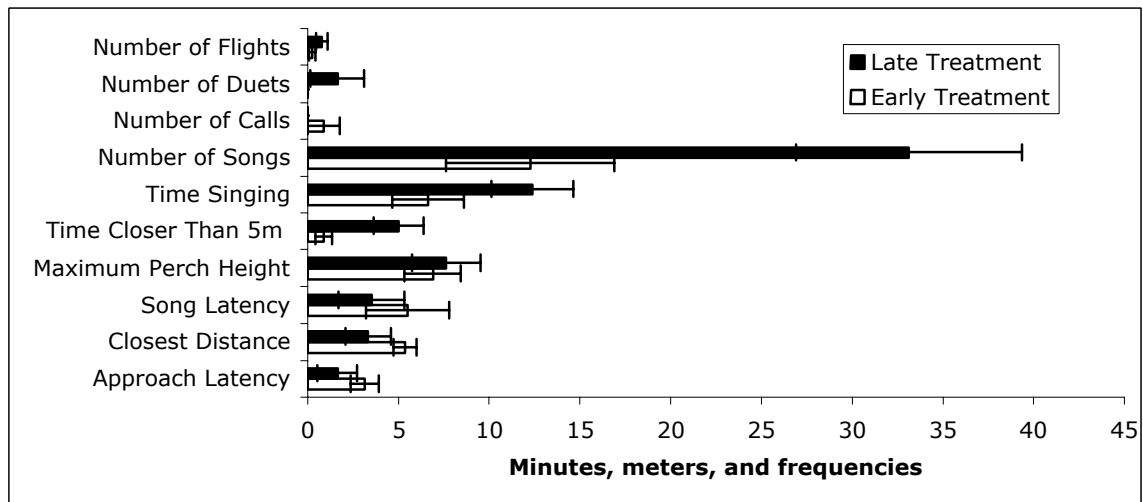
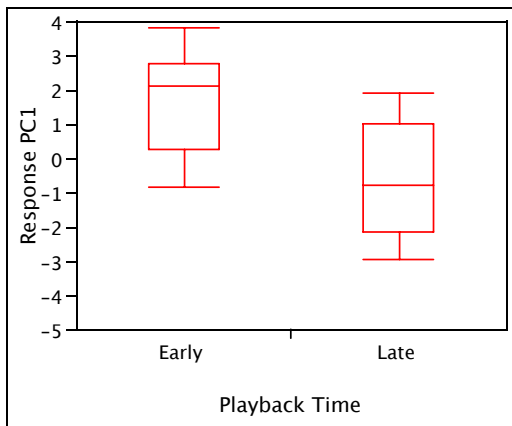


Figure 1. Mean responses (\pm SE) of (A) early-singing and (B) late-singing species to early and late playback treatments. A strong response is indicated by a small value for approach latency, closest approach, and song latency, and a large value for maximum perch height, time spent less than 5 meters from the speaker, number of minutes singing, number of songs, number of calls, number of duets, and number of flights.

(A)



(B)

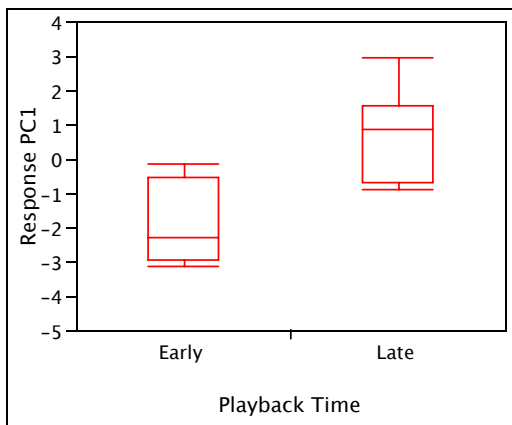


Figure 2. Boxplots showing the overall strength of response (A) early-singing species and (B) late-singing species to different playback treatments. Positive PC values indicate stronger responses than negative PC values. The line in the middle represents the median, the lower and upper boundaries of the boxes represent 25th and 75th percentiles, respectively, and the lower and upper bars relate to the 10th and 90th percentiles, respectively.

**ACOUSTIC SIGNAL SPACE AND
PERCEPTUAL SPACE: A COMPARISON IN
A COMPLEX NEOTROPICAL AVIFAUNA**

ABSTRACT

Species-specific communicatory signals allow species recognition for mate choice and territory defense. In many cases, communication occurs in the presence of other species with similar signals, a situation that hinders discrimination of conspecific from heterospecific signals. To reduce acoustic interference, species could partition acoustic space, both in production and in perception of signals. I investigated this possibility for two Neotropical suboscine birds that are distantly related but widely sympatric and acoustically similar. To assess partitioning of signal space, I compared variation in features of their songs. As with most other sympatric species, these two produced signals that occupied distinct regions of signal space, with a gap between them. To assess partitioning of perceptual acoustic space, I played synthesized versions of the two species' songs and three intermediate versions to individuals of both species in the field. Both species responded to versions outside the normal range of songs that they produced. All synthetic versions received responses from one or the other species, but there was little overlap between the responses to different versions by each species. Unlike signal space, acoustic perceptual space between these two species was fully occupied. These

results help to explain the evolution of signals that appear to be more distinct than necessary for species-specificity.

INTRODUCTION

Species-specific signals allow individuals to recognize conspecifics, to choose optimal mates, and to settle territorial disputes (Bradbury & Vehrencamp 1998). Acoustic interference from background noise can decrease the efficiency of intraspecific communication by affecting the detectability and discriminability of conspecific signals (Endler 1992; Wiley 1994; 2006; Brumm & Slabbekoorn 2005). Detectability is a receiver's ability to separate a signal from background noise, whereas discriminability is the ability to separate two signals. Background noise is ubiquitous in natural environments, from both biotic and abiotic sources. In addition many animals communicate in aggregations, such as frog choruses and avian dawn choruses, that make it especially difficult to detect and to discriminate conspecific from similar heterospecific signals (Bremond 1978; Gerhardt & Huber 2002; Pfennig 2000; Wollerman 1999; Wollerman & Wiley 2002a). To avoid the negative effects of acoustic interference, signalers should evolve signals that contrast with the background noise of their environment (Endler 1993; Miller 1982; Wiley 1994; Wiley 2006).

Heterospecific signals are a common source of background noise with the potential to disrupt intraspecific communication (Nelson and Marler 1990; Wiley 1994; Wollerman 1999; Wollerman & Wiley 2002b). Similar heterospecific signals have a greater chance of causing acoustic interference and creating receiver errors than less similar signals. Features of signal structure that differ distinctly from those of other species should have advantages for conspecific recognition (Emlen 1972; Falls 1963; Marler 1960; Nelson

1988; Nelson & Marler 1990). Thus signals might diverge in multidimensional acoustic space, as defined by acoustic features such as dominant frequency, duration, number of notes, and any other features that characterize the structure of a signal (Littlejohn 1959; Marler 1960; Miller 1982). If species partition acoustic space in this way, in the production of signals, they must also partition perceptual space in a corresponding way. If signal evolution were not matched by receiver evolution communication would fail.

Syntopic birds usually have songs that occupy distinct regions of acoustic space, often separated by gaps between their signals in acoustic space (Nelson & Marler 1990). In effect, acoustic space is not fully occupied for the production of signals. These gaps might serve to enhance the distinctiveness of signals and to reduce errors in signal detection. It remains unclear whether or not the regions of acoustic space in which receivers of different species respond to signals are also disjunct. Alternatively, regions occupied by different species in perceptual space could be overlapping or contiguous. In this case, perceptual space would be fully occupied. Such a disparity between the disjunct occupation of signal space and the continuous occupation of perceptual space might allow for variation in the perception of signals degraded during transmission through the environment (Wiley and Richards 1980, 1982; Naguib and Wiley 2001). Overall, acoustic partitioning would fully occupy the available space, despite the occurrence of gaps in the production of signals. This situation would explain how natural selection can produce the evolution of signals separated in acoustic space more than necessary for species-specificity.

Avian dawn choruses in tropical forests provide an example of communication in the presence of high levels of heterospecific background noise. The combination of high species diversity and a narrow window of time in which the majority of species broadcast

their signals increases opportunities for acoustic competition and limits possibilities for signal divergence. In addition, many Amazonian species live in the forest interior, which increases their reliance on acoustic signals for communication. Although it is clear that each species has a distinct species-specific song, we know little about how these species-specific songs are perceived in acoustically crowded environments.

This study investigates how syntopic species partition their perceptual acoustic space to improve intraspecific acoustic communication. It focuses on two species of Neotropical suboscine passerines that are distantly related but acoustically similar and often syntopic. I manipulated features of both species' songs to create synthetic songs typical of each species and three intermediate versions between their songs. Recognition of songs was tested in experiments that measured the responses of each species to its own song, the other species' song, and the three intermediate versions. The intermediate versions, along a continuum between the two species' songs, allowed me to determine whether or not these species partition their perception of signals in acoustic space disjunctly (with gaps), as they do with the production of signals.

METHODS

Location and species studied

All experiments took place at the Rio Cristalino Private Natural Heritage Preserve, 40 km north-east of the town of Alta Floresta in the state of Mato Grosso, Brazil (9° 41' S, 55° 54' W). Most of the site is lowland tropical moist forest (see Zimmer et al. 1997). In 2004 I collected standardized replicated recordings between 0530 and 0830 in terra firma habitat at Rio Cristalino. In these censuses I detected 51 suboscine species, which sang during more than 1% of the acoustic censuses. To compare their songs I measured 15

acoustic features of songs from 3 individuals of each species. I used principal components analysis (PCA) of the 15 measures to reduce the number of acoustic features to independent variables that could be used to calculate the acoustic space occupied by each species. The first 4 principal components (PCs) had eigenvalues >1 and explained 73 percent of the variation. I averaged the individual PC values for each species to calculate a species mean PC score. To identify nearest-neighbors in acoustic space, I calculated the Euclidean distance between species' mean songs in 4D space, defined by the first 4 PCs (see Luther 2007). Twenty-one species had nearest-neighbors that were reciprocal. From the group of species that were reciprocal nearest-neighbors, I selected *Thamnophilus schistaceus* and *Piprites chloris*, which had the second smallest nearest-neighbor distance (NND), for playback experiments. The species with the smallest NND were not selected because they sang primarily before sunrise and would have been difficult to observe during playback experiments.

Playback experiments on sixteen individuals, 8 Plain-winged Antshrikes *T. schistaceus* and 8 Wing-barred Piprites *P. Chloris*, were conducted in September and October 2006. Both species are territorial and non-migratory. Territories of individuals were delimited by following the movements of singing birds and marking the locations of counter-singing individuals with flagging.

Preparation of songs for playback

Exemplars for playback were prepared from recordings of 5 individuals of each species from Rio Cristalino. These recordings were obtained in May 2006 with a Marantz PMD660 digital recorder (44 kHz digitizing rate, 16-bit accuracy WAV format) and a Sennheiser ME67 ultra directional microphone from distances of 4 - 10 m. They were normalized to maximal amplitude with Wildspectra1 v.051027, www.unc.edu/~rwhiley. One-minute tracks were produced with 4 songs at close to the natural rate of singing. For each playback I randomly chose a track of a male song recorded at least 3 territories away (>500 m).

Song synthesis

To synthesize songs with intermediate features I used Sound Synthesis2 v.060906, www.unc.edu/~rwhiley, a program that uses a spreadsheet of frequencies and amplitudes to specify successive parts of notes. To synthesize each species' natural song I measured songs of 3 individuals from each species and averaged the amplitude, timing, and frequency values for the songs and the notes. The averages specified a mean song for each species. These values were also used to specify intermediate songs with features 2/3, 1/2, and 1/3 the distance between the two species' mean songs (Figure 1). Throughout this paper the synthesized songs will be referred to as 100%, 67%, 50%, 33%, and 0% morphs of a species' song. A 0% morph of one species' song is equal to a 100% morph of the other species' song. The song parameters measured and altered include the length of each note, time between notes, highest frequency of each note, lowest frequency of

each note, shape (number of elements, length of each element, and bandwidth of each element) of each note, length of each song, dominant frequency of each song, number of notes in a song, rate of the song, note with the highest amplitude, bandwidth of the song, the slope of the note, and the change in rate of the song (Table 1). I presented all morphs (100% through 0%) to each individual of both species.

Procedures for playback

All playbacks were conducted within four hours of sunrise. Presentations of natural songs and 100% morphs were conducted before presentations of intermediate morphs. This was necessary to confirm that individuals would respond to synthesized songs. The playback speaker, a RadioShack mini amplifier speaker (9V), was set near the center of a subject's territory, 2 m above the ground, connected with a 5 m lead to an iPod. Since the range of frequencies in the playbacks was limited, frequency response of the speaker had little influence on the fidelity of the played songs. After the speaker was in place, I selected a playback song at random (by rolling a die), subject to the constraints of the experimental design. Playback trials began when the subject had been silent for at least 5 minutes. Each trial lasted 26 min (5 min before playback, 1 min of playback, and 20 min afterwards). All playbacks to an individual were conducted within 5 m of the same location near the center of its territory. Treatments were separated by at least 48 hours to minimize habituation and each subject received the treatments in a random order. Territorial neighbors of the same species were not tested on the same day. All playbacks had the peak sound pressure level (SPL) adjusted to approximate that of natural songs (81dB at 1 m, Realistic digital sound level meter set at C weighting, fast response). I was unable to obtain accurate SPL readings for the two species under study because they sang

5-10 m above ground. Instead I used a level measured for 4 other species of suboscines found in this region (Seddon & Tobias 2006; Seddon & Tobias 2007; see chapter 3).

Individuals were presented their species' natural song and a synthesized song to test whether they would respond equally to both natural songs and synthesized songs.

Playbacks of natural and synthetic songs included 10 subjects, 6 *T. schistaceus* and 4 *P. chloris*. Intermediate song treatments included 16 individuals, 8 from each species.

Thirteen of these 16 subjects received 5 treatments of synthetic songs (Figure 1). The remaining 3 individuals, 2 *P. chloris* and 1 *T. schistaceus* did not receive the treatment of 50% morphs, but did receive the other 4 treatments. They did not receive this treatment because rain prevented or interrupted these experiments.

Response of subjects

During the periods before, during, and after each playback I recorded (1) time from the start of playback to the first visible flight toward the speaker (latency of approach in min), (2) closest distance to the speaker (in m), (3) time spent less than 5 m from the speaker (in min), (4) time from the start of playback to the first song (latency of song in min), (5) total number of minutes singing, (6) number of songs, (7) number of call notes, (8) number of duets, and (9) number of flights by the subject within 1 m of the speaker. Low values for measures (1), (2), and (4) and high values for (3), (5), (6-9) indicated strong responses to playback.

Analysis

SYNTHETIC AND NATURAL SONGS

Since many of the behavioral responses were correlated, I used Principal Component Analysis (PCA) to reduce the measures of response to a smaller number of independent variables. This analysis extracted 3 PCs with eigenvalues >1 which together explained 70% of the variation. PC1, which explained 29% of the variation, was used as the response variable in Wilcoxon signed-ranks matched-pairs tests to compare individual responses to natural and synthesized songs. Statistical tests were calculated with JMP 5.1.

SYNTHETIC INTERMEDIATE SONG FORMS

I again used a PCA to reduce the response measures to a smaller number of independent variables. This analysis extracted 3 PCs with eigenvalues >1, which together explained 77% of the variation (Table 2). PC1, which explained 51% of the variation, was used as a response variable in all tests. An initial investigation of the response variable showed that its relationship to the predictor approximated a logistic S-shaped curve (Figure 2). Based on this observation I fit a nonlinear model in which PC1 was treated as a logistic function of song morph. I rescaled the PC1 response variable with the highest response as 1 and the lowest response as 0 so that I could fit 2-parameter, $y=1/(1+\exp(c+dx))$, and 3-parameter, $y=b/(1+\exp(c+dx))$, logistic functions. To account for multiple observations of individuals nested within bird species, I used mixed-effects models in which each parameter as well as each parameter combination was random. Mixed-effects models offer flexibility by allowing for within-group correlation, which is often present in grouped data. Separate mixed-effects logistic regressions were calculated

for each species with the NLME library of R. I used NLME for the analysis because of its ability to handle grouped data in nonlinear mixed-effects models (Pinheiro & Bates 2000). Using the Akaike Information Criterion (AIC), I compared both fixed-effects and mixed-effects linear, 2-parameter non-linear, and 3-parameter non-linear models.

COMPARISON OF SONG PRODUCTION AND PERCEPTION

To compare song production by the two species, I measured the same parameters used to create the synthesized morphs of songs (Table 1) in randomly selected songs of 7 individuals of each species. PCA reduced parameters to a smaller number of independent variables. This analysis extracted 4 PCs with eigenvalues >1 that together explained 81% of the variation. PC1 and PC2 explained 61% of the variation and were used to calculate the mean and 2 standard deviations around the mean for each species in two-dimensional signal space. To compare song perception, I analyzed individuals' responses to each of the synthesized morphs. PC1 and PC2, which explained 65% of the response variation (Table 2), were used to calculate the mean response and 2 standard deviations around the mean response in two-dimensional response space.

RESULTS

SYNTHETIC AND NATURAL SONGS

Both species responded aggressively to natural songs and 100% morphs. *T. schistaceus* showed essentially equal response toward both playbacks in latency of response, proximity to the speaker, number of minutes singing, number of duets, and the number of songs. *T. schistaceus* spent more time closer to the speaker after natural songs, but flew by the speaker and called more frequently after the 100% morphs. *P. chloris*

spent more time close to the speaker and flew by the speaker more frequently after natural song playbacks, but also responded with a shorter latency of song, spent more time singing and calling, and sang more songs after the 100% morphs. There was no statistical difference ($N = 10$, $T = 12.5$, $p = 0.232$) in responses to synthetic and natural songs (Figure 3). Responses to synthetic and natural songs had mean PC1 scores close to zero (0.37 and -0.37 , respectively).

SYNTHETIC INTERMEDIATE SONG FORMS

All 8 *T. schistaceus* responded to the 100% morphs while only 7, 6, 2, and 0 individuals responded to versions with 67%, 50%, 33%, and 0% of conspecific features, respectively. All 8 *P. chloris* responded to 100% and 67% morphs, while only 5, 2, and 2 individuals responded to 50%, 33%, and 0% morphs, respectively. Both species responded more strongly to 100% and 67% morphs (with respect to their own species) than to the other 3 treatments. In general the strong responses included shorter latency of approach and song, closer approaches, a greater number of songs, calls, duets, number of minutes singing, number of flights past the speaker, and time spent closer to the speaker (Figure 4).

Each species also responded in characteristic ways. In a comparison of both species' responses to 100% morphs, *T. schistaceus* showed shorter latency of song, spent more time singing, and sang more songs and duets, while *P. chloris* spent more time close to the speaker and flew by the speaker more frequently. In responses to 67% morphs, *P. chloris* was closer to and spent more time next to the speaker, and showed a shorter latency of song, and *T. schistaceus* spent more time singing and sang more duets than *P. chloris*. In response to 50% morphs, *P. chloris* was closer to the speaker, but showed

longer latency of approach than *T. schistaceus*. A comparison of responses to 33% and 0% morphs revealed that the two species responded at equally low levels. In general, strong responses by *T. schistaceus* involved more singing and more time spent singing, while responses of *P. chloris* included a closer proximity to the speaker and more time spent near the speaker.

For both species the best models for predicting responses to song morphs were 3-parameter non-linear fixed-effects models (Table 3, Figure 5). The 3-parameter and 2-parameter mixed-effects models that incorporated multiple random parameters failed to converge. The 2- and 3-parameter mixed-effects models that included one random parameter converged on fixed-effects models, with no random effects. In the best model for *T. schistaceus* and *P. chloris*, parameters c and d, associated with the inflection point of the model's curve, were highly correlated with each other (-0.93 and -0.98, respectively). Parameter b, associated with the steepness of the curve, was moderately correlated with parameters c and d in the *P. chloris* model (0.72 and -0.66, respectively) but less so in the best model for *T. schistaceus* (-0.39 and 0.64, respectively). 3-parameter model coefficient b was almost identical for *T. schistaceus* and for *P. chloris* ($b = 0.68 \pm 0.09$, $b = 0.68 \pm 0.08$, respectively). Coefficients c and d had similar but inverse values, because the inflection points of both species' response curves were in opposite directions ($c = 3.38 \pm 1.08$ and $d = -6.48$ for *T. schistaceus* and $c = -4.28 \pm 2.40$ and $d = 8.40 \pm 4.01$ for *P. chloris*).

DISPERSION OF SONG PRODUCTION AND PERCEPTION

Song production for both species was disjunct (Figure 6). Even with a buffer of 2 standard deviations around each species' song there was no overlap in song production. The intermediate morphs were farther than 2 standard deviations from the 100% morphs. Song perception was more crowded than song production. Two standard deviations around responses to each morph revealed that 100% and 67% morphs received similar responses (Figure 6). The responses to 50% morphs overlapped with responses to 100% and 67% morphs.

DISCUSSION

Songs of two acoustically similar avian species were synthesized to test the hypothesis that acoustic perceptual space is partitioned to optimize correct responses to conspecific acoustic signals in complex noisy environments. Both species responded similarly to natural and synthetic versions of their songs. In fact, responses to synthetic songs were slightly stronger, perhaps due to the lack of background noise in the synthetic songs. Responses were strong to 100% and 67% morphs, moderate to low to 50% morphs, and low to absent to 33% and 0% morphs. The diminishing responses between 67%, 50%, and 33% morphs exhibited by both species indicate a contiguity in signal perception along the conspecific-heterospecific continuum. For these species, the acoustic perceptual space is full with no perceptual gap between these 2 species' signals.

This contiguous acoustic perceptual space could be a product of the species' locations in the acoustic community signal space. Acoustic community signal space is the acoustic signal space occupied by all of the vocally active syntopic species. The species in this

study are near the center of the acoustic community signal space. As a consequence, most of their signal features are similar to the signal features of other species in the community (see chapter 2). Both the acoustic signal space and the acoustic perceptual space of each species should be more tightly packed than those spaces would be for species with signals near the periphery of the acoustic community signal space (Nelson & Marler 1990; Wollerman & Wiley 2002b). Crowding at the center of signal space should result in increased acoustic interference, which in turn could lead to increased pressure for partitioning of both acoustic signal space and acoustic perceptual space.

Both species' songs occupied similar signal space. Most of the features of their songs had values that overlapped (Table 1). However the combination of all measured features in a principal components analysis revealed that the two species' songs are separated by a gap. The signal space is thus disjunct while the perceptual space is full.

The results were analyzed with a mixed-effects model to include the individual variation within a species' behavioral responses to different morphs. Despite the inclusion of random-effects to explain the individual variation, the best models were fixed-effects models. The small sample size of 8 individuals per species combined with individual responses to 5 morphs appears to make estimating mixed-effects models impractical because the variation with each individual is greater than the variation between individuals. Thus the models settled on the population averages, the fixed-effects, rather than the individual variation, the random-effects. Despite the small sample size and large amount of individual variation, the curvilinear pattern of mean responses by both species supports the suggestion that the two species occupy acoustic perceptual space completely but with minimal overlap.

Previous studies of acoustic partitioning have focused on differences in signal production (Chek et al. 2003; Drewry & Rand 1983; Duellman & Pyles 1983; Hodl 1977; Littlejohn 1959) rather than signal perception. These studies have documented avoidance of interspecific overlap of signals in birds (Cody & Brown 1969; Ficken et al. 1974), frogs (Littlejohn 1959; Schwartz & Wells 1984), and insects (Greenfield 1988), but documenting partitioning of signal space has been more difficult. Results from studies that have investigated temporal (Sueur 2002), spectral (Chek et al. 2003; Hodl 1977; Littlejohn 1959) and spatial (Chek et al. 2003; Drewry & Rand 1983; Duellman & Pyles 1983) signal partitioning have documented differences in syntopic species' signals and signaling behavior but have not conclusively supported signal partitioning. Most of these studies described the differences in acoustic signals, spatial separation of signalers, and timing of signaling among species in the same community. Check et al. (2003) used null models to test for overdispersion among species-specific acoustic signals and found evidence for overdispersion in 3 out of 11 communities of frogs. The communities with the highest diversity exhibited the most dispersion. While these studies of partitioning have focused on patterns of signal production, there has been no previous attention to partitioning of perceptual space.

In realistic situations, receivers usually must detect and discriminate signals in the presence of background noise. Signals are more effectively masked by noise in the spectral region of the signal than by noise in other parts of the spectrum (Lohr et al. 2003). Noise from other individuals and species can interfere with detection and discrimination of signals (Gerhardt & Klump 1988; Wollerman 1999; Wollerman & Wiley 2002a). Together these results indicate that acoustic interference from heterospecific signals can be a serious problem for intraspecific communication.

Acoustic interference depends on a receiver's auditory tuning as well as the signal's frequency. Amezcuita et al (2006) studied geographic variation of both signal and perceptual properties in the frog *Allobates femoralis* to determine whether or not the variation in calls is affected by the presence of *Epipedobates trivittatus*, a sympatric species with calls that overlap in frequency. Sympatric populations of *A. femoralis* responded to a smaller range of frequencies than did allopatric populations, especially at low frequencies where the possibility of confusion was greatest. This is one example among several of perceptual tuning influenced by sympatric species (Gerhardt 1994; Hobel & Gerhardt 2003). No previous study, however, has attempted to determine if perceptual space is fully occupied, as indicated by the present experiment.

Saturated perceptual space could be an evolutionary response to communication in a noisy environment. Between the time when a signal is broadcast and received, it often becomes degraded by the physical environment and mixed with background noise (Wiley & Richards 1982; Naguib & Wiley 2001). Consequently receivers cannot afford to be too narrowly focused on the exact parameters of a clean signal. Broad perceptual tuning could also explain why there are gaps in acoustic signal space. Signals should contrast with each other more than minimally in order to allow receivers to perceive the differences between signals that have been degraded during signal transmission. Partitioning of signal space in this situation is more disjunct than would be necessary to avoid overlap in the absence of degradation and background noise.

Acknowledgements

Haven Wiley helped in all aspects of this project. Jack Weiss provided statistical advice. Maria Alice dos Santos Silva and Mario Cohn-Haft helped with Brazilian

research visas, and John Luther, Amy Upgren, Brad Davis, Vitoria da Riva Carvalho, and the staff of the Rio Cristalino RPPN assisted in the field. Amy Upgren and Barbara Ballentine provided helpful comments to early versions of this manuscript. Support for this research came from the Mellon Foundation, Explorer's Club, International and Latin American Studies at UNC, the UNC Graduate School, and the Biology Department's Behavioral Research Fund.

REFERENCES

- Amezquita, A., Hodl, W., Lima, A. P., Castellanos, L., Erdtmann, L. & Carmozina De Araujo, M. 2006 Masking interference and the evolution of the acoustic communication system in the Amazonian dendrobatid frog *Allobates femoralis*. *Evolution* **60**, 1874-1887.
- Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*: Sunderland, Mass. : Sinauer Associates.
- Bremond, J. C. 1978 Acoustic competition between the song of the wren (*Troglodytes troglodytes*) and the songs of other species. *Behaviour* **65**, 89-98.
- Brumm, H. & Slabbekoorn, H. 2005 Acoustic communication in noise. *Advances in the Study of Behavior* **35**, 151-209.
- Chek, A. A., Bogart, J. P. & Loughheed, S. C. 2003 Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecology Letters* **6**, 235-247.
- Cody, M. L. & Brown, J. H. 1969 Song asynchrony in neighboring bird species. *Nature* **222**, 778-780.
- Drewry, G. E. & Rand, A. S. 1983 Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus*. *Copeia* **1983**, 941-953.
- Duellman, W. E. & Pyles, R. A. 1983 Acoustic resource partitioning in anuran communities. *Copeia* **1983**, 639-649.
- Emlen, S. T. 1972 An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* **41**, 130-171.
- Endler, J. A. 1992 Signals, signal conditions, and the direction of evolution. *American Naturalist* **139**, S125-S153.
- Endler, J. A. 1993 The color of light in forests and its implications. *Ecological Monographs* **63**, 1-27.
- Falls, J. B. 1963 Properties of bird song eliciting response from territorial males. In *Proceedings of the International Ornithological Congress*, vol. 13, pp. 259-271.
- Ficken, R. W., Ficken, M. S. & Hailman, J. P. 1974 Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* **183**, 762 - 763.
- Gerhardt, H. C. 1994 The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics* **25**, 293-324.

- Gerhardt, H. C. & Huber, F. 2002 *Acoustic communication in insects and anurans: common problems and diverse solutions*. Chicago: University of Chicago Press.
- Gerhardt, H.C. & Klump, G.M. 1988 Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Animal Behaviour* **36**, 1247-1249.
- Greenfield, M. D. 1988 Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* **36**, 684-695.
- Hobel, G. & Gerhardt, H. C. 2003 Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* **57**, 894-904.
- Hodl, W. 1977 Call differences and calling site segregation in anuran species from central amazonian floating meadows. *Oecologia* **28**, 351-363.
- Littlejohn, M. J. 1959 Call differentiation in a complex of seven species of *Crinia* (Anura, Leptodactylidae). *Evolution* **13**, 452-468.
- Lohr, B., Wright, T. F. & Dooling, R. J. 2003 Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour* **65**, 763 - 777.
- Marler, P. 1960 Bird songs and mate selection. In *Animal sounds and communication*, vol. 7 (ed. W. E. Lanyon & W. N. Tavolga), pp. 348-367. Washington D.C.: American Institute of Biological Sciences.
- McGarigal, K., Cushman, S. & Stafford, S. 2000 *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- Miller, E. H. 1982 Character and variance shift in acoustic signals of birds. In *Acoustic communication in birds*, vol. 1 (ed. D. E. Kroodsma & E. H. Miller), pp. 253-295. New York: Academic Press.
- Naguib, M. & Wiley, R.H. 2001 Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour* **62**, 825-837.
- Nelson, D. A. 1988 Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* **106**, 158-182.
- Nelson, D. A. & Marler, P. 1990 The perception of bird song and an ecological concept of signal space. In *Comparative perception, Vol. 2, Complex signals*, vol. 2 (ed. W. C. a. B. Stebbins, M.A.), pp. 443-78. New York: Wiley.
- Pfennig, K. S. 2000 Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behavioral Ecology* **11**, 220-227.

- Pinheiro, J. C. & Bates, D. M. 2000 *Mixed-effects models in S and S-Plus*. Statistics and Computing. New York: Springer.
- Schwartz, J. J. & Wells, K. D. 1984 Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behavioral Ecology and Sociobiology* **14**, 211-224.
- Seddon, N. & Tobias, J. A. 2006 Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behavioral Ecology* **17**, 73-83.
- Seddon, N. & Tobias, J. A. 2007 Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biological Journal of the Linnean Society* **90**, 173-188.
- Sueur, J. 2002 Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera : Cicadomorpha : Cicadidae). *Biological Journal of the Linnean Society* **75**, 379-394.
- Wiley, R. H. 1994 Errors, exaggeration, and deception in animal communication. In *Behavioral mechanisms in evolutionary ecology* (ed. L. A. Real), pp. 157-189. Chicago: University of Chicago Press.
- Wiley, R. H. 2006 Signal detection and animal communication. *Advances in the Study of Behavior* **36**, 217-247.
- Wiley, R.H. & Richards, D. G. 1982 Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 131-181. New York & London: Academic Press.
- Wollerman, L. 1999 Acoustic interference limits call detection in a neotropical frog *Hyla ebreccata*. *Animal Behaviour* **57**, 529 - 536.
- Wollerman, L. & Wiley, R. H. 2002a Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour* **63**, 15-22.
- Wollerman, L. & Wiley, R. H. 2002b Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* **52**, 465-473.
- Zimmer, K. J., Parker, T. A., Isler, M. L. & Isler, P. R. 1997 Survey of a southern amazonian avifauna: the Alta Floresta region, Mato Grosso, Brazil. *Ornithological Monographs* **48**, 887-918.

Table 1. Parameters of synthesized songs. Frequencies are in Hertz and times are in milliseconds.

Song Type	Number of Notes	Length of Note			Low Frequency of Note			High Frequency of Note			Distance Between Notes			Number of Elements per Note			
		First	Average	Last	First	Average	Last	First	Average	Last	First	Second	Last T.	First	Average	Last	
Piprites chloris 100%	8.0	119.0	86.6	87.0	1378.0	1464.0	1464.0	1464.0	1550.0	.0	136.0	191.8	104.0	NA	1.0	2.6	1.0
P. chloris 67%									1550								
T. schistaceus 33%	8.3	139.3	99.7	98.3	1521.3	1492.7	1291.7	1578.7	1607.3	.0	186.3	190.7	112.0	NA	1.0	1.7	2.0
P. chloris 50%									1550								
T. schistaceus 50%	8.5	149.5	106.2	104.0	1593.0	1507.0	1205.5	1636.0	1636.0	.0	211.5	190.1	116.0	37.0	1.0	1.3	2.0
P. chloris 33%									1550								
T. schistaceus 67%	8.7	159.7	112.8	109.7	1664.7	1521.3	1119.3	1693.3	1664.7	.0	236.7	189.5	120.0	NA	1.0	1.3	2.0
Thamnophilus schistaceus 100%	9.0	180.0	125.9	121.0	1808.0	1550.0	947.0	1808.0	1722.0	.0	287.0	188.4	128.0	37.0	1.0	1.0	2.0
Difference between P. chloris & T. schistaceus	1.0	61.0	53.6	34.0	430.0	86.0	517.0	344.0	172.0	0.0	151.0	100.2	24.0	37.0	1.0	1.0	2.0
Confidence intervals																	
P. chloris N=7	1	19.3	33.7	21.7	48.2	50.3	44.0	68.1	58.9	96.3	44.6	63.7	39.0	NA	0.0	0.4	0.0
Confidence intervals																	
P. schistaceus N=7	0	36.8	29.8	20.6	79.9	82.7	71.2	70.9	73.5	68.1	15.8	15.2	NA	15.5	0.0	0.0	0.0
Overlap between species N=7	2	12	77	64	86	86	345	86	115	258	-12	112	371	NA	0	2	-1

TABLE 2. Factor loadings for the first three principal components derived from behavioral responses to playback experiments (see Figure 4).

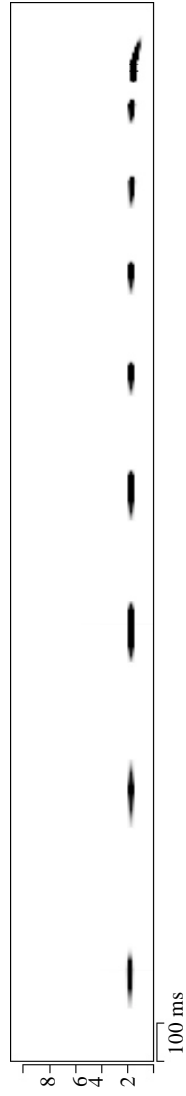
	PC1	PC2	PC3
Eigenvalue	4.58	1.29	1.05
Percent of variation explained	50.86	14.38	11.71
Latency of response (min)	-0.37	0.05	0.36
Closest distance to speaker (m)	-0.36	0.29	-0.16
Time spent less than 5 m (min)	0.36	-0.31	0.30
Latency of song (min)	-0.38	-0.05	0.37
Number of minutes singing response (min)	0.42	0.24	-0.08
Number of songs	0.38	0.37	-0.04
Number of calls	0.10	-0.49	-0.49
Number of duets	0.21	0.54	0.21
Number of flybys	0.29	-0.30	0.57

Bold denotes variables with factor loading > 0.3 (McGarigal et al. 2000).

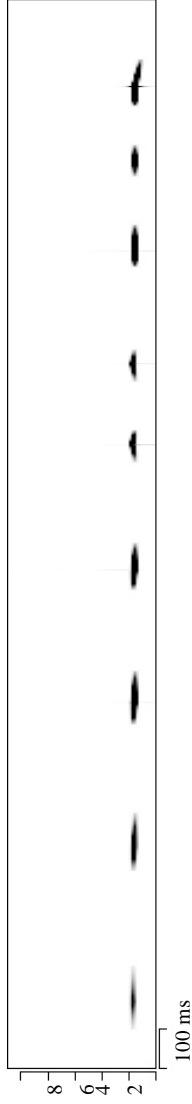
Table 3. Comparison of models. The AIC score with the lowest value represents the model with the best fit.

Model	Description	Parameters	<i>T. schistaceus</i>		<i>P. chloris</i>	
			AIC	LogLik	AIC	LogLik
1	Linear	1	-18.18	12.09	-5.68	5.84
2	Fixed-effects	2	-18.18	12.09	-7.44	6.72
3	Mixed-effects, c	2	-14.26	12.13	-4.78	7.39
4	Mixed-effects, d	2	-14.45	12.23	-4.2	7.1
5	Fixed-effects	3	-19.15	13.58	-7.98	7.99
6	Mixed-effects, c	3	-15.42	13.7	Failed to converge	
7	Mixed-effects, d	3	-15.59	13.8	-5.85	8.92

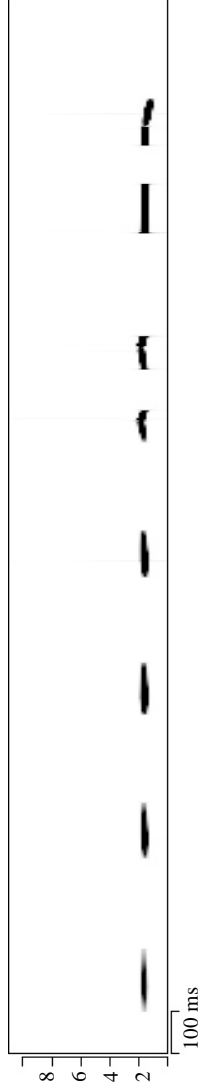
100% *T. schistaceus*
0% *P. chloris*



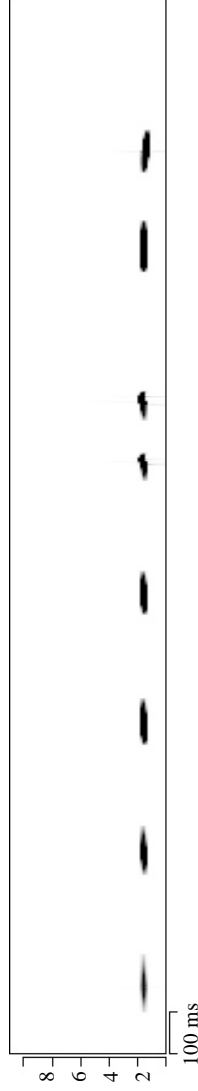
67% *T. schistaceus*
33% *P. chloris*



50% *T. schistaceus*
50% *P. chloris*



33% *T. schistaceus*
67% *P. chloris*



100% *P. chloris*
0% *T. schistaceus*

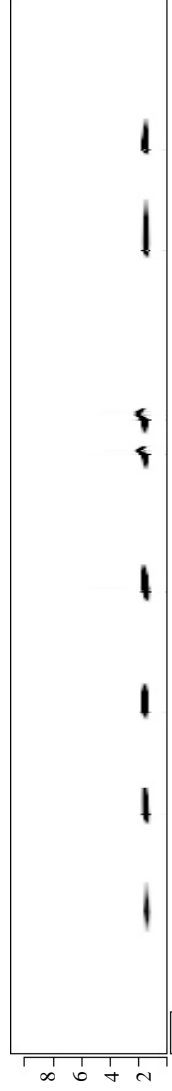


Figure 1. Sonograms of synthesized songs (see text for explanations of the different morphs).

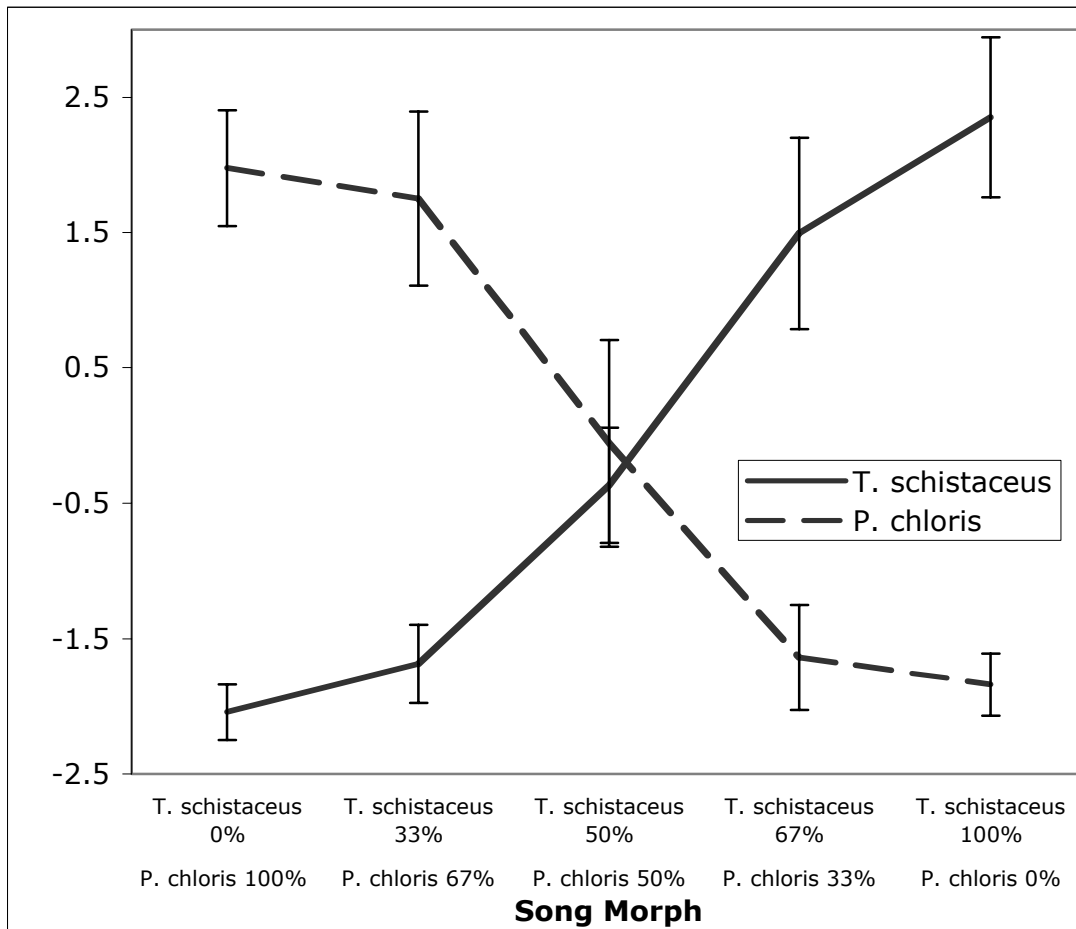


Figure 2. Mean responses (\pm SE) of each species to the different synthesized morphs.

High values of PC1 represent a strong response.

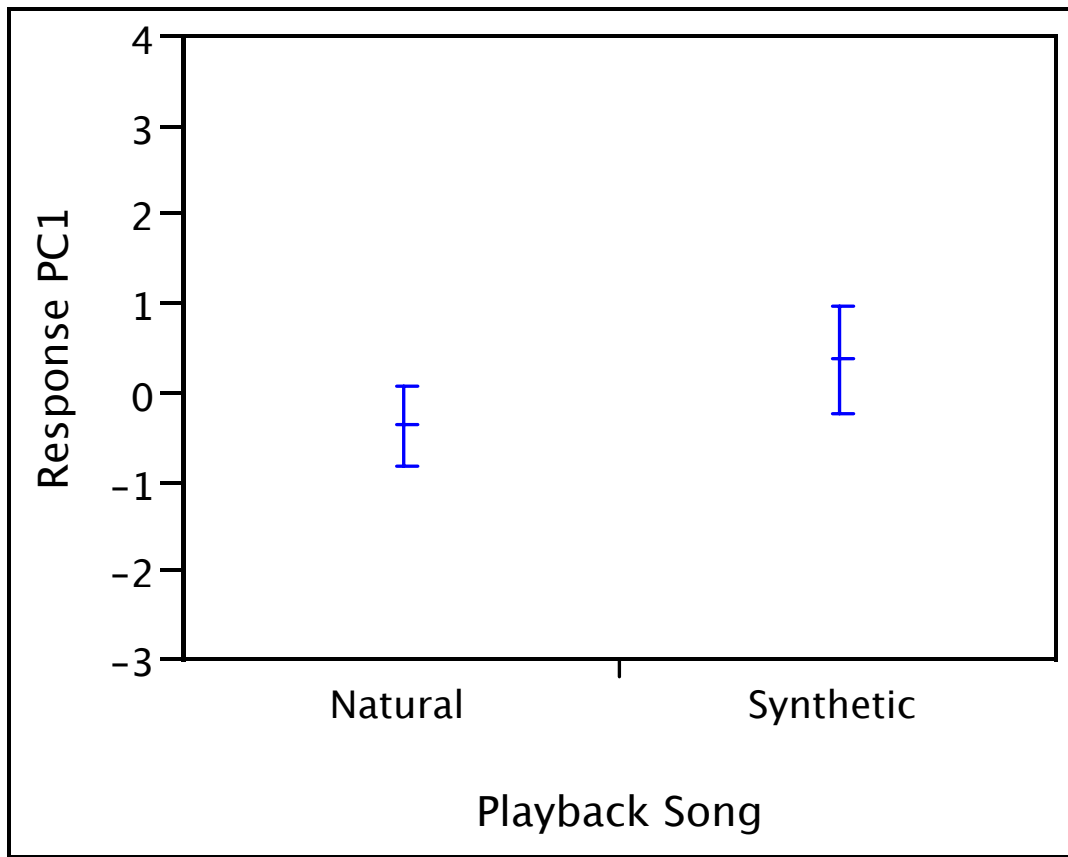
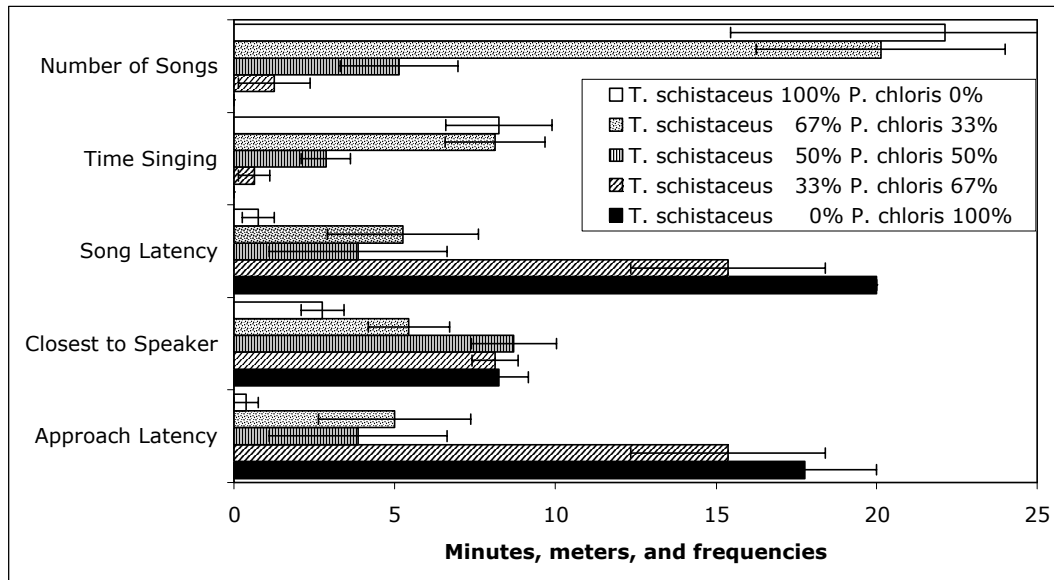


Figure 3. Mean responses (\pm SE) of *T. schistaceus* and *P. chloris* to playback of natural songs and synthesized songs. High values of PC1 represent a strong response.

(A)



(B)

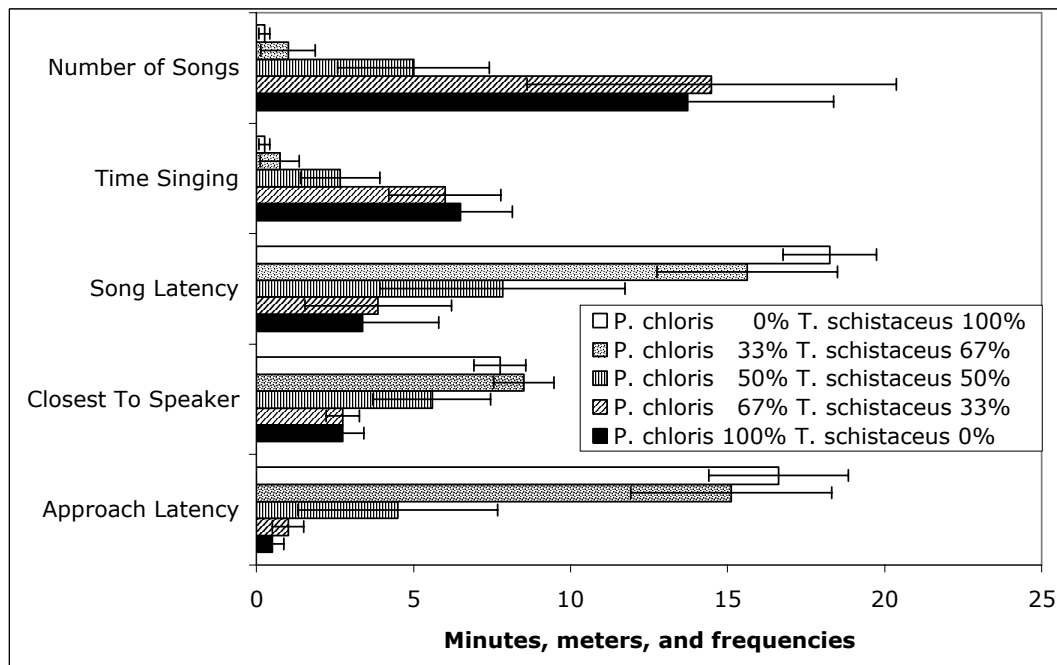


Figure 4. Mean responses (\pm SE) of (A) *Thamnophilus schistaceus* and (B) *Piprites chloris* to different morphs. See text for description of measures.

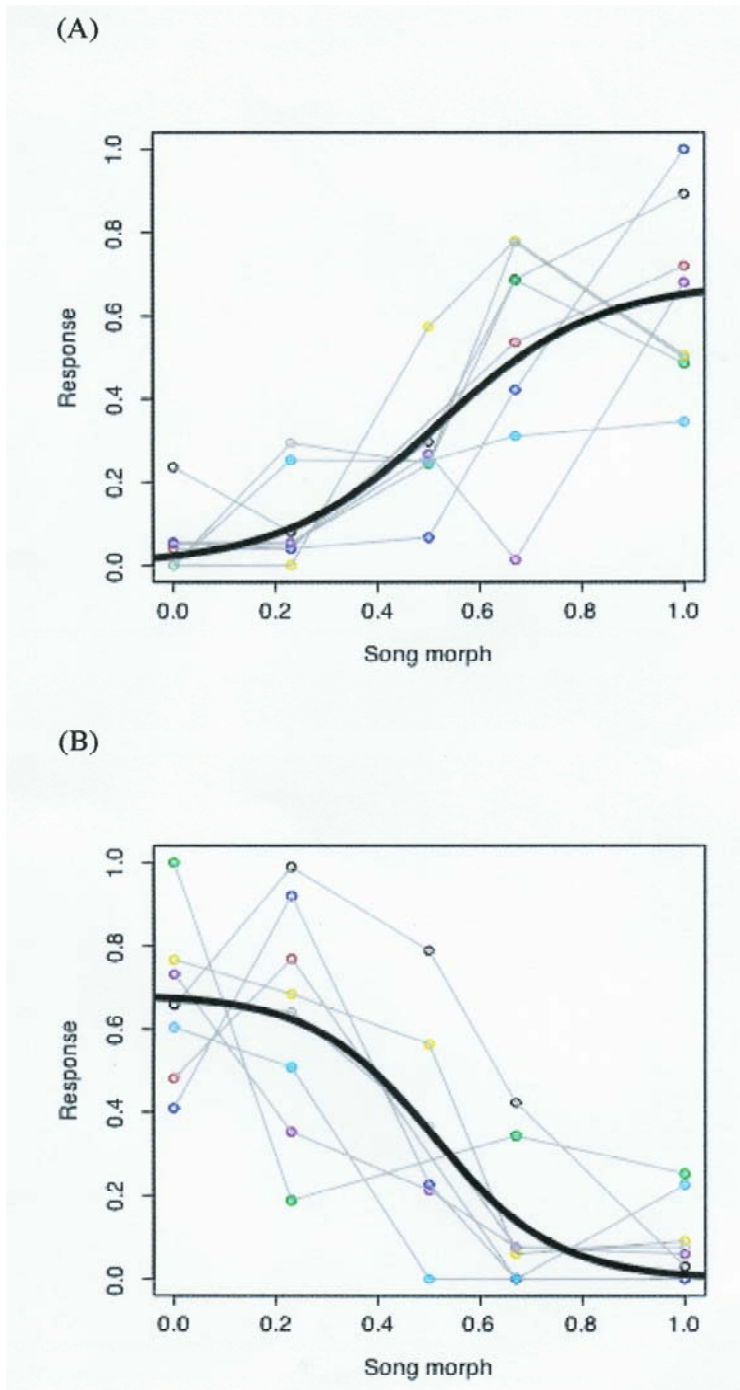


Figure 5. Logistic regression of behavioral responses by (A) *Thamnophilus schistaceus* and (B) *Piprites chloris*, y-axis, to each morph, x-axis. 1.0 is 100% of a species' song and 0.0 is 100% of the acoustic nearest-neighbor's song. Light gray lines represent individual responses.

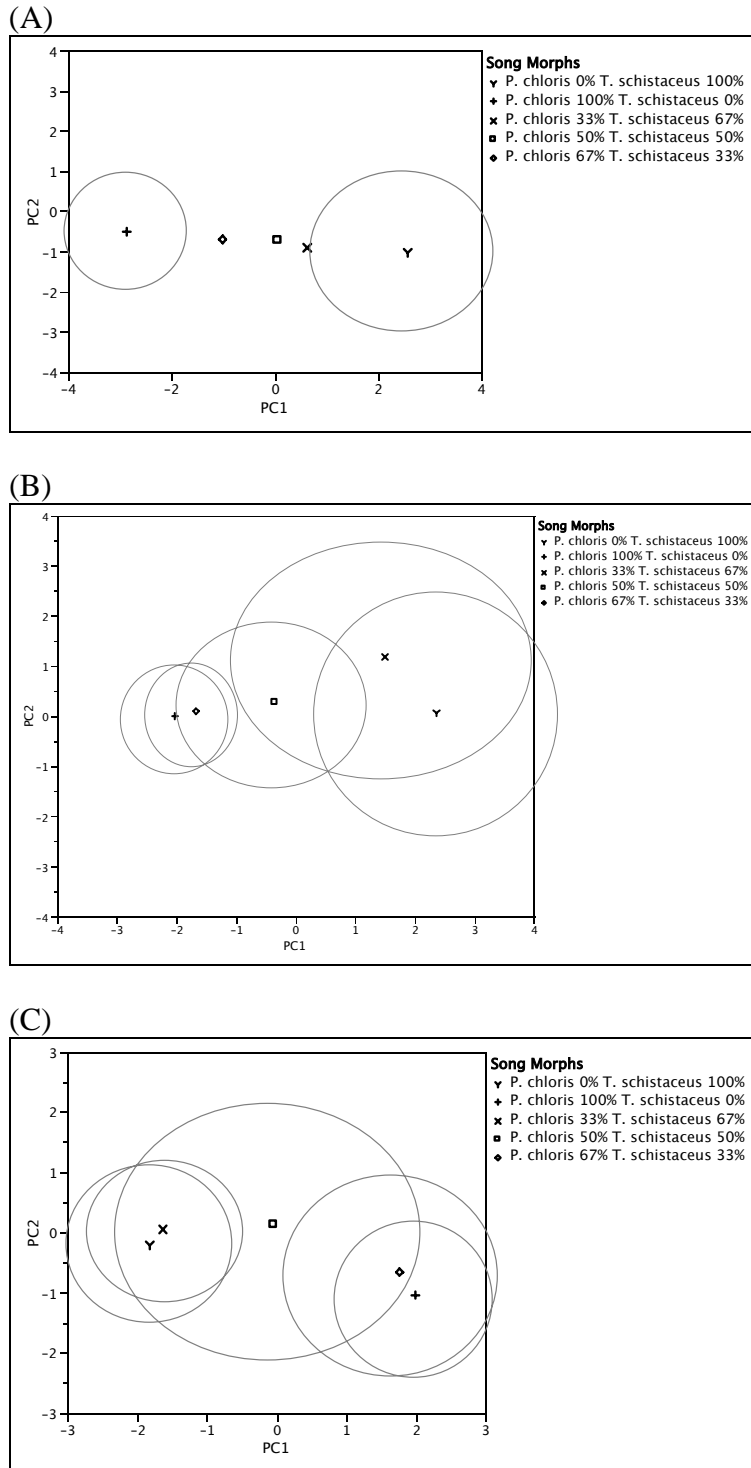


Figure 6. Means and 2-standard-deviation ellipses for morphs of songs in (A) signal space and in perceptual space for (B) *Thamnophilus schistaceus* and (C) *Piprites chloris*.

CONCLUSION

Animals rely on long-range communication for species recognition, mate selection, and territorial defense. The study of these signals improves our understanding of evolutionary processes such as sexual selection and speciation, yet environmental influences on the evolution of these signals are not well understood. To communicate efficiently, animals must produce signals that are obvious to receivers in their environment. Studies have shown that the physical environment influences the transmission and evolution of species' acoustic signals. In contrast, little is known about the influence of background noise on animal communication. Background noise can come from both abiotic and biotic sources, such as wind, water, distantly related taxa, heterospecific species, and conspecific individuals. To avoid errors in communication, signals, such as bird songs, should evolve to contrast with background noise.

Before a receiver can react to a signal, it must detect and discriminate the signal against the background noise of its environment, including other species' signals. For effective communication, and to avoid potential errors of recognition, species' signals need to be distinguishable from one another. Such errors include responses to signals from different species, which could lead individuals to mate with inappropriate species, or the lack of a response to appropriate signals, which could result in additional time and risks in finding a mate and defending resources. Therefore, species' signals that overlap in space and time might diverge through natural selection to minimize confusion with similar signals from other species.

To reduce potential confusion with other species' signals, species might partition acoustic signal space, the multidimensional space defined by features of signals, such as dominant frequency, duration, note length, and any other feature that is important for signal recognition. Thus, through natural selection, species' signals could evolve to maximize differences with other species' signals in the same community. However, partitioning acoustic signal space will only be effective if acoustic perceptual space is partitioned in a corresponding way. If signal evolution were not matched by receiver evolution communication would fail.

Previous studies of acoustic partitioning have focused on differences in signal production rather than signal perception. In addition, these studies investigated temporal, spectral, and spatial acoustic signal space partitioning in birds, frogs, and insects, and found differences in syntopic species' signals and behavior but have not conclusively supported competition for acoustic space as the cause of signal divergence. Previous studies described the differences in acoustic signals, spatial separation of signalers, and timing of signaling among species living in the same community but did not conduct statistical community-wide comparisons of signal dispersion in acoustic signal space. While these studies of partitioning have focused on patterns of signal production, to my knowledge there has been no investigation of acoustic perceptual space partitioning.

My research analyzed bird songs to determine whether the timing of signal transmission, the structure of signals, or both, serve to partition the acoustic space among different species' signals. I used a combination of acoustic censuses and field experiments to investigate acoustic partitioning. With the censuses, I documented the exact times and places at which species sing, and measured the song features that determine the location of each species' song in acoustic space. Playback experiments in

the field enabled me to test predictions about acoustic partitioning of a song's features and the timing of signal transmission in both acoustic signal space and acoustic perceptual space. Combined the census and experimental data provided me with the means to examine the influence of background noise from heterospecific species on the evolution of acoustic communication in both signalers and receivers.

To investigate acoustic signal space partitioning I examined the dispersion of 82 species' songs, relative to each other, in acoustic space. I also examined the dispersion of congeners in comparison to other pairs of species and the degree of crowding in the center of occupied acoustic space in comparison to the periphery. Analyses of the acoustic censuses revealed that songs of species that were in the same strata and sang during the same 30-min intervals had more dispersed signals than species that sing together over the course of the whole morning or species that sing in different strata. Therefore, it appears that the songs of species that sing near each other most frequently have coevolved to reduce acoustic interference from each other's songs.

Songs of congeners were no more dispersed than random species' songs, providing evidence that congeners face no greater consequences for recognition errors to conspecific signals than to the signals of distantly related species. Songs near the center of acoustic space were more crowded than songs near the periphery, which indicates that species near the center face different challenges in communication than species on the periphery. In addition, species near the center sang more frequently than species further from the center. By repeating their songs more frequently individuals increase the chances that their songs will be detected in a noisy environment.

To investigate temporal partitioning of acoustic perceptual space I tested the responsiveness of territorial birds to conspecific songs at typical and atypical times

during the dawn chorus. The study focused on four species, 2 that sing primarily early and 2 that sing primarily late in the dawn chorus. Each of the four species responded more to playbacks at its- own typical time of vocalization. The results indicate that syntopic species of birds temporally partition the dawn chorus both in production and perception in a way that would reduce heterospecific interference in communication.

A novel experimental procedure allowed me to compare the partitioning of acoustic signal space and acoustic perceptual space. To assess partitioning of acoustic signal space, I measured and compared the features of acoustically similar songs of 2 sympatric species. As with most other sympatric species, these 2 produced signals that occupied disjunct regions of signal space, with a gap between them. To assess partitioning of perceptual acoustic space, I played synthesized versions of the 2 species' songs and three intermediate versions to individuals of both species in the field. Both species responded to versions outside their normal range of songs. All song versions received responses from one or the other species, but with little overlap between the 2 species' responses. Unlike signal space, perceptual space had no gaps between species. Acoustic perceptual space between these 2 species was fully occupied.

This study attempted to characterize the locations of species-specific signals relative to each other in acoustic space, as well as the spatial, temporal, and phylogenetic factors that might determine their dispersion in acoustic space. In addition, it is the first study to investigate acoustic perceptual space in a multi-species community. The results of this study indicate that signalers and receivers have evolved distinct strategies to reduce errors in recognizing conspecific signals. The first experiment indicated that signalers and receivers coordinate the timing of their communication within the dawn chorus. This correspondence could result from mutual coevolution to find distinct channels for

communication, a coincidence of limitations on activity, or a signalers exploitation of receiver predisposition. In the present case, the first possibility seems the most likely. The second experiment revealed that, at least for some species, partitioning of acoustic signal space is disjunct, with gaps between nearest species' signals, but partitioning of acoustic perceptual space is saturated. Since signals are degraded as they travel through the environment, receivers must respond to degraded signals mixed with background noise. This situation could help to explain the disjunct partitioning of acoustic signal space more than that necessary to avoid overlap. Receivers allow more variation in perception of signals than signalers include at the source.

APPENDIX A

LIST OF SPECIES IN THE ACOUSTIC COMMUNITY

Species	PC1	PC2	NND	Majority of singing during the morning
Crypturellus cinereus	-2.71	-1.83	0.38	equal
Crypturellus obsoletus	-1.03	0.27	0.32	before sunrise
Crypturellus strigulosus	-2.92	-1.35	1.34	8AM
Crypturellus variegatus	-1.71	0.20	0.61	around sunrise
Micrastur cryptic	-0.22	1.21	1.91	before sunrise
Penelope jacquacu	-1.39	1.37	0.84	before sunrise
Columba plumbea	-2.78	0.81	0.78	8AM
Columba subvinacea	-2.57	1.32	0.63	7AM & 8AM
Leptotila rufaxilla	-3.61	-0.79	1.22	8AM
Otus watsonii	-2.33	2.21	1.00	before sunrise
Nyctiphrynus ocellatus	-2.72	-1.61	0.37	before sunrise
Trogon collaris	-1.33	1.49	0.50	equal
Trogon melanurus	-2.16	2.03	1.00	equal
Trogon violaceus	-1.64	1.04	0.17	7AM
Trogon viridis	-1.37	1.28	0.50	equal
Momotus momota	-3.14	-0.08	1.27	before sunrise
Galbula cyanicollis	-0.71	-0.30	0.99	equal
Jacamerops aurea	-1.70	-2.44	0.64	before sunrise
Monasa morphoeus	-0.58	1.39	1.84	equal
Pteroglossus beauharnaesii	-1.32	1.51	0.94	equal
Ramphastos tucanus	-2.68	-1.32	0.06	7AM & 8AM
Ramphastos vitallinus	-1.75	-1.86	0.59	8AM & 7AM
Celeus torquatus	-1.05	0.52	0.64	sunrise
Veniliornis affinis	0.77	1.15	1.01	before sunrise
Glyphorhynchus spirurus	9.80	1.98	6.99	8AM
Dendrexetastes rufigula	0.62	2.48	0.93	before sunrise
Xiphocolaptes promeropirhynchus	-0.25	0.73	1.10	before sunrise
Dendrocolaptes certhia concolor	-0.31	0.82	0.41	before sunrise
Xiphorhynchus guttatus eytoni1	-0.34	1.91	1.02	before sunrise
Xiphorhynchus guttatus eytoni2	-0.99	-0.02	0.69	before sunrise
Xiphorhynchus spixii	3.98	2.23	2.54	8AM
Campylorhamphus procurvoldes multistriatus	-0.45	0.88	1.12	sunrise & 7AM
Synallaxis cherriei	1.05	0.12	0.82	before sunrise

<i>Hyloctistes subulatus</i>	-0.32	-1.78	1.05	equal
<i>Automolus dorsalis</i>	-0.71	0.62	0.45	7AM
<i>Automolus rufipileatus</i>	1.69	1.16	1.31	equal
<i>Xenops minutus</i>	4.94	-1.26	2.33	equal
<i>Sclerurus rufigularis rufigularis</i>	2.39	-1.11	0.57	equal
<i>Cymbilaimus lineatus</i>	-1.66	0.92	0.17	equal
<i>Thamnophilus palliatus palliatus</i>	-0.34	0.88	0.83	8AM
<i>Thamnophilus schistaceus</i>	-1.55	0.22	0.61	before sunrise
<i>Thamnomanes caesius</i>	2.66	0.61	1.35	sunrise
<i>Myrmotherula brachyura</i>	0.03	0.06	0.90	equal
<i>Myrmotherula hauxwelli</i>	1.92	-1.10	1.19	sunrise
<i>Myrmotherula leucophthalma sordida</i>	4.01	-3.28	2.45	equal
<i>Myrmotherula longipennis transitiva</i>	0.72	-1.20	0.93	equal
<i>Microrhophias quixensis emiliae</i>	2.12	-1.23	0.95	equal
<i>Dichrozona cincta</i>	0.07	-0.26	1.62	equal
<i>Drymophila devillei subochracea</i>	3.53	-0.26	1.70	equal
<i>Cecromacra cinerascens</i>	-0.87	0.05	0.41	equal
<i>Cecromacra manu</i>	-1.52	0.35	1.34	around sunrise
<i>Myrmoborus leucophrys</i>	1.10	1.61	0.62	sunrise
<i>Myrmoborus myiotherinus</i>	1.64	-0.49	0.47	sunrise
<i>Hypocnemis cantator striata</i>	1.47	-0.63	0.90	sunrise
<i>Rhegmatorhina gymnops</i>	0.80	-2.16	0.99	sunrise
<i>Hylophilax naevia ochracea</i>	2.72	-1.05	0.57	sunrise
<i>Phlegopsis nigromaculata bocumani</i>	-0.74	-2.36	1.05	sunrise
<i>Formicarius analis</i>	-0.99	0.52	0.69	7AM
<i>Formicarius colma</i>	1.02	1.81	0.62	7AM
<i>Grallaria varia</i>	-2.47	1.61	0.73	equal
<i>Hylopezus macularius paraensis</i>	-2.39	1.32	0.63	before sunrise
<i>Conopophaga aurita snethlageae</i>	2.56	1.25	1.35	before sunrise
<i>Attila spadiceus</i>	-0.73	0.92	0.64	before sunrise
<i>Rhytipterna simplex</i>	-0.17	1.03	0.41	equal
<i>Lipaugus vociferans</i>	2.00	-1.09	2.14	equal
<i>Pipra rubricapilla</i>	1.90	-2.49	1.29	8AM
<i>Piprites chloris</i>	-1.09	0.67	0.45	equal
<i>Schiffornis turdinus</i>	-0.03	-1.32	0.93	equal
<i>Ornithion inerme</i>	5.06	-0.85	1.70	equal
<i>Myiopagis gaimardii</i>	0.91	-3.68	1.39	7AM
<i>Lophotriccus galeatus</i>	1.84	2.38	1.80	equal
<i>Ramphotrigon megacephala</i>	-2.70	-1.36	0.06	equal
<i>Platyrrhynchus platyrhynchos</i>	1.77	2.52	1.90	equal
<i>Onychorhynchus coronatus</i>	-0.29	-2.73	1.05	equal

<i>Lathrotriccus euleri</i>	1.08	-2.79	1.39	equal
<i>Myairchus tuberculifer</i>	-1.48	-2.19	0.47	equal
<i>Thryothorus genibarb</i>	-0.85	0.14	0.32	equal
<i>Microcerculus marginatus</i>	0.42	1.62	2.60	equal
<i>Ramphocaenus melanurus</i>	0.68	0.69	0.90	equal
<i>Vireolanius leucotis</i>	-1.85	-2.23	0.47	equal
<i>Hylophilus semicinereus</i>	0.72	0.13	1.02	sunrise & 8AM
<i>Granatellus pelzelni</i>	1.28	-0.51	0.47	equal
<i>Pitylus grossus</i>	-0.77	-1.04	0.99	equal