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UNIVERSITY OF MIAMI

ECOLOGY AND EVOLUTION OF SOFT SONG, A COMPLEX BEHAVIOR, IN TURDUS THRUSHES

By

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The development and evolution of low amplitude ‘soft song’ was investigated in thrushes of the genus *Turdus*. Sharing of soft song was studied in the white-throated thrush (*T. assimilis*) and compared to sharing of broadcast song in the same species, in order to draw inferences about how both song modes are acquired. It was found that most of the song repertoires of each song mode are unique to particular white-throated thrushes, suggesting that this species relies more on invention than imitation during song development. The spatial pattern of sharing between local males differed between song modes. Broadcast song sharing peaks with neighbors located at intermediate distance while soft song sharing has no association with geographical distance. The implication of these patterns for the song learning strategy of soft song are discussed and a potential role for sexual selection is highlighted. In addition, the possible function of soft song to avoid eavesdropping and its adaptations to increase habitat-induced degradation and attenuation were analyzed by means of a field sound propagation experiment. The effect of basic acoustic features on excess attenuation, blur ratio and signal-to-noise ratio was evaluated and compared between song modes while controlling for amplitude differences. The acoustic structure of soft syllables undergoes significantly more habitat-induced degradation than does the acoustic structure of broadcast syllables. These results are consistent with the eavesdropping avoidance hypothesis and suggest that soft signals design is adapted to limit eavesdropping by third party receivers such as predators or conspecifics. Finally, the correlated evolution of body size, beak morphology and habitat structure (i.e. closed vs open habitats) with the acoustic structure of both song modes was investigated in a comparative study of 26 species of *Turdus*. Based on the assumption that morphology effects are independent of signal communication range and the acoustic adaptation hypothesis, it was predicted that both song modes are correlated with morphological traits but only broadcast with habitat structure. Results showed that both song modes are indeed correlated with morphological traits, but each song mode has evolved different correlated responses. Novel and interesting associations between soft song structure and beak morphology were found. Contrary to expected, broadcast song was not correlated with habitat. Soft song showed a correlation with habitat but in the opposite direction to that expected under the acoustic adaptation hypothesis. Since soft song is a signal mainly used for short-range communication, selection favoring habitat-induced degradation in closed habitats is a plausible explanation.

To my parents Rocío y Enrique,

and Lili, with love.

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"It is not only for the intrinsic interest, inspiration and beauty of bird song that we should esteem it, but also because a sense of continuity with the past is important for our spiritual health as life becomes more complex. Despite the changes in man's attitude, his response to the utterances of birds has retained so much from the past that in appreciating bird song and what has been written about it we become alive to insights and sentiments widely shared."

Edward A. Armstrong

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INTRODUCTION

Acoustic communication has important interactions with fundamental biological processes such as species recognition, sexual selection and ecological adaptation (Andersson 1994, Gerhardt and Huber 2002, Searcy and Nowicki 2005, Bradbury and Vehrencamp 2011). The study of bird vocalizations in particular, has contributed significantly to our understanding of how behavior patterns develop, change over space and diversify over evolutionary time (Marler 1970, Grant and Grant 1996, Price and Lanyon 2002, Slabbekoorn and Smith 2002, Nottebohm 2004, Seddon 2005, Podos and Warren 2007). Among avian vocalizations, bird song has been the subject of extensive research (Baker 2001), conceivably because of its essential role in achieving reproductive success by facilitating the formation of breeding pairs and territorial defense in songbirds (Catchpole and Slater 1995).

Bird song research, as well as most studies in acoustic communication, has predominantly focused on high amplitude signals or ‘broadcast song’ (Reichard and Anderson 2015). Nonetheless, low amplitude signaling has been recognized as a different form of communication, tightly associated with courtship displays and agonistic interactions leading to physical attack over a wide range of animal taxa (Dabelsteen et al. 1998, Searcy et al. 2006, Reichard and Anderson 2015). Still, even in the rich bird song literature, low amplitude ‘soft song’ remains poorly understood. This gap of knowledge led Dabelsteen et al. (1998) to designate soft song as an ‘overlooked phenomenon’, while arguing that soft song may be in fact a widespread behavior during the breeding season of songbirds. Supporting this idea, Dabelsteen et al. (1998) presented evidence for the occurrence of soft song in six passerine species of the passerine families Turdidae (common blackbirds *Turdus merula*, redwings *T. iliacus*, fieldfares *T. pilaris* and robins *Erithacus rubecula*) and Prunellidae (dunnocks *Prunella modularis* and alpine accentors *P. collaris*). Subsequently, Morton (2000) reported that 24 species of new world passerines also show soft singing behavior, generally in the context of territory defense following playback of conspecific song. Furthermore, it has been found that non-passerine birds (Rek and Osiejuk 2011), crickets (Robinson and Hall 2002) and bats (Behr and von Helversen 2004) also produce low-amplitude vocalizations during close range interactions with conspecifics. In sum, low amplitude signaling is indeed a widespread behavior among different animal taxa.

Recent and successful efforts have investigated soft song from a functional perspective (Searcy et al. 2006, Hof and Hazlett 2010, Akçay et al. 2011, Reichard et al. 2013, Xia et al. 2013). But we are still lacking information on other important aspects of this acoustic modality. For example, how is soft song acquired? What is the effect of the environment on the evolution of soft signal design? Is soft song correlated with the evolution of other morphological or ecological traits? My dissertation aims to contribute in this regard by approaching the study of low amplitude signals from these new points of view, with the main goal of generating further insights into the intricacies of this form of communication.

What is soft song?

Besides the typical repertoires of broadcast songs, some songbird species sing low amplitude song when conspecific individuals approach within short distances (<10 m)

(Dabelsteen et al. 1998). Soft song may be lower amplitude versions of a broadcast song patterns or structurally very different songs (Dabelsteen et al. 1998, Anderson et al. 2008, Reichard et al. 2011). Low amplitude seems to be an adaptation for short range communication.

Some songbird species sing broadcast songs composed by a single song type to attract mates or repel rivals, which they maintain during their whole lives (Kroodsma 1996, Hough et al. 2000), but other species instead have larger broadcast song repertoires, ranging from a few to hundreds or thousands of song types (Kroodsma and Parker 1977, Krebs et al. 1978, Todt and Hultsch 1996). A third level of complexity could be added, due to the fact that yet other songbird species also possess a soft song repertoire (Figure I.1.), but the size and composition of soft song repertoires has been very little studied.

Soft song sharing and learning

In songbirds, song components or whole songs are commonly acquired through vocal imitation of conspecifics (Marler 1970). Song learning involves both memorizing song models during a sensitive period, and rehearsing songs to match vocal output with previously memorized models (Brenowitz and Beecher 2005). This type of vocal learning may result in song sharing among local males. Song sharing allows neighboring males to interact through matching, counter-matching, or repertoire matching, possibly indicating escalation or de-escalation of aggressive intent during agonistic encounters and facilitating territory defense (Akçay et al. 2013).

The extent of song sharing between a focal male and other males usually changes with distance between their territories. This small scale (micro) spatial pattern of song sharing is mainly a function of the length of the song learning period and juvenile dispersal distance; both ecological factors interact to produce different spatial patterns of song sharing (Wilson et al. 2000). Therefore, the spatial patterns of song sharing provide a guide to examine how songs are being learned, as it is possible to infer probable song learning strategies and dispersal behaviors that are compatible with these patterns.

The processes described above have been widely studied for broadcast songs, but how soft song develops still remains unknown. Soft song has lower amplitude relative to broadcast song and usually has different acoustic structure as well (Figure I.1). Thus, compared to broadcast songs, soft song learning by imitation poses additional problems because of the difficulties of hearing soft song models. Even though it is known that soft song functions in agonistic encounters in a few species (Dabelsteen et al. 1998, Searcy et al. 2014), no data on soft song sharing has been provided, except for one study indicating that a number of soft syllables were shared between a local group of males (in grey thrushes *Turdus cardis*; (Ishizuka 2006)).

Here I investigate whether soft syllables are learned by imitation in white-throated thrushes (*Turdus assimilis*) and compare the song learning strategy of soft song with that of broadcast song in the same population (Vargas-Castro 2015). In Chapter 1, I measure the extent of song sharing and determine the spatial pattern of sharing in broadcast syllables. Using that as a point of reference, I then calculate the amount and spatial pattern of soft song sharing in Chapter 2. Based on the comparison of spatial patterns of song sharing between song modes, the behavioral contexts in which soft song is used and soft song signal design, I then identify a compatible mechanism for soft song acquisition.

Signal design and eavesdropping avoidance

It has been suggested that soft song is a signal adapted to avoid predator interception and/or eavesdropping by con-specifics, an idea known as the eavesdropping avoidance hypothesis (McGregor and Dabelsteen 1996, Dabelsteen et al. 1998). During aggressive encounters or courtship displays, eavesdroppers could gain information about the signaler that may be used in subsequent interactions, which poses a cost to being eavesdropped upon. According to this hypothesis, soft song has evolved to limit detection by eavesdroppers through reduced signal transmission range. A number of adaptations have been suggested to reduce signal transmission range including higher maximum frequency, broader bandwidth, higher frequency modulation and lower amplitude (Dabelsteen 2005), but only the last one has been demonstrated experimentally (Dabelsteen et al. 1993, Rek 2013). The main goal of Chapter 3 will be to test one prediction of the eavesdropping avoidance hypothesis: that aspects of the structure of soft song in addition to low amplitude are adapted to limit song transmission. Sound propagation trials in the natural habitat of the study species will be conducted to test this hypothesis experimentally.

Comparative analysis of morphology and habitat effects on the acoustic structure of both song modes

The 'acoustic adaptation hypothesis' proposes that animal sounds are shaped by selection dependent on habitat structure (Morton 1975). As sounds propagate through the environment, different structural characteristics and habitat conditions interact with the physical properties of sounds. Dense vegetation acts as a barrier to sound propagation causing reverberations and amplitude (loudness) attenuation in closed habitats like forests (Morton 1975, Wiley and Richards 1978, Badyaev and Leaf 1997).

Since different habitats pose different selective pressures on sounds, it is expected that the acoustic properties of animal signals will be adapted to prevent early degradation in their environments and promote efficient transmission to the intended receivers. However, this hypothesis assumes that signals are used in long range communication (Morton 1975). Broadcast songs are used in long range communication while soft songs are mainly used during short range interactions (Dabelsteen et al. 1993, Dabelsteen et al. 1998, Searcy and Beecher 2009). Thus, environmental selection for adaptations that increase propagation distance are expected in broadcast songs but not in soft songs, where increased sound degradation may be favored instead (Dabelsteen 2005).

Moreover, different morphological factors may also affect song structure. Body mass (Ryan and Brenowitz 1985, Badyaev and Leaf 1997, Tubaro and Mahler 1998, Palacios and Tubaro 2000, Bertelli and Tubaro 2002, Seddon 2005) and beak size (Palacios and Tubaro 2000, Podos 2001) have been associated with song frequency. In Chapter 4, I measure frequency and temporal variables in the broadcast and soft songs of *Turdus* thrushes to test for correlated evolution between habitat structure and morphology with the acoustic parameters of each song mode using a comparative approach. This avian group provides a good opportunity to analyze the effects of ecological and morphological traits on the design of these two acoustic modalities.

Song of the White-throated Thrush, *Turdus assimilis*

Thrushes are widely known for their long, varied and melodious broadcast songs, but their repertoires also include soft song components (Grabowski 1979, Dabelsteen 1984, Lampe 1991, Dabelsteen et al. 1998, Morton 2000, Ishizuka 2006, Johnson 2006, Vargas-Castro et al. 2012, Vargas-Castro 2015). In white-throated thrushes, songs are composed of syllable sequences, highly variable in length, containing anywhere from one up to more than a hundred syllables. A syllable may be composed of a single continuous element or (more often) of multiple elements that are repeated in a stereotypic way. In the broadcast song mode, the syllable sequence is composed mostly of broadcast syllables, but soft syllables may be embedded, although less frequently, into different parts of the sequence as well. Conversely, in the soft song mode the sequences are composed mostly or completely of soft syllables. The song mode is determined by the behavioral context of the singing bird. For example, broadcast syllables are more common than soft syllables during spontaneous singing behavior, comprising 84% and 16% of the total syllables produced, respectively (Vargas-Castro 2015), whereas soft syllables become the dominant song mode during short-range conspecific interactions.

Broadcast syllables and soft syllables have different acoustic structure. This difference in acoustic structure between soft syllables and broadcast syllables facilitates song mode classification making white-throated thrushes an appropriate model species for this research.

In the present dissertation, I analyze different aspects of soft song using experimental approaches and detailed analysis to better understand the acquisition and adaptations of this vocal behavior. I use the white-throated thrush as a model species to address questions related to a) song learning and acquisition of soft syllable types, as inferred from the comparison of the spatial patterns of song sharing in the two song modes (Chapters 1-2) and b) the acoustic design of both song modes in relation to signal transmission range and conspecific eavesdropping avoidance (Chapter 3). In addition, I estimate c) ecological and morphological effects on the acoustic properties of both song modes using a comparative approach with 26 species of the genus *Turdus* (Chapter 4). Therefore, the proposed research project constitutes an integrated approach to investigate low amplitude signaling, involving three of the four fundamental questions suggested by Tinbergen (1963) when studying animal behavior: development (Chapters 1-2), function (Chapter 3) and phylogeny (Chapter 4).

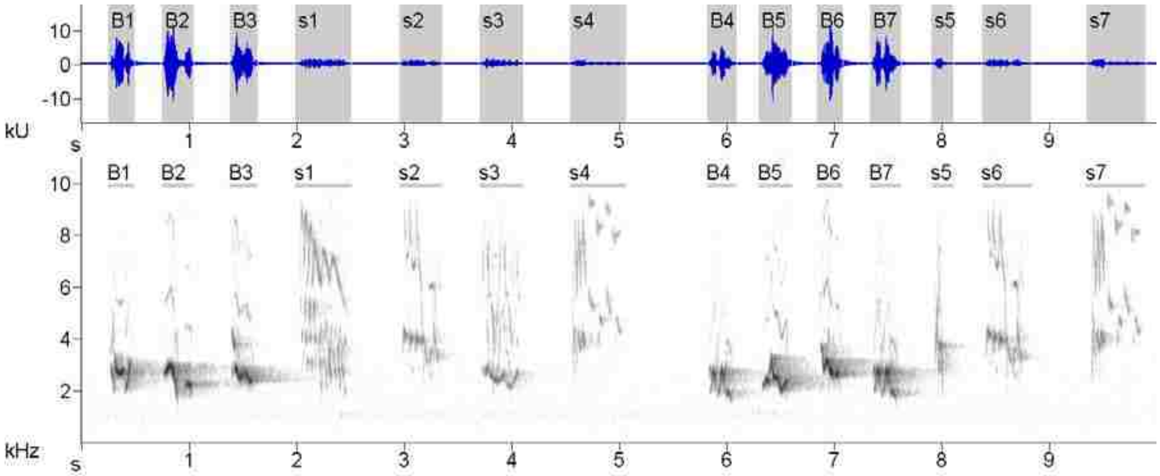

Figure I.1. Waveform (upper panel) and spectrogram (lower panel) showing a section of the song the American robin *Turdus migratorius*. Syllables labeled with uppercase ‘B’ indicate broadcast syllables, while those labeled with ‘s’ correspond to soft syllables. The relative amplitude difference between song modes can be observed in the differences of the amplitude values of the waveform and darkness of the signals in the spectrogram (where louder sounds are darker).

Chapter 1

Spatial pattern of syllable sharing in White-throated Thrushes: implications for song learning and dispersal behaviors

OVERVIEW

In songbirds, song components or whole songs are commonly acquired through vocal imitation of conspecific individuals (Marler 1970, Marler and Peters 1981, Beecher and Burt 2004). This type of vocal learning may result in song sharing among local males (Marler and Tamura 1964, Beecher and Brenowitz 2005). Song sharing allows neighboring males to interact through matching, counter-matching, or repertoire matching, possibly indicating escalation or de-escalation of aggressive intent during agonistic encounters and facilitating territory defense (Krebs et al. 1981, Beecher et al. 1996, Burt et al. 2001, Beecher and Brenowitz 2005). The extent of song sharing between a focal male and other males usually changes with distance between their territories (Wilson et al. 2000). This small scale (micro) spatial pattern of song sharing is a function of a number of ecological factors that affect particular species. Juvenile dispersal distance (from the place where an individual is born to the location where it establishes its territory) and length of the song learning period seem to be the main factors that interact to produce different spatial patterns of song sharing (Slater 1989, Wilson et al. 2000, Koetz et al. 2007), although extent of imitation during song development and seasonal migration may also affect the tendency for males to share songs with local neighbors (Kroodsma 1974, Nelson et al. 1995, Kroodsma et al. 1999, Handley and Nelson 2005). Thus, by analyzing the spatial pattern of song sharing it is possible to infer probable song learning strategies and dispersal behaviors. Here I will infer these two factors based on the spatial pattern of song sharing in the White-throated Thrush *Turdus assimilis*, a Neotropical species.

Wilson et al. (2000) describe three common patterns of microgeographic variation in song sharing (Figure 1.1) and their respective associations with dispersal and learning behaviors. First, little variation in the song sharing level between neighbors and a general decline with distance is indicative of open-ended learners or age-restricted species in which learning occurs after dispersal (Figure 1.1A) (Slater 1989, Wilson et al. 2000). The songs of Village Indigobirds *Vidua chalybeata* (Payne 1985), Great Tits *Parus major* (Mcgregor and Krebs 1989), American Redstarts *Setophaga ruticilla* (Lemon et al. 1994) and the dialect neighborhoods of the Chowchilla *Orthonyx spaldingii* (Koetz et al. 2007) follow this pattern of song sharing. Second, higher variation of song sharing levels between close neighbors and a subsequent fall in the average song sharing level with distance suggests age-restricted learners that tend to disperse short distances but may get established in distant areas in the absence of suitable territorial space nearby (Figure 1.1B). The western subspecies of Song Sparrows *Melospiza melodia* studied by Wilson et al. (2000) show this spatial pattern. Some species of wrens including the Banded Wren *Thryothorus pleurostictus* (Molles and Vehrencamp 1999), the Carolina Wren *Thryothorus ludovicianus* (Morton 1987) and Bewick's Wren *Thryomanes bewickii* (Kroodsma 1974) also have been found to follow this type of pattern. In the third pattern, song sharing levels peak at intermediate distances and close neighbors thus have a relatively lower song sharing level (Figure 1.1C). This pattern is associated with age-restricted learners that have non-random dispersal towards locations where males sing different songs or with open-ended learners that avoid performing shared songs with close neighbors (Hultsch and Todt

1981, Slater 1989, Wilson et al. 2000). Following this type of pattern, Common Nightingales *Luscinia megarhynchos* (Hultsch and Todt 1981) and Common Blackbirds *Turdus merula* (Todt 1981) share more song types with neighbors at intermediate distances (90-240 m and 50-150 m, respectively) than with adjacent neighbors.

Another factor that must be considered when analyzing microgeographic variation in song sharing is the extent and accuracy of vocal imitation (Krebs and Kroodsma 1980). Species in which invention (or improvisation) plays an important role during song development are expected to have lower overall song sharing levels among males than those that have repertoires based on extensive and accurate imitation (Kroodsma et al. 1997). In analyzing learned songs, it is challenging to distinguish between invention and improvisation. While the former does not require a previous song model, the later refers to changes in song structure over time from an original song model to a point where the new version (improvised song) may not resemble the model anymore (Johnson 2006). Hereafter invention and improvisation will be denoted together simply as invention, but with the understanding that both processes may be involved.

Even though most studies of geographic variation have focused on whole songs rather than song components, evidence suggests that song learning could also be based on imitation of song subunits, such as syllables or elements, and different song learning mechanisms (whole songs imitation versus copying song components) seem to occur even at the intraspecific level (Nelson et al. 1995, Hughes et al. 1998). Variation in these learning mechanisms may result in different spatial patterns of sharing at different song structural levels. Indeed, a number of studies have assessed spatial patterns in syllable sharing between males (House Finches *Carpodacus mexicanus* (Pytte 1997); (Tracy and Baker

1999); White-crowned sparrows *Zonotrichia leucophrys* (Nelson et al. 2001); Serins *Serinus serinus* (Mota and Cardoso 2001); Thrush Nightingales *Luscinia luscinia* (Grießmann and Naguib 2002); Chowchillas *Orthonyx spaldingii* (Koetz et al. 2007); and Skylarks *Alauda arvensis* (Briefer et al. 2008)).

Song sharing plays an important role in the communication system and social interactions of several species. In Song Sparrows for example, (Beecher et al. 2000) found that males that shared more songs with their adjacent neighbors were able to hold their territories for a longer time than those that shared fewer songs. Additionally, first year Indigo Buntings *Passerina cyanea* that imitated the song type of a neighboring adult male experienced higher reproductive success and survival than those that did not (Payne 1982, 1983). Shared songs could also provide a badge of familiarity in groups and among territorial neighbors (Beecher 2008), where males honestly signal their high social status and mate quality through their ability to sing local songs because immigrants or first year males may find them difficult to imitate, as has been postulated for the dialects in Brown-headed Cowbirds *Molothrus ater* (Rothstein and Fleischer 1987). Moreover, song sharing has also been positively associated with lifetime social pairing success in White-crowned Sparrows *Zonotrichia leucophrys* (Nelson and Poesel 2013). Thus, the functional significance of sharing likely differs between species (Slater 1989) and selection acting directly on sharing might influence the spatial patterns of song sharing (Podos and Warren 2007).

Most research studies on vocal geographic variation have been conducted in temperate regions (Podos and Warren 2007), and little is known about song geographic variation in tropical bird species, especially about spatial patterns of song sharing (Koetz et al. 2007). I investigated the spatial pattern of syllable sharing in the songs of Neotropical White-throated Thrushes in three different sites (located 2.5-21 km from each other) to provide insights into the song learning strategy, juvenile dispersal and extent of imitation in this avian species. The song of White-throated Thrushes is a sequence of syllables, highly variable in length, delivered in bouts containing anywhere from one to more than a hundred syllables. The objectives of this study were: first, to determine if the syllable sharing level between males changes with the geographic distance between their territories at a broad scale (all sites combined); second, to determine if the extent of song sharing between males differs according to distance categories within sites (adjacent, intermediate or far neighbors and non-neighboring males); and third, to make inferences about the song learning strategy and dispersal behavior of this avian species from its spatial pattern of song sharing.

METHODS

Study species and sites

The White-throated Thrush *Turdus assimilis* is a Neotropical species of humid forest with a range from Mexico through Ecuador (Ridgely and Gwynne 1976, Stiles and Skutch 1989). It favors middle levels of mature forest and second growth habitat (Garrigues and Dean 2007). In southern Costa Rica, it breeds between March and June (Skutch 1960) and successfully nests in pastures and agricultural fields, but requires some threshold of forest area nearby to maintain viable populations (Cohen et al. 2004, Cohen and Lindell 2005). Males defend a small territory, mainly for nesting purposes as foraging often takes place in other areas. It is a resident year-round, usually found from 800-1800 m asl but individuals may migrate to lower elevations during the non-breeding season (Skutch 1960, Garrigues and Dean 2007).

I recorded songs from 23 male white-throated thrushes (only the males sing) distributed among three different sites in southern Costa Rica, on the Pacific slope of the Talamanca mountain range in the province of Puntarenas. The first site (8 males) was the Wilson Botanical Garden (08°47’N, 82°58’W), a property of 12 ha that is part of Las Cruces Biological Station. This site has an elevation of 1200 m above sea level and receives 4000 mm of rainfall per year, with a dry season between December and April. The Wilson Botanical Garden is a large collection of plants scattered over open areas and forest cover. A second site (8 males), Finca Cantaros (08°49’N, 82°58’W) is located approximately 2.5 km north of the Wilson Botanical Garden and is composed of 7 ha of secondary forest mixed with garden areas. A third site (7 males), Las Alturas (08°57’N, 82°50’W), is a cattle farm with abandoned coffee plantations, pastures and forest fragments located approximately 21 and 18 km northeast of the Wilson Botanical Garden and Finca Cantaros respectively. Las Alturas has an elevation of 1500 m above sea level and is composed of montane wet forest habitat (Holdridge et al. 1971).

Song recordings

Songs were recorded in the field using a Marantz PMD661 digital recorder and a Sennheiser ME66/K6 microphone. Recordings were stored as *.wav* files with a 44.1 kHz sampling rate and 16 bit resolution. Most individuals (16/23) were recorded during a single day, while recordings separated by two, three and eight days were used for four, two and one male, respectively. Individuals were identified by their location and the syllable repertoire of their songs, which contain syllables that are unique to particular males. GPS waypoints (Garmin Map 60CSx) were marked for each singing location so that distances between male territories could be calculated. Males regularly use the same singing perches within the territory. Recordings were made throughout the day between 0500 and 1730 hours. Only spontaneous singing bouts were used in the analysis. All recordings were made between May and June in 2012.

The songs of the white-throated thrush include two categories of syllables: broadcast syllables (or whistles) and soft syllables. These two syllable categories are also found in other thrushes (Grabowski 1979, Rasmussen and Dabelsteen 2002, Johnson 2006, Vargas-Castro et al. 2012). Broadcast syllables are more frequently used, compared to soft syllables, during spontaneous singing in white-throated thrushes (84% of 8505 syllables classified here were broadcast syllables). These ‘broadcast songs’ can travel long distances, over 2-4 male territories (Dabelsteen et al. 1993). Soft syllables have lower amplitude and more complex acoustic structure than broadcast syllables (Figure 1.2). It has been shown that other songbird species use soft songs in close-range communication (< 10m), particularly in agonistic interactions, courtship displays, or both (Dabelsteen et al. 1998, Searcy and Beecher 2009). This study focuses on broadcast syllables, which are commonly produced to advertise territory ownership in long range communication between male territories. In addition, only broadcast songs have been analyzed in previous studies of spatial patterns of song sharing in other species, allowing further comparisons.

Syllable classification

Sound spectrograms were produced of each recording with a 1000 samples Fast Fourier Transform, using a Hann type window with 21.5 Hz frequency resolution, 5.67 ms time resolution and 75% overlap using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, New York, USA). Syllables are the basic structural units of a song (Figure 1.2). Songs are highly variable in number of syllables and sequence; therefore repertoire size was measured as the total number of different syllable types in the songs of a given male. Two observers visually inspected the syllables of each male in order to identify the different syllable types composing the repertoires. I aimed at recording at least 300 syllables of each male because cumulative curves showed that 250 syllables are enough to detect full male repertoires (Figure 1.3). On average, 362 syllables (range = 290-656) were recorded and classified per male.

I reexamined the syllable type classification using spectrogram correlation and non-metric multidimensional scaling analysis (MDS) (Nowicki and Nelson 1990). Three renditions of each syllable type (within repertoires) with high recording quality were selected to make an audio library of male repertoires. I performed spectrogram correlations between all pairs of syllables that belonged to each male independently, using the batch correlator tool in Raven Pro 1.5. 'Normalize' and 'linear power' options were selected and a 1000-4000 Hz band-pass filter was applied to all files to decrease background noise effects outside of the frequency range of the songs. Normalized correlations compare the overall shape of acoustic signals while ignoring differences in amplitude (Charif et al. 2010), which is appropriate for uncalibrated field recordings, where amplitude differences have little meaning (Zollinger et al. 2012). Spectrogram correlation computations based on linear power, as opposed to logarithmic power, provide a wider spread of correlation values between visually different spectrograms (Charif et al. 2010). The spectrogram correlation square matrix was converted into a dissimilarity matrix by subtracting each value from 1. Dissimilarity matrices were used to conduct a multidimensional scaling analysis using the MASS package in R (R Development Core Team, Vienna, Austria) solving for two dimensions. As a result, syllables were spread on a bi-dimensional geometric space according to their similarity in acoustic structure.

Syllable sharing analysis

In order to assess syllable sharing between male repertoires, I used the library of male repertoires to print spectrograms of three renditions of all syllables from every male. Three different observers visually inspected these spectrograms to identify shared syllables types between pairs of males according to the similarity of acoustic structure pattern. Male ID was unknown to the observers during this process. The percentage of comparisons in which pairs of observers agreed was high (range = 99.8-99.9%). I considered as shared syllable types those matches that were identified by at least two of the observers, resulting in 60 matches in total out of 63,903 possible comparisons; 30 of these matches were indicated by all three observers.

Syllable repertoire sharing was calculated for all pairs of males using the song sharing index $S = 2N_s/(R_1+R_2)$, where N_s is the number of shared syllable types between the two males and R_1 and R_2 are the repertoires sizes of each male (Mcgregor and Krebs 1982). The syllable sharing index value was subtracted from 1 to obtain a repertoire dissimilarity measure between pairs of males. Mantel tests were used to test whether repertoire dissimilarity was linearly correlated with geographic distance (Manly 1997, Legendre and Fortin 2010), with an estimated p value based on 9,999 permutations.

Additionally, the syllable sharing measurements for each male were grouped in categories within and between sites. I averaged the syllable sharing index of each male over all other males within its own site and also over all other males from the other two sites. I also averaged the syllable sharing index of each male over males located in adjacent territories (≤90 m), those located at intermediate distance (>90 but ≤180 m), far distance (>180 but ≤250 m) and between non-neighboring males (>250 m) within sites. It has been suggested that in a closely related species, the Common Blackbird *Turdus merula*, males are able to discriminate song components at distances up to 250 m (Dabelsteen et al. 1993). Likely, White-throated Thrushes may also discriminate song syllables from males whose territories are located within this distance range. Moreover, the average syllable sharing for each male over males located in a close site (Wilson Botanical Garden vs. Finca Cantaros; range = 2.5-3.0 km) and of each male over those males from far sites (Las Alturas males vs. all others; range = 18-21 km) were also calculated. I then compared the mean syllable sharing values of each category using non-parametric Wilcoxon signed-rank tests. A similar procedure to reduce the 'male x male' matrix to other categories, such as 'male x population' has been used in other studies (Tracy and Baker 1999, Koetz et al. 2007). All statistical tests were conducted using R 2.14.0 (R Development Core Team, Vienna, Austria), the R package "ade4" was used for the Mantel tests. Values are reported as means ± SD.

RESULTS

MDS diagrams based on spectrogram correlations showed substantial agreement with the visual classification of syllable types. Syllable renditions of the same type, as classified by the observers, generally segregated into distinct groups in the MDS analysis (Figure 1.4). In some cases, syllables that were visually classified as different types failed to emerge as well-defined groups in the MDS diagrams (syllables C, N and Q in Figure 1.4C). However, the stereotyped pattern with which these syllables are reproduced, as observed in the spectrogram of the different renditions, clearly showed discrete syllable types rather than continuous variation in syllable structure (Figure 1.4D). Moreover, further segregation of these not well-defined groups (e.g. C, N, and Q in Figure 1.4C) into clusters equivalent to those obtained by visual classification was achieved when the MDS analysis was based on this subset of syllables (C, N and Q) alone instead of the full male repertoire.

Overall, our visual classification of syllable types was supported by the MDS reexamination and subsequent analyses were based on the former method.

I classified 8505 syllables into a total of 296 syllable types. Overall mean repertoire size was 15 (range = 8-25) syllable types. Male repertoire size was similar in all sites (Wilson Botanical Garden = 15 ± 3, Finca Cantaros = 15 ± 4, and Las Alturas = 17 ± 3; $F_{2,20} = 0.9$, $p = 0.44$). There were 60 shared syllables types in total (see Figure 1.5 for examples). Most males (18/23) shared syllables with three or more males and all males shared at least one syllable type with one other male. However, most syllable types were unique to particular males as shown by the low mean syllable sharing indices of S = 0.03 ± 0.02 within sites and S = 0.02 ± 0.03 overall. Mean syllable sharing was not associated with repertoire size (within sites: $r = 0.14$, $N = 23$, $p = 0.53$; overall: $r = 0.14$, $N = 23$, $p = 0.53$).

Within sites, syllable repertoire dissimilarity and territory distance among males were not correlated (Mantel tests: Wilson Botanical Garden $z = -0.23$, $p = 0.90$; Finca Cantaros $z = 0.27$, $p = 0.07$; Las Alturas $z = 0.28$, $p = 0.11$) (Figure 1.6). However, at a larger scale, repertoire dissimilarity increased with geographic distance between male territories when all sites were combined (Mantel test $z = 0.27$, $p < 0.001$) (Figure 1.7). Males within sites (≤ 465 m) had the highest level of syllable sharing and there was no significant difference in the extent of repertoire sharing between males located a few kilometers away (2.5-3.0 km) or considerably farther apart (18-21 km) (Wilcoxon test $z = 141.0$, $N = 16$, $p = 0.61$). Additionally, a second analysis involving distance categories within sites, showed that syllable sharing was higher between males whose territories are located at intermediate distances than between males with adjacent territories (Wilcoxon test $z = 6.0$, $N = 14$, p

<0.01) or between males with territories that were farther apart at least up to 250 m (Figure 1.8).

DISCUSSION

The low overall level of syllable sharing between males (mean repertoire sharing index of 0.03 within sites) should be taken into account when inferring the song learning strategy of White-throated Thrushes. Low levels of sharing suggest that invention plays a greater role than imitation during song development (Krebs and Kroodsma 1980). Hand-rearing experiments and field recordings showed that American Robins *Turdus migratorius* appear to invent or improvise most (75-82% of element types) of their repertoires (Johnson 2006). Similarly, about half or more of the song components forming the repertoires of Clay-colored Thrushes *T. grayi* (72% of syllable types, (Vargas-Castro et al. 2012)) and Common Blackbirds *T. merula* (48% of start motifs, (Rasmussen and Dabelsteen 2002)) were not shared with other males. These findings suggest that invention could be a widespread mechanism of song acquisition among *Turdus* species.

The extent of song sharing between a focal White-throated Thrush and other conspecific males varies according to distance between their territories. At a broad scale, song sharing level decreases with the geographic distance between male territories. Within sites, the extent of syllable sharing was highly variable and a number of males did not share any syllable types even though their territories were quite close to each other. Moreover, the extent of syllable sharing between males from close sites (2.5-3.0 km) was similar to that between males from far sites (18-21 km), indicating that at a larger scale geographic distance has no effect on the proportion of shared syllable types. A variable sharing level between close neighbors and an overall decrease in song sharing with geographic distance between male territories is described by the second pattern in Figure 1.1, which is compatible with pre-dispersal learning and a tendency to disperse short distances unless there is not suitable territorial space nearby (Wilson et al. 2000).

However, at a narrower scale (within sites), further analysis involving distance categories showed that males shared a higher proportion of syllable types with neighbors at an intermediate distance (90-180 m) than with adjacent neighbors. This smaller scale spatial pattern of song variation is comparable to the third pattern (Figure 1.1C) and has only been documented in Common Nightingales *Luscinia megarhynchos* (Hultsch and Todt 1981), Common Blackbirds *Turdus merula* (Todt 1981) and Chaffinches *Fringilla coelebs* (Lachlan and Slater 2003). Compared to white-throated thrushes, nightingales and blackbirds share more song types at a similar distance (90-240 m and 50-150 m, respectively), while in chaffinches song sharing peaks at a longer distance (≥500 m). The distance at which song sharing peaks for these different species may be associated with their respective territory size. For instance, in chaffinches song sharing peaks at a greater distance compared to the other species and chaffinches also have the largest territory area, averaging 6700 m2 (Marler 1956). Common nightingales and common blackbirds follow this trend with territories of 1832 m2 (mean) and 1619-2428 m2 (range) respectively (Snow 1956, Holt et al. 2010). An estimate of white-throated thrushes territory size, based on the minimum distance at which two neighboring territories have been observed (40 m, this study) and using half of this value as a radius while assuming circular areas, results in minimum territory sizes of 1256 m2. Thus, territory size is another variable that may be relevant to describe the interactions of song learning and dispersal behaviors that are compatible with a given spatial pattern of song sharing. Lower song sharing with adjacent neighbors than with other males has also been reported in White-eyed Vireos *Vireo griseus* (Bradley 1981), Cactus Finches *Geospiza conirostris* (Grant 1984) and Sage Sparrows *Amphispiza belli* (Rich 1981), but sharing with intermediate neighbors was not higher or evaluated in these cases. A comparative examination of factors that might favor low song sharing between adjacent neighbors will become useful as data from more species is gathered.

Two possible mechanisms are compatible with the spatial pattern in which the syllable sharing level of a focal male peaks with intermediate neighbors. First, songs could be learned before dispersal and then males establish their territories through non-random dispersal in locations where males sing different songs (repulsion hypothesis) (Hultsch and Todt 1981, Slater 1989, Catchpole and Slater 2008). Alternatively, this pattern could arise through active avoidance of the acquisition (Wilson et al. 2000) or retention (Nelson 2000) of shared songs between adjacent males during and after settling. At this point, neither mechanism has been directly tested, but some support for the first strategy comes from laboratory studies with Common Blackbirds, showing they avoid perching on song posts broadcasting playbacks that matched their own songs with a short time delay (overlapping the subject's song) (Todt 1981).

A preference for particular locations based on song neighborhoods during the territory establishment of White-throated Thrushes has not been documented. Cohen et al. (2004) radio-tracked fledglings in the same region as the present study and found that they moved on average 297.5 m (range = 90-500 m) on the first day they dispersed from the place they were born, at around 31 days of age. Cohen et al. (2004) also observed a juvenile

>1 km away from its natal area more than a month after dispersal. Although these measurements do not correspond to juvenile dispersal distances (from the place were an individual is born to the location where it establishes its territory), they provide minimum values to expect if a fledgling's movement remains unidirectional as during the time period observed by Cohen et al. (2004). These fledgling movement distances are greater than the distance range among intermediate neighbors in which syllable sharing was higher and therefore are compatible with the idea that males could establish their territories in locations where males sing different songs, but it also does not rule out the possibility of active avoidance of shared syllables by neighboring males. Playback studies are needed to determine if active avoidance of shared syllables between neighboring males occurs and therefore could be the mechanism responsible for the observed spatial pattern of song sharing in White-throated Thrushes.

A relatively lower sharing level with adjacent neighbors and such a low level of sharing in general suggest that there is no selection on White-throated Thrushes to share songs. Adjacent neighbors have few or no shared syllables to interact with through song matching, a common social function of song sharing (Beecher and Brenowitz 2005), and perhaps even avoid matching. Avoidance of matching has previously been observed in Wood Thrushes *Hylocichla mustelina*, both in laboratory and field studies, showing that subjects reply to stimulus songs with identical or highly similar songs significantly less than expected by chance (Whitney and Miller 1983, Whitney 1991). Comparable field experiments with playbacks or simultaneous recordings of adjacent males would test if White-throated Thrushes avoid syllable matching as well, rendering further support for a lack of selection to share songs in this species.

Based on these results, I suggest that White-throated Thrushes learn a small number of syllables before dispersing, inventing the rest. Juvenile dispersal distance is then variable and probably less than 2.5 km, which produces higher and more variable syllable sharing level in males within sites than between sites. Finally, during territory establishment, males may prefer locations where residents sing different syllables from their own, or males may avoid incorporating syllables sung by their neighbors into their own repertoires, producing the lower sharing level with adjacent neighbors than with intermediate neighbors. Further studies on this speciose genus, *Turdus*, with more than 60 species worldwide, will reveal the generality of this song learning strategy and its adaptive significance to the evolution of song within this avian group.

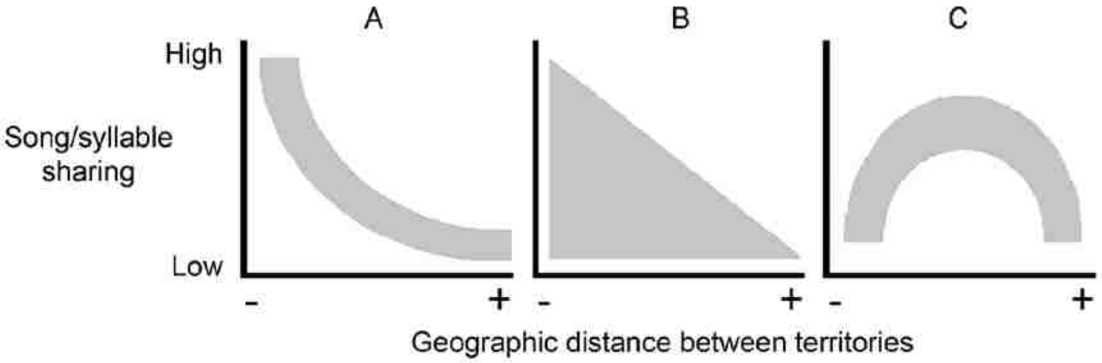

Figure 1.1. Three patterns of spatial variation in song sharing (or syllable sharing) between pairs of conspecifics. Each spatial pattern is compatible with different song learning and dispersal behavior interactions.

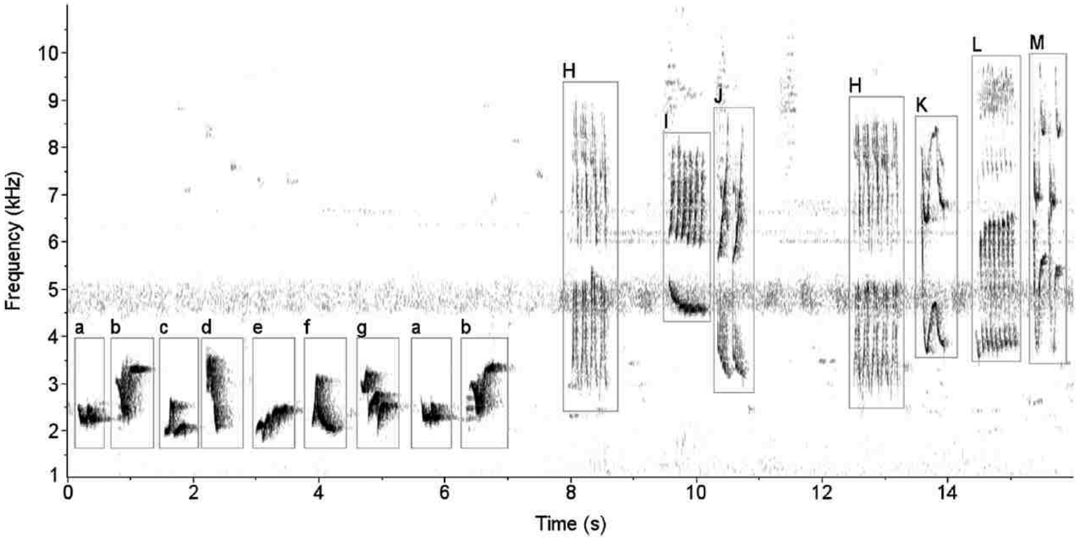

Figure 1.2. Song of a male White-throated Thrush from Las Cruces Biological Station, Costa Rica, in May 2012. Songs are composed of syllable sequences, highly variable in length, containing anywhere from one up to more than a hundred syllables. A syllable may be composed of a single note or (more often) of multiple notes. Syllables last 0.59 ± 0.18 sec and are separated by silent intervals of 0.32 ± 0.17 sec in length within songs (mean ± SD, n = 7 males, 2118 syllables). Consecutive songs are separated by silent intervals ≥ 1 sec. Loud syllables (a-g) have a frequency range of 1000-4000 Hz; soft syllables (H-M) have higher maximum and minimum frequencies and broader frequency range. Syllables marked with the same letter correspond to the same syllable type.

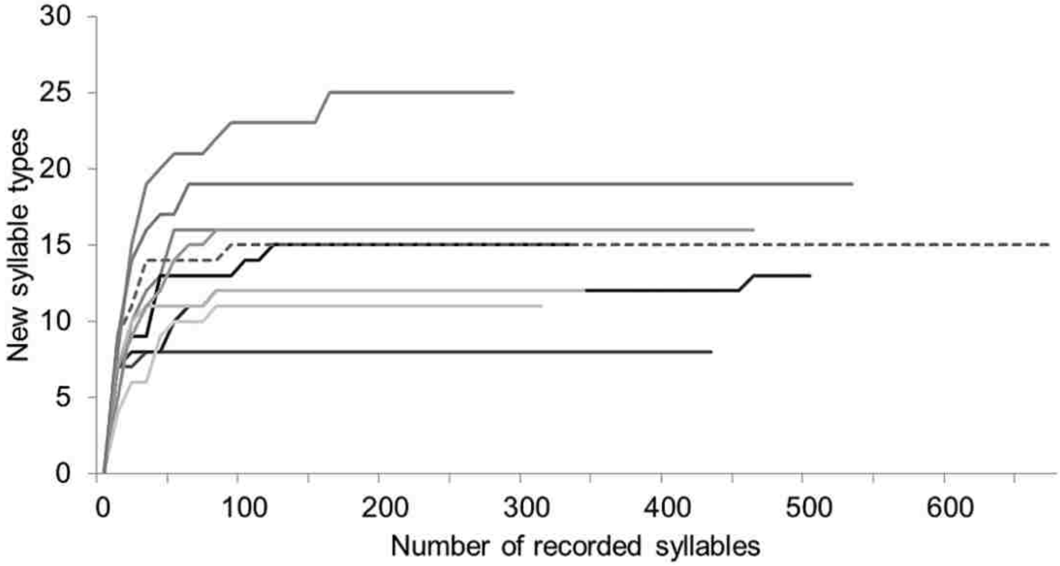

Figure 1.3. Cumulative curves of new syllable types according to the number of syllables recorded in the songs of 10 male White-throated Thrushes. Puntarenas, Costa Rica, 2012.

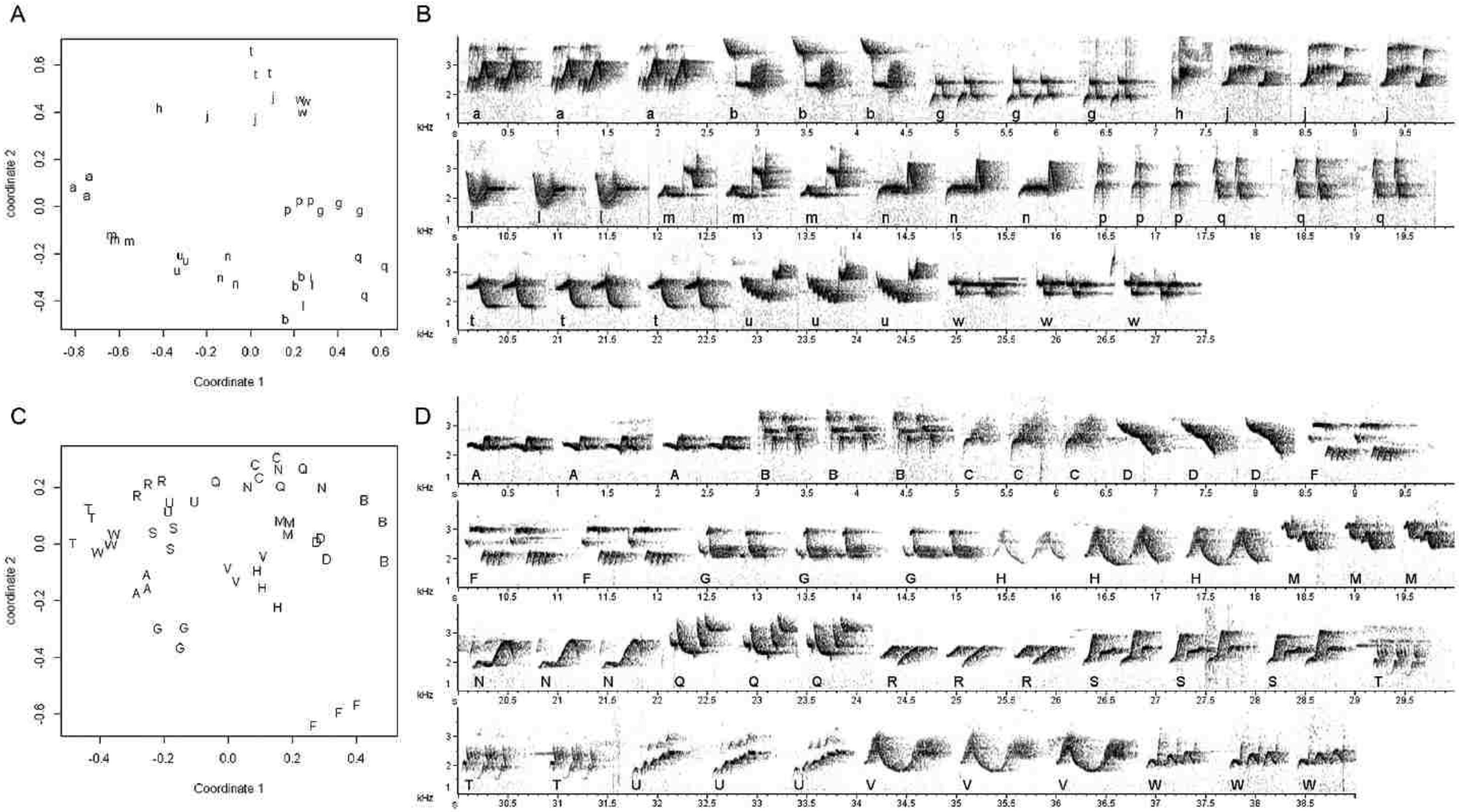

Figure 1.4. MDS diagrams (left) based on spectrogram correlations of the syllable repertoires of two males: 104 (**A-B**) and 303 (**C-D**). Each letter denotes a syllable type shown in the respective spectrogram (right). Three different renditions of each syllable were used, except for syllable h (recorded only once). Time axis is presented only for scale purposes; this syllable arrangement does not constitute a natural song.

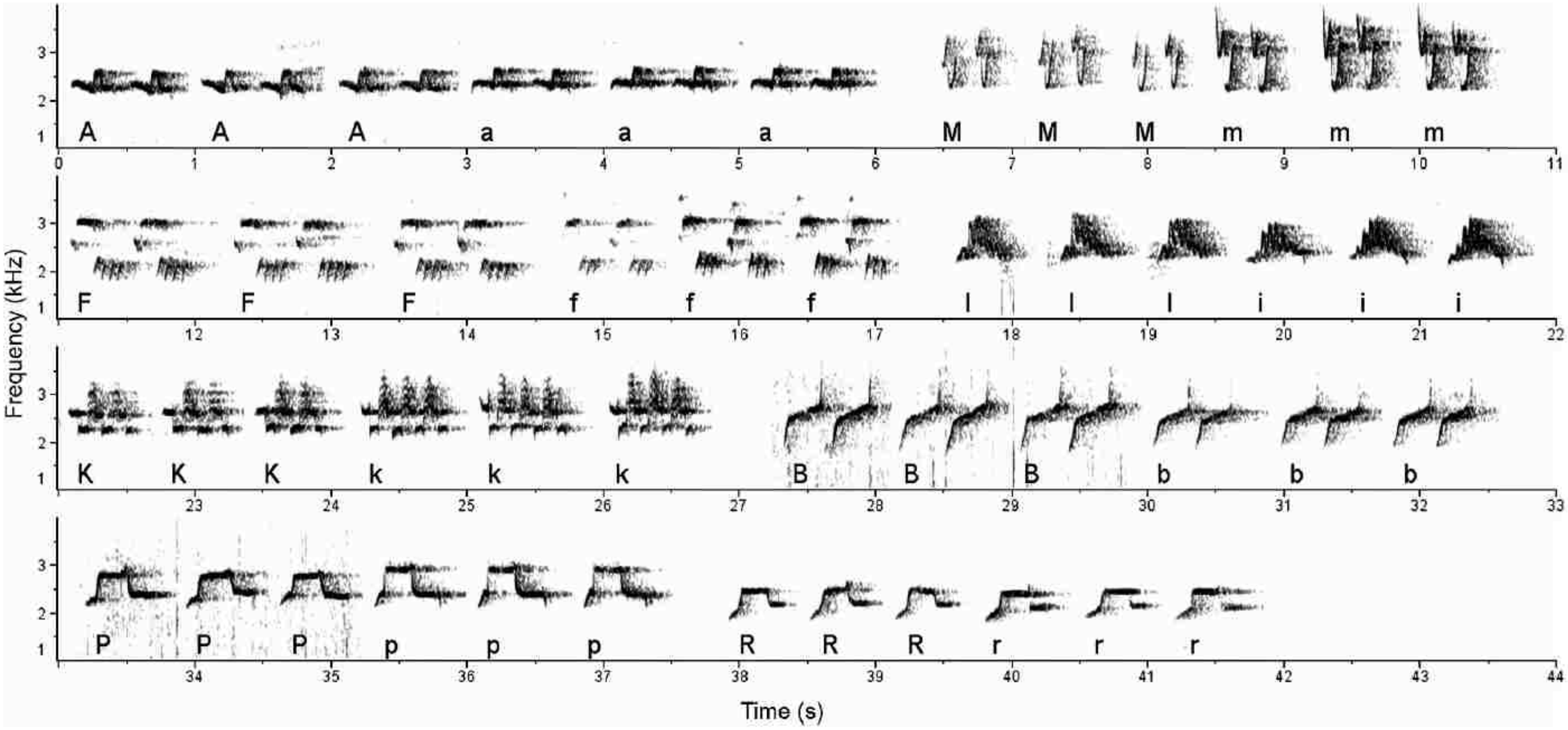

Figure 5.1. Eight examples of shared syllable types between pairs of males. Three renditions of each syllable type are shown and denoted by the same letter. Uppercase letters indicate syllables produced by one male and lowercase letters indicate those produced by the other male. Time axis is presented only for scale purposes.

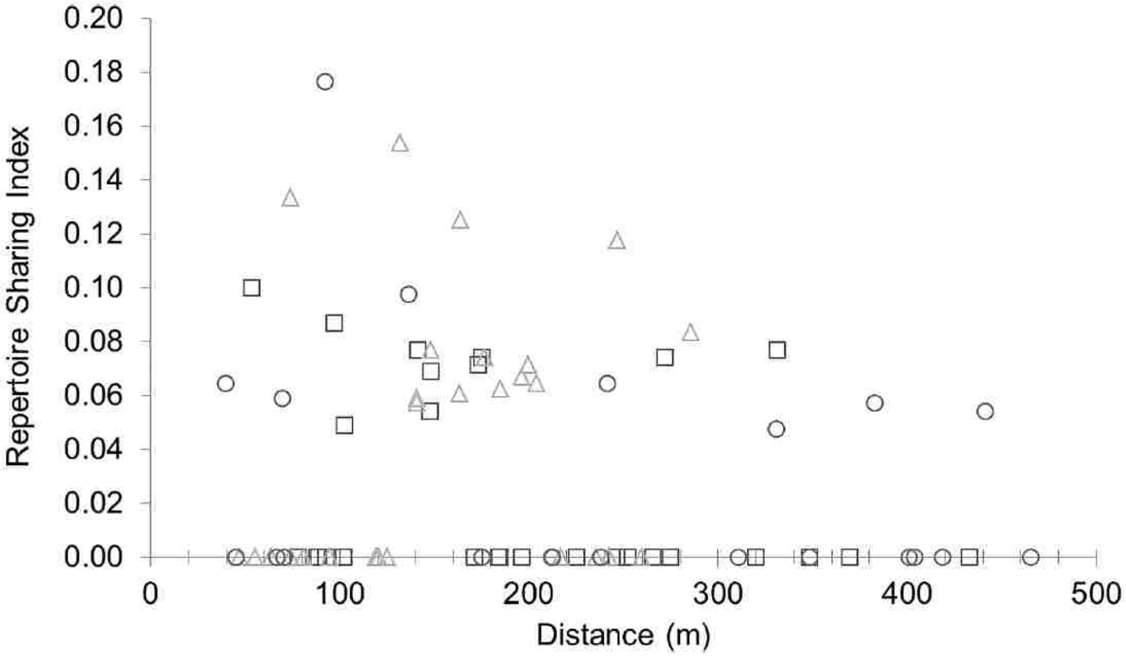

Figure 1.6. Syllable sharing among male White-throated Thrushes within sites: Wilson Botanical Garden (triangles), Finca Cantaros (squares) and Las Alturas (circles); southern Pacific region, Costa Rica.

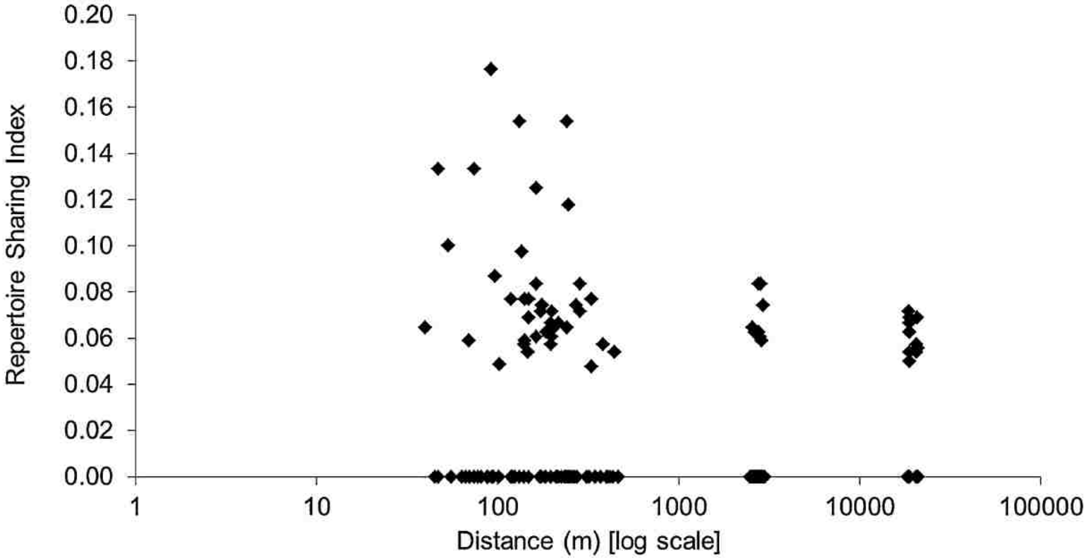

Figure 1.7. Syllable sharing index between male White-throated Thrushes according to geographic distance of their territories. Males were recorded in three different sites (2.5-21 km from each other) in the southern Pacific region of Costa Rica. The leftmost cluster contains pairwise comparisons within sites, the middle cluster contains comparisons between the two close sites (Wilson Botanical Garden and Finca Cantaros), and the rightmost cluster contains comparisons between Las Alturas and the other two sites.

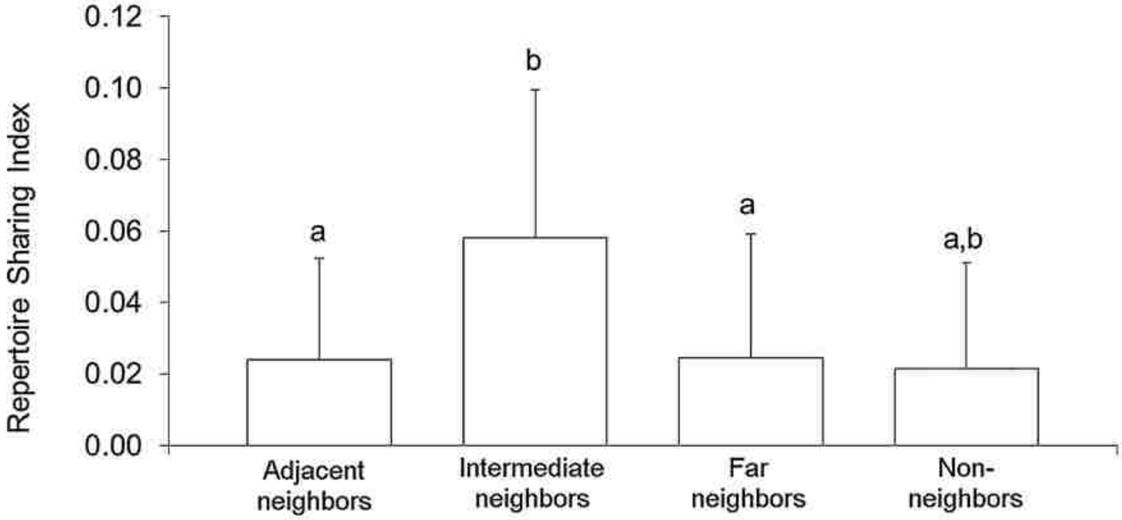

Figure 1.8. Mean (+SD) syllable sharing in White-throated Thrush song within sites between adjacent neighbors (territories located ≤90 m), intermediate neighbors (>90 but ≤180 m), far neighbors (>180 but ≤250 m) and non-neighboring males (>250 m) in southern Puntarenas, Costa Rica. Different letters indicate a significant difference (alpha value = 0.05) in mean syllable sharing level between paired distance categories using Wilcoxon tests.

Chapter 2

Song learning strategies for acquiring soft song

OVERVIEW

Songbirds may learn their songs by different processes, ranging from accurate imitation of previously existing song models (Marler 1970, Marler and Peters 1981, Beecher and Burt 2004) to innovation of novel songs (Slater and Lachlan 2003). Imitation of complete songs or song subunits from the repertoires of other individuals results in song sharing (model-copy) within populations (Marler and Tamura 1964, Brenowitz and Beecher 2005). Song sharing may play an important role in territorial defense by facilitating vocal interactions, such as song matching or repertoire matching, in which use of shared and unshared song types indicates different levels of aggressive intent during agonistic encounters (Krebs et al. 1981, Beecher et al. 1996, Burt et al. 2001, Akçay et al. 2013, Searcy et al. 2014). Even though it is well documented that soft song (i.e. low amplitude signals) functions in agonistic encounters in a number of species (Dabelsteen and Pedersen 1990, Dabelsteen et al. 1998, Ballentine et al. 2008, Hof and Hazlett 2010, Xia et al. 2013, Searcy et al. 2014), it is not known whether individuals engage in song matching interactions using their soft song repertoires. Only one study has provided evidence for soft song sharing (Ishizuka 2006), and no studies to our knowledge have addressed soft song development. Soft song learning by imitation poses special problems because of the difficulties of hearing soft song models at any distance. In this study, I will analyze the pattern of sharing of soft song in white-throated thrushes (*Turdus assimilis*) and then draw inferences about the learning strategy for soft song.

The degree of song sharing between a given male and other males often changes as a function of distance between their territories. Juvenile dispersal distance and song learning strategies (e.g. open-ended vs age-restricted learners) interact to produce different spatial patterns of song sharing (Slater 1989, Wilson et al. 2000, Koetz et al. 2007). For species like common nightingales *Luscinia megarhynchos* (Hultsch and Todt 1981), common blackbirds *Turdus merula* (Todt 1981) and white-throated thrushes *T. assimilis* (Vargas-Castro 2015), the extent of song sharing peaks with neighbors located at intermediate distances (90-240 m, 50-150 m, and 90-180, respectively) while closer neighbors have relatively lower song sharing. This spatial pattern of song sharing is compatible with two mechanisms. First, individuals could learn songs before dispersal and then, during territory establishment, favor locations where males sing different songs from their own ('repulsion hypothesis') (Hultsch and Todt 1981, Slater 1989, Catchpole and Slater 1995). Second, this pattern could arise by active avoidance of the acquisition of shared songs between adjacent males, during and after settling (Catchpole and Slater 1995, Wilson et al. 2000).

These two mechanisms, however, are unlikely to have important effects on soft syllable sharing mainly because of two factors: a) soft syllables have low amplitude and limited transmission range (Dabelsteen et al. 1993), making soft syllables more difficult to detect, and b) soft syllables are mainly used during specific short range behavioral contexts, such as aggressive encounters or courtship (Dabelsteen and Pedersen 1988, Dabelsteen et al. 1998, Searcy and Beecher 2009), making them less abundant overall and less likely to be heard. Based on what is known about spatial patterns of sharing in broadcast songs and their implications for song learning, the behavioral contexts in which soft song is used and soft song signal design, I predict that soft song will show a different spatial pattern of song sharing compared to broadcast song.

Besides imitation, songs may also be acquired by innovation, invention or improvisation (Slater and Lachlan 2003, Johnson 2006). These three processes mainly differ in the degree to which a given song model is used as an initial template during song learning. Innovation is when new behavior patterns are derived from modifying pre-existing ones (Janik and Slater 2000). In contrast, invention is defined as the appearance of novel behaviors, not derived from any pre-existing ones that the animal could have been exposed to (Janik and Slater 2000). Improvisation can be defined as new patterns that arise in a given moment, ephemeral and not necessarily based on pre-existing ones (Slater and Lachlan 2003). Hereafter I will refer to these three processes as ‘invention’, as it is challenging to distinguish between them while studying song repertoires. None or lower overall song sharing among males is expected when species rely largely on invention during song development, compared to those that acquire songs based on extensive and accurate imitation (Krebs and Kroodsma 1980, Kroodsma et al. 1997).

The objectives of this study are: 1) to estimate the extent of soft syllable sharing between neighboring males; 2) to determine if the syllable sharing level between males changes with the geographic distance between their territories; and 3) to infer the song learning strategy that is compatible with the spatial pattern of soft song sharing. To our knowledge, no other study has attempted to investigate the song learning strategy for acquiring soft song, perhaps because soft song is an inconspicuous vocal behavior by nature and thus is difficult to observe and record. These results will provide insights to fundamental questions about soft song that will help understand how this complex signaling system develops.

METHODS

Species and study site

This study was conducted at the Wilson Botanical Garden, Las Cruces Biological Station (08°47'N, 82°58'W), located on the southern Pacific slope of the province of Puntarenas, Costa Rica. The Wilson Botanical Garden is a large collection of plants distributed over open grassy areas, partially surrounded by forest cover. The garden has an elevation of 1200 m above sea level, 4000 mm of rainfall per year and a dry season that extends December-April.

I studied a local group of male white-throated thrushes whose breeding territories were scattered through the study site (Figure 2.1). As this species sings throughout the day, I recorded between 0400-1800 hours. All recordings were made between May 9 and June 6, 2015.

Audio Recordings

Songs were recorded in the field using an Olympus LS-10 or Marantz PMD661 digital recorder connected to a Sennheiser ME62/K6 microphone attached to a Sony PBR-

400 parabola. Playback of conspecific song was commonly used to stimulate the production of soft song by territorial males and thus facilitate obtaining recordings including soft syllables. Recordings were stored as uncompressed *.wav* files with a 48 kHz sampling rate and 16 bit resolution. Individuals were identified by their location and syllable repertoires, which contain unique syllable types (Vargas-Castro 2015). The singing location of each male was marked using GPS waypoints (Garmin Map 60CSx) to calculate horizontal distances between male territories.

Syllable Classification

Sound spectrograms for each recording were produced based on a 2048 samples DFT, using a Hann type window, with 66.4 Hz bandwidth, 23.4 Hz frequency resolution, and 50% overlap using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, New York, USA). Two observers visually inspected the sound spectrograms to retrieve individual song syllables, classify them into different types and calculate repertoire size. Repertoire size was measured as the total number of different syllable types in the songs of a given male. I analyzed the repertoire of each song mode independently; therefore, a 'broadcast repertoire' and 'soft repertoire' was identified for each male. A total of 10751 syllables were originally identified from 13 males. Two males were dropped from the analysis due to 1) sample size and 2) not being able to find the individual in following days after first recording it. This study focuses exclusively on soft song as broadcast song has previously been analyzed elsewhere (Vargas-Castro 2015). Thus, the final sample includes 4226 soft syllables from 11 different males. Cumulative curves have shown that 200 syllables are often enough to detect full broadcast syllable repertoires (Vargas-Castro 2015), but a larger sample may be required for soft syllable repertoires. For this particular analysis, I analyzed an average of 384 soft syllables (range: 228-608) per male.

Three renditions of each syllable type with high recording quality were selected when possible. All renditions from the syllable types that belong to a given male were grouped together to make an audio library of each male repertoire. I used the batch filter tool in Raven Pro 1.5 to apply a 1500-12000 Hz band-pass filter to decrease background noise effects outside of the frequency range of the songs. I reexamined syllable type classification (within males) using a protocol develop by Große Ruse et al. (2016) for MATLAB. Briefly, the method uses multitaper spectrograms, filtered ambiguity spectrum and hierarchical clustering to produce dendrograms that cluster syllable types according to their similarity in acoustic structure.

Syllable Sharing Analysis

In order to assess syllable sharing between male repertoires, I used the library of male repertoires to print spectrograms of three renditions of all syllables from every male. I visually inspected these spectrograms to identify shared syllables types between pairs of males according to the similarity of acoustic structure pattern. A second observer also inspected spectrograms for 8/11 males to identify shared syllable types and the inter-observer agreement was high (99.9%). Male ID was unknown to the observers during this process.

Syllable repertoire sharing was calculated for all pairs of males using the Sørensen similarity index (hereafter ‘repertoire sharing index’), $S = 2N_s / (R_1+R_2)$, where N_s is the number of shared syllable types between the two males and R_1 and R_2 are the repertoires sizes of each male (Mcgregor and Krebs 1982). Standard errors for the song sharing values of each pairwise comparison were calculated using bootstrapping based on a sample size of 300 syllables and 100 iterations (Table 2.1). The sharing index value was subtracted from 1 to obtain a repertoire dissimilarity matrix between pairs of males. A Mantel test was then used to test whether repertoire dissimilarity was linearly correlated with geographic distance (Manly 1997, Legendre and Fortin 2010), with an estimated P value based on 999 permutations.

Additionally, I also calculated the average syllable sharing between each male and all other males located in adjacent territories (≤90 m), those located at intermediate distance (>90 but ≤180 m), far distance (>180 but ≤250 m) and between non-neighboring males (>250 m). I compared the mean syllable sharing values of each category using non-parametric Wilcoxon signed-rank tests. A similar procedure to reduce the ‘male x male’ matrix to other categories, has been used in other studies (Tracy and Baker 1999, Koetz et al. 2007). All statistical tests were conducted using R 3.2.5 (R Development Core Team, Vienna, Austria). The R packages ‘ade4’ and ‘vegetarian’ were used for the Mantel test and bootstrapping method, respectively.

RESULTS

A PCA of 500 syllables (250 of each song mode) based on 20 acoustic parameters described up to 75% of the variation in acoustic structure with two principal components. The spread of values in the PCA plot shows two clearly separated groups (Figure 2.3), providing support for the classification of syllables in two different song modes: broadcast and soft syllables. In addition, a comparison of amplitude differences within pairs of syllables produced under the same conditions showed that soft syllables had significantly less amplitude than broadcast syllables (mean amplitude difference -17.6 dB, $t = -14.44$, $df = 8$, $p < 0.001$) (Figure 2.4).

Soft song repertoire size averaged 22 syllables (range = 12-34) per individual. Across the 11 males there were 220 different soft syllable types, of which 23 were shared types (Figure 2.2 for examples). All males had shared syllable types in their repertoires, with individuals on average sharing 5 soft syllable types (range = 2-9) with other males. However, most syllable types were unique to particular males as shown by the low mean repertoire sharing index of 0.03 ± 0.03 (SD). Pairwise standard error values for this index are shown in Table 2.1.

Syllable repertoire dissimilarity and territory distance among males were not correlated (Mantel test: $z = -0.04$, $p = 0.64$) (Figure 2.5). A second analysis using distance categories between adjacent neighbors, intermediate neighbors, far neighbors and non-neighbors, showed no significant differences in mean soft syllable sharing between any pairwise comparison of distance categories (Wilcoxon tests paired by individuals, all p-values > 0.05) (Figure 2.6).

DISCUSSION

The low levels of syllable sharing among local males suggests that invention may be the main learning mechanism by which soft song is acquired in white-throated thrushes. A vast majority of soft syllables, up to 90% of 220 syllable types, were unique to the repertoires of particular males. The extent of soft repertoire sharing between males was not associated with geographical distance between their territories, demonstrating that the spatial pattern of soft song sharing and that of broadcast song sharing differs.

Spatial patterns of syllable sharing in broadcast and soft song

In white-throated thrushes, the extent of syllable sharing between local males is similar in both song modes. I found the same mean repertoire sharing index (0.03) in this study for soft song, as that for broadcast song in the same population (Vargas-Castro 2015). However, the spatial pattern of sharing changes between song modes. The spatial pattern of shared songs is associated with particular song learning and dispersal behaviors (Slater 1989, Wilson et al. 2000). White-throated thrushes shared a higher proportion of broadcast syllable types with intermediate neighbors (territories separated by 90-180 m) than with adjacent neighbors (≤90 m) (Vargas-Castro 2015). This spatial pattern of song sharing is compatible with age-restricted learners preferring locations where residents sing songs different from their own during territory establishment, or open-ended learners avoiding the incorporation of syllables sung by their neighbors into their own repertoires (Hultsch and Todt 1981, Slater 1989, Wilson et al. 2000). These two mechanisms, however, are not expected to apply to soft syllable sharing mainly because of two reasons. First, soft syllables have low amplitude and limited transmission range, making their detection more difficult. Second, soft syllables are mainly used within short range during specific behavioral interactions, which makes them less abundant relative to broadcast syllables and less likely to be heard.

In relation to the first reason, I showed there are important amplitude differences between song modes, with soft syllables having relatively less amplitude. Also, field experiments have shown that after sound transmission through distances of only 10 and 20 m, soft syllables showed more than two and three times greater 'excess attenuation', respectively, than broadcast syllables and also higher blur ratios and lower signal-to-noise ratios (Vargas-Castro et al. *In review*). Thus soft song has a very limited propagation range and is unlikely to be transmitted between territories, which are often separated by more than 40 m in white-throated thrushes. Similarly, in common blackbirds, sound propagation studies have shown that the soft components (twitters) of the full songs are not transmitted over distances greater than one territory diameter, while the loud components of the songs can travel over 2-4 territories (Dabelsteen et al. 1993).

Secondly, soft syllables are mainly used during short range interactions when conspecifics approach each other, such as agonistic encounters and courtship, making them less common than broadcast syllables in the typical song bouts that characterize the spontaneous singing behavior of territory owners. In white-throated thrushes for example, only 16% of 8505 syllables recorded during spontaneous song bouts were soft syllables (Vargas-Castro 2015). Both aspects, limited transmission range and association with particular behavioral contexts, suggest that a considerably greater amount of time and closer physical approach would be required for a given male to efficiently monitor another male’ soft syllable repertoire and imitate soft syllable models. In fact, it is startling that there is soft song sharing at all. The above mechanisms that are compatible with the spatial pattern of broadcast song sharing (non-random dispersal and active avoidance of shared types) are unlikely to affect soft syllables sharing and therefore no pressure on their spatial pattern.

Invention as a mechanism to acquire soft song

Most soft syllable types were found to be unique to the repertoires of particular males. The low levels of sharing suggest that invention is a more important mechanism to develop and acquire soft syllables rather than imitation. As long as invented songs do not deviate from the typical species range of acoustic variation, which could potentially impair communication, invented songs may be functionally equivalent to imitated songs (Hughes et al. 2002, Slater and Lachlan 2003). In the case of soft syllables, the relatively large bandwidth and diverse temporal patterns provide ample space for variation in acoustic structure within the species limits. Since soft song is mainly used during behavioral interactions that involve mate attraction or territorial defense, it is reasonable to expect that soft song repertoires may be under sexual selection favoring larger repertoire size (Searcy and Andersson 1986, Andersson 1994), which is consistent with the observed larger size of soft syllable repertoires compared to those of broadcast syllables. As Hughes et al. (2002) proposed, imitation and invention could be alternative developmental strategies for increasing repertoire size.

Table 2.1. Sample size (diagonal) and standard errors for each song sharing index between pairs of males calculated using bootstrapping (sample size = 300, number of iterations = 100)

	A	B	C	D	E	F	G	H	I	J	K
A	370										
B	0.000	233									
C	0.003	0.014	534								
D	0.000	0.000	0.001	262							
E	0.000	0.000	0.001	0.003	333						
F	0.000	0.002	0.000	0.000	0.000	343					
G	0.000	0.000	0.011	0.008	0.000	0.019	608				
H	0.000	0.000	0.001	0.000	0.001	0.000	0.000	342			
I	0.000	0.000	0.000	0.000	0.000	0.001	0.005	0.000	228		
J	0.019	0.001	0.001	0.004	0.014	0.001	0.007	0.000	0.020	588	
K	0.001	0.000	0.000	0.003	0.001	0.000	0.000	0.001	0.000	0.015	385

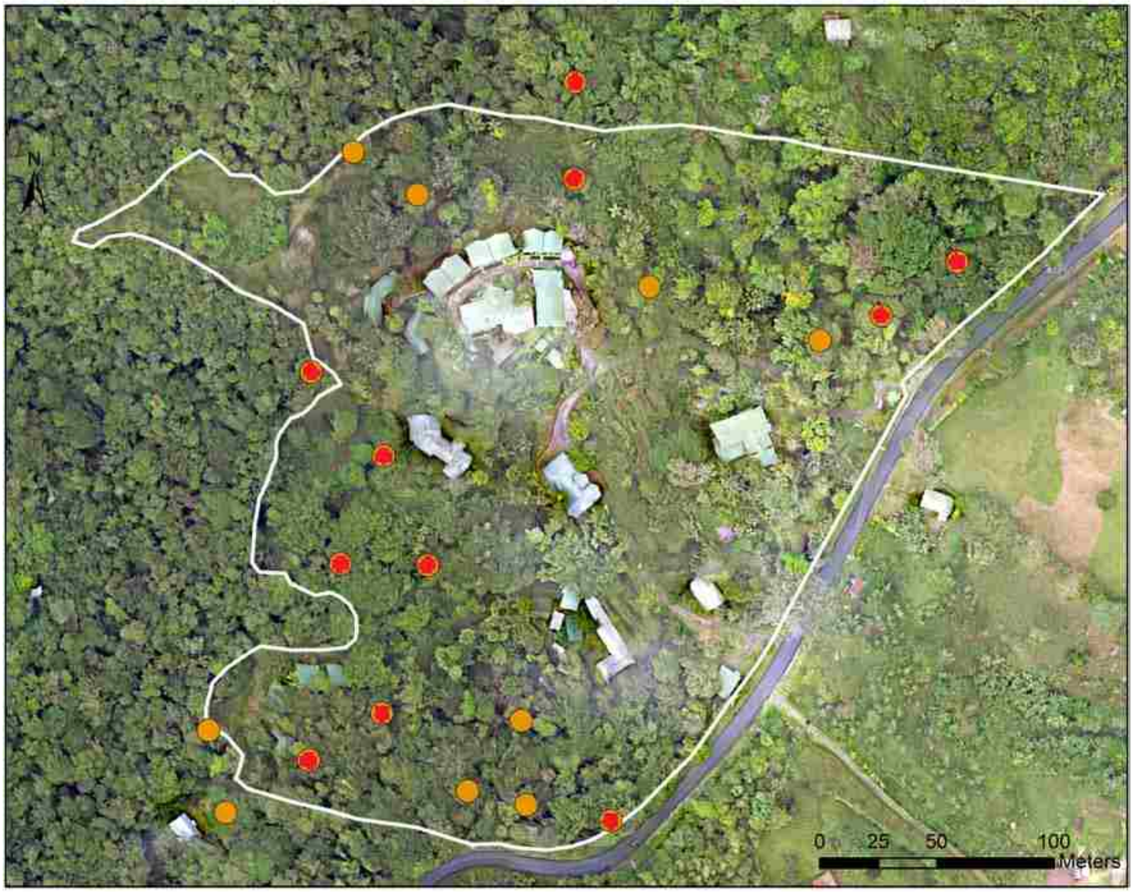

Figure 2.1. Map showing the spatial distribution of white-throated thrush (circles) at the Wilson Botanical Garden, in the southern Pacific slope of Puntarenas, Costa Rica. The males from territories highlighted in red were analyzed in this study. Some individuals were not included in the analysis because the number of soft syllables recorded was deficient or they did not hold stable territories.

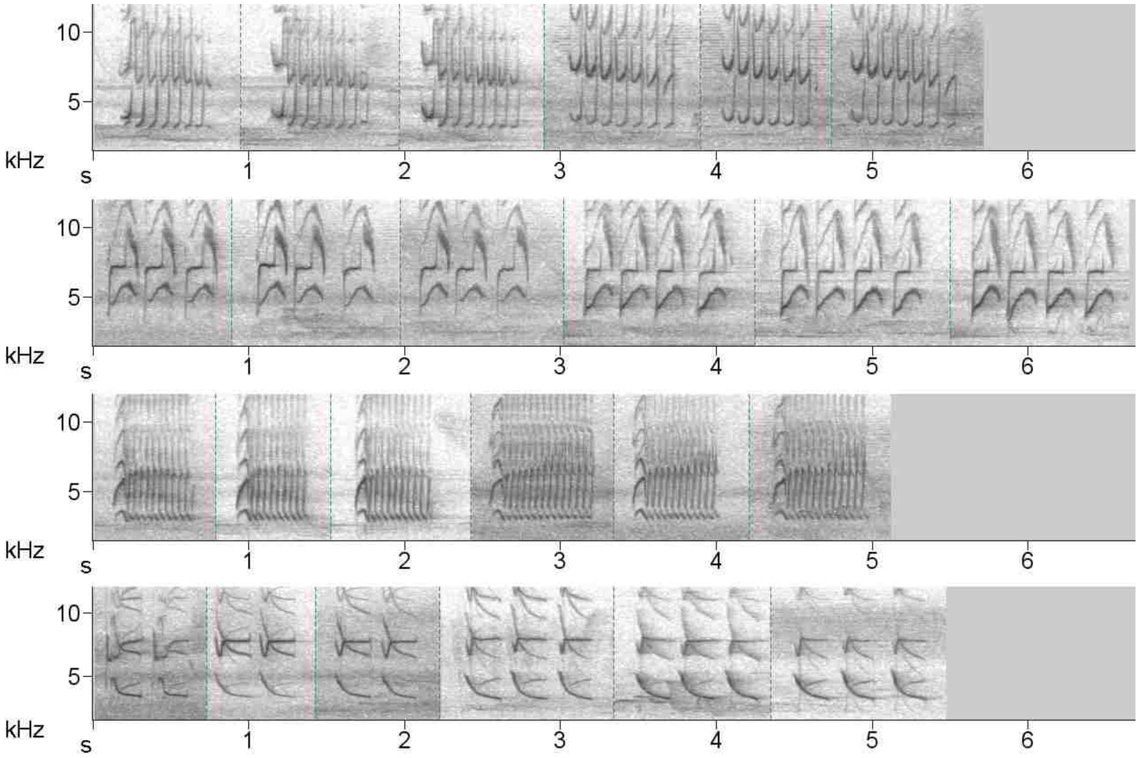

Figure 2.2. Four examples of shared syllable types between males. Each example is composed by three renditions of the first male's version followed by three renditions of the second male's version of a given type.

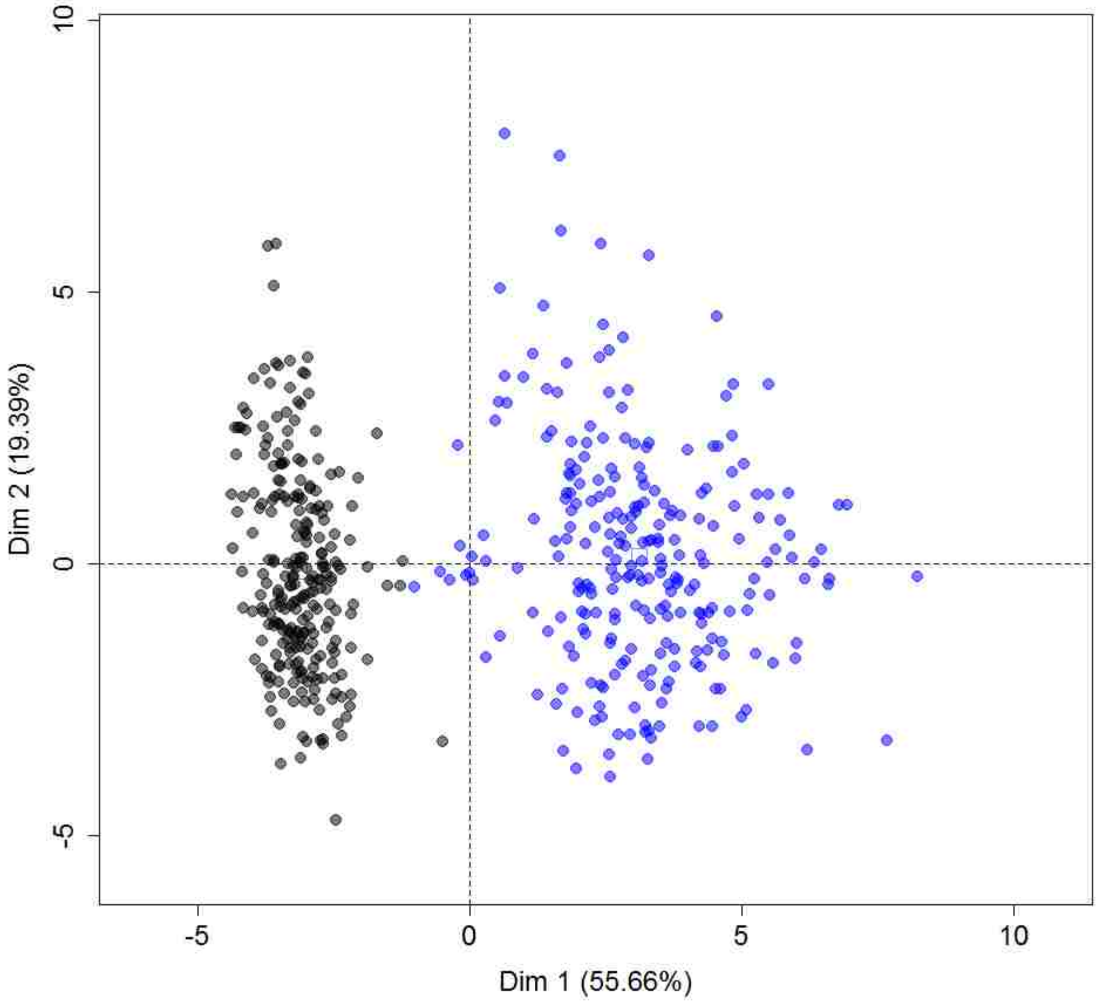

Figure 2.3. Scatter plot of the first two principal components describing the acoustic structure of a sample of 500 syllables (250 of each syllable mode). Broadcast and soft syllables are shown in black and blue, respectively. PCA was based on 20 acoustic parameters calculated using Raven Pro 1.5.

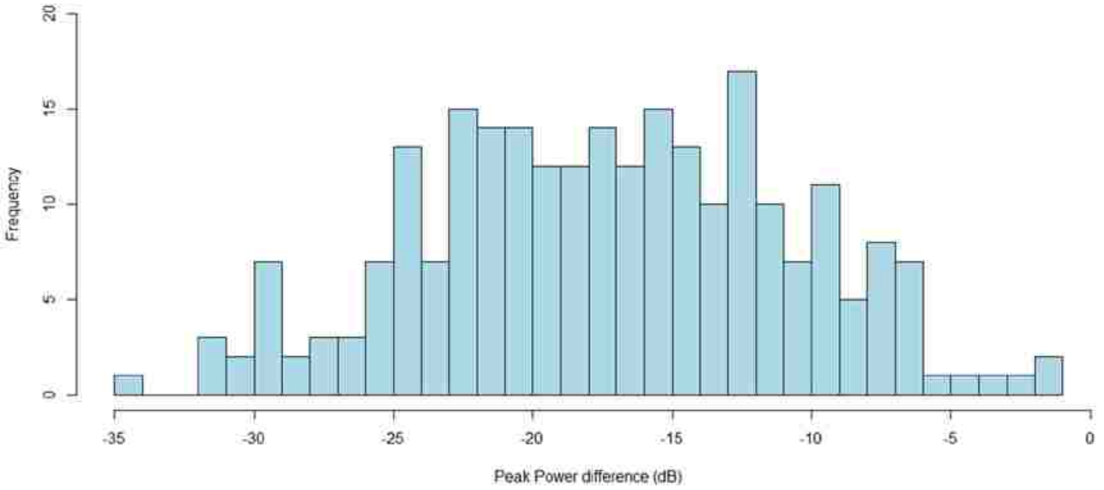

Figure 2.4. Histogram showing amplitude differences between broadcast and soft syllables. Amplitude differences were calculated by subtracting peak power values of broadcast syllables from those of soft syllables produced immediately after (≤1 s). Data shows 250 events (pairs of syllables, one of each song mode) in 9 different males.

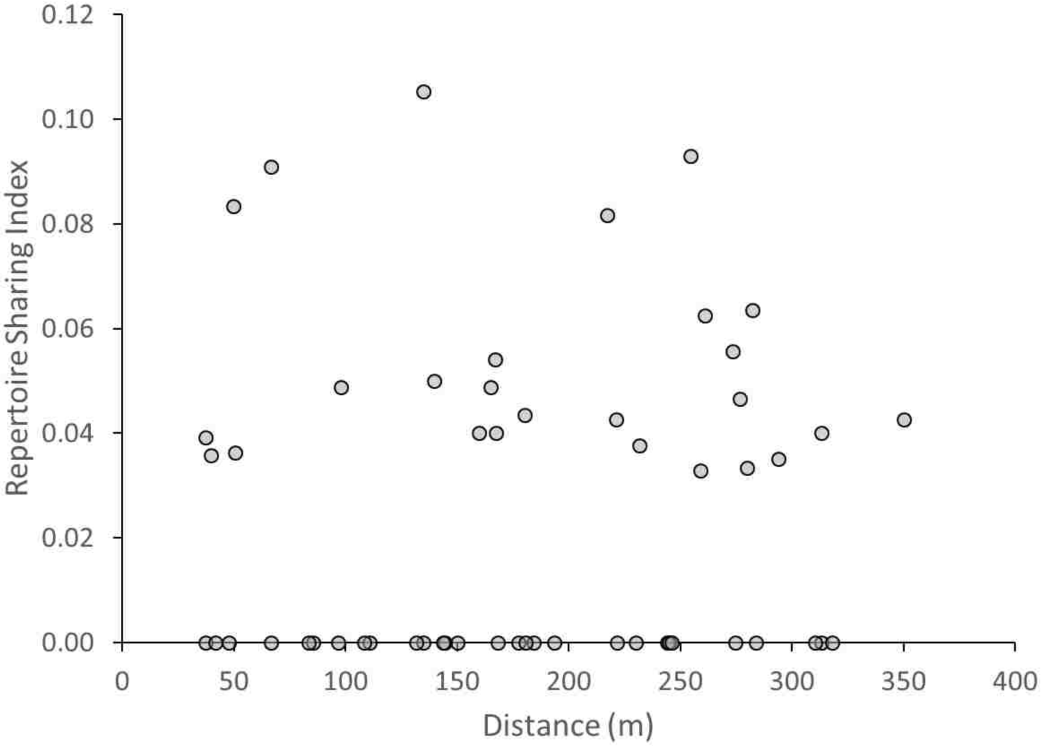

Figure 2.5. Soft song repertoire sharing in white-throated thrushes according to geographic distance between their territories. Individuals were recorded in the Wilson Botanical Garden, Puntarenas, Costa Rica in 2015

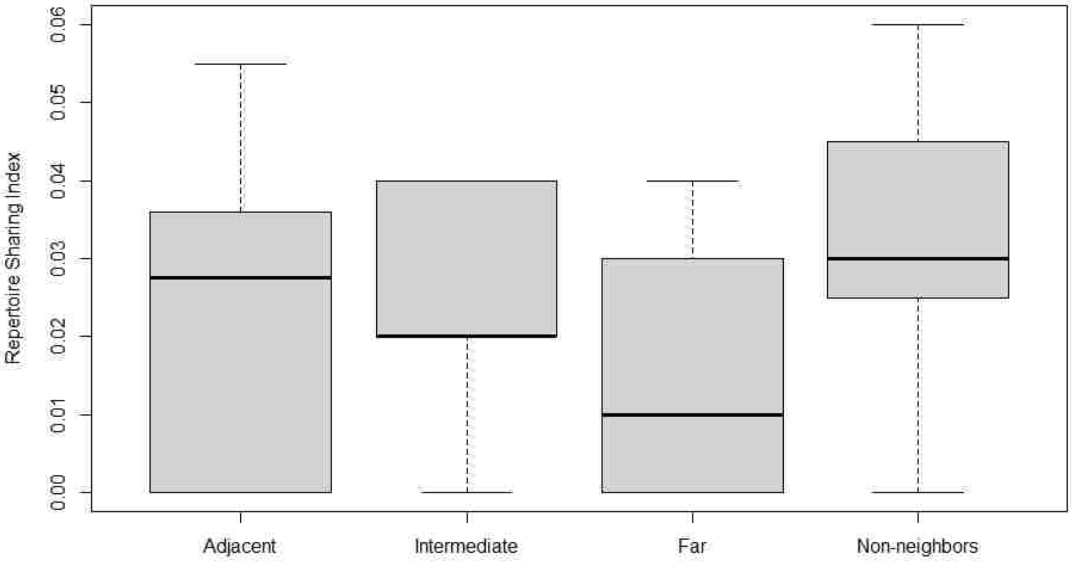

Figure 2.6. Soft syllable sharing in white-throated thrushes between adjacent neighbors (territories located ≤90 m), intermediate neighbors (>90 but ≤180 m), far neighbors (>180 but ≤250 m) and non-neighboring males (>250 m) in southern Puntarenas, Costa Rica.

Chapter 3

Eavesdropping avoidance and sound propagation: the acoustic structure of soft song

OVERVIEW

In animal communication, acoustic signals can be transmitted longer distances relative to other sensory channels (Catchpole and Slater 1995). Long range sounds may reach multiple receivers, including individuals not directly involved in the interactions that can nevertheless gather information by eavesdropping upon these signals (McGregor 1993). During agonistic encounters, eavesdroppers may obtain information about an unknown intruder's fighting ability relative to their own by comparing the outcome of its interactions with neighbors of known fighting ability (McGregor 1993, McGregor and Dabelsteen 1996). Intruders may benefit from concealing their agonistic interactions and avoiding assessment of their fighting ability. In turn, male territory owners may also benefit by concealing the outcome of their agonistic interactions from their mates, especially if they lose (McGregor and Dabelsteen 1996). For instance, male black-capped chickadees *Poecile atricapilla* that lose in singing interactions during simulated intrusions lose paternity in their nests as a consequence of eavesdropping by their mates (Mennill et al. 2002). Additionally, signaling males may benefit from not being detected by unintended male receivers during courtship interactions. Eavesdropping third party males may try to interrupt copulation attempts to seek copulations themselves once they gain information about the fertility status of nearby females (Dabelsteen et al. 1998). Males seeking extra-pair mating may also benefit from preventing eavesdropping on their signals by the social mates of females they are courting (Dabelsteen et al. 1998). Thus signalers may benefit in different ways from modifying their signals so as to minimize eavesdropping by conspecifics.

Predators constitute another category of potential unintended receivers (Dabelsteen et al. 1998). Individuals engaged in signaling interactions may be distracted and therefore more vulnerable to predation (Jakobsson et al. 1995). Examples of signaling systems in which predators cue on acoustic signals include fringe-lipped bats (*Trachops cirrhosus*) eating tungara frogs (*Physalaemus pustulosus*) during their chorus activity (Tuttle and Ryan 1981, Ryan et al. 1982), Mediterranean house geckos (*Hemidactylus tursicus*) attracted to calling male decorated crickets (*Gryllodes suplicans*) and preying on females as they approach males (Sakaluk and Belwood 1984), and brown skuas (*Catharacta antarctica*) cuing on nocturnal sexual advertisement calls to locate and prey on male petrels (Mougeot and Bretagnolle 2000). Therefore, selection imposed by predators intercepting signals may favor signals that avoid these unintended receivers.

McGregor and Dabelsteen (1996) suggested that soft song is a signal adapted to avoid eavesdropping by con-specifics and/or predators through reduced transmission range, an idea known as the eavesdropping avoidance hypothesis. During agonistic interactions, courtship displays, or both, males of some songbird species sing low amplitude song when conspecific individuals approach within short distances (Dabelsteen et al. 1998, Anderson et al. 2007, Searcy and Beecher 2009, Reichard et al. 2013). Males may use lower amplitude versions of the broadcast songs or structurally different low amplitude songs (Dabelsteen et al. 1998, Anderson et al. 2008, Reichard et al. 2011), therefore, this mode of singing has been termed ‘soft song’.

Two experimental studies with song sparrows *Melospiza melodia* found negative results on predictions of the eavesdropping avoidance hypothesis concerning the use of soft song. Soft song use decreased when territorial intrusions were simulated under a high risk of predation context, using conspecific alarm calls (Searcy and Nowicki 2006) or predator (Cooper's hawk *Accipiter cooperi*) calls (Akçay et al. 2016), relative to control stimuli. Also, Searcy and Nowicki (2006) found no significant difference in the intrusion time per trial between interactions in which simulated territory owners replied with broadcast songs versus soft songs. Up till now, these song sparrow playback studies constitute the only experimental tests dealing with the functional role of soft song within the context of the eavesdropping avoidance hypothesis. Nonetheless, more species and aspects of this hypothesis remain to be tested, for instance those concerning signal design.

The physical structure of animal sounds is subject to selection derived from environmental acoustics (Morton 1975, Wiley and Richards 1978). In a homogeneous frictionless medium, sound spreads spherically from a source that is small relative to the sound's wavelength (Morton 1975). Due to this spherical spreading, the intensity of the sound wave decreases at a rate of 6 dB per each doubling of distance (Wiley and Richards 1978). However, natural environments are structurally complex (e.g. vegetation cover, ground texture) and as sound propagates the energy of sound waves is reduced or redirected (Morton 1975). Processes such as absorption and multiple scattering, in addition to spherical spreading, cause attenuation or gradual loss in sound intensity (Wiley and Richards 1978, Bradbury and Vehrencamp 2011). Moreover, selective frequency filtering, reverberation and atmospheric turbulence produce blurring or distortion of amplitude and frequency patterns (Wiley and Richards 1978, 1982, Dabelsteen et al. 1993). This environmental or habitat induced degradation alters the initial characteristics of the signal and thus may limit information transfer between individuals (Aubin et al. 2014). In addition, the amount and nature of ambient noise affects the signal-to-noise ratio (Dabelsteen et al. 1993, Slabbekoorn 2004), which in turn affects the detectability of the signal by receivers (Klump 1996).

The eavesdropping avoidance hypothesis proposes that selection to avoid detection of the signal by eavesdroppers has favored the evolution of low amplitude in soft song to lower transmission range. If selection has indeed favored lowering transmission, then other features of soft song (besides amplitude) should also be adapted to lowering transmission. Spectral features can lower sound transmission in two ways: by leading to increased excess attenuation and degradation, and by leading to greater masking by ambient noise (Searcy and Yasukawa 2016). Dabelsteen (2005) suggested that higher maximum frequency, broader bandwidth and higher frequency modulation represent adaptations to reduce signal transmission range and increase privacy in acoustic signals. In accordance with these suggestions, higher maximum frequency and/or broader frequency range are common characteristics of the soft songs of song sparrows *Melospiza melodia* (Anderson et al. 2008), the short-range songs of dark-eyed juncos *Junco hyemalis* (Titus 1998, Reichard et al. 2011), the courtship diving songs of whitethroats *Sylvia communis* (Balsby et al. 2003) and the twitter elements in the songs of redwings *Turdus iliacus* (Lampe 1991) and common blackbirds *Turdus merula* (Dabelsteen 1984, Dabelsteen et al. 1998).

Empirical data comparing the transmission of soft and broadcast song comes mainly from three sound propagation studies (Dabelsteen et al. 1993, Balsby et al. 2003, Rek 2013). Dabelsteen et al. (1993) played motif sounds (broadcast song) and twitter sounds (soft song) of common blackbirds *Turdus merula* at their natural amplitudes and observed relatively more degradation in soft song. Nonetheless, signal-to-noise ratio differences between the two song modes probably resulted mainly from the initial amplitude differences in the test sounds. Balsby et al. (2003) compared the transmission of 'perch song' (broadcast song) and 'diving song' (soft song) in whitethroats *Sylvia communis*, after equalizing their peak amplitudes, and observed greater excess attenuation and lower signal-to-noise ratios for diving songs transmitted across 12.5-50 m. Later, Rek (2013) conducted an experiment using broadcast calls and soft calls in corncrakes *Crex crex* and found that when played at similar amplitude, one of two soft call components (gurgling notes) had lower signal-to-noise ratio than broadcast calls after being transmitted across 10-40 m. As gurgling notes have low frequency and narrower bandwidth, greater masking by low-frequency environmental noise may explain their lower signal-to-noise ratios (Rek 2013). These transmission studies provide support for the eavesdropping avoidance hypothesis, but direct evidence regarding intrinsic signal design is still deficient.

Our main goal is to test predictions of the eavesdropping avoidance hypothesis concerning the acoustic structure of soft song. I argue that if soft song has evolved under selection to avoid eavesdroppers' detection by reducing signal transmission range, then the spectral traits of soft song should be adapted to reduce signal propagation distance. Our objectives are: 1) to test if the acoustic structure of soft song, besides amplitude, reduces transmission range and 2) to analyze the effect of specific spectral traits on signal degradation.

METHODS

Study site and species

I conducted a sound propagation experiment using songs of white-throated thrushes *Turdus assimilis* in the forest of Las Tablas Protected Area, part of the primary forest in La Amistad Biosphere Reserve, adjacent to Las Alturas Biological Station (08°57’N, 82°50’W) on the Pacific slope of the Talamanca mountain range in southern Costa Rica. The habitat is characterized by montane wet forest (Holdridge et al. 1971) at an elevation of 1500 m above sea level. Mean (±SD) tree density is 557.5 ± 160 trees per hectare, and mean tree DBH (diameter at breast height) is 25.0 ± 2.9 cm, as estimated by Lindell and Smith (2003) using trees ≥10 cm in DBH. Also, mean canopy cover is high, reaching 95.9 ± 4.8 % (Lindell and Smith 2003). In this area, the nesting season of white-throated thrushes extends from March to August with a peak in May (Cohen and Lindell 2005).

The study was conducted in three sites nearby active white-throated thrush territories from May 20-28 in 2014. The experiment (see sound propagation experiment) involved placing the speaker at a given site and then placing the microphone at three different positions, varying in distance and angle from the speaker. The transects between the speaker and microphone were different for each horizontal distance within sites. I selected sites that were relatively flat and located all speaker and microphone positions in the forest edge, contained within an area situated 50 m from the forest border towards the forest interior, where white-throated thrushes typically sing throughout the day during the breeding season.

Test Sounds

A series of test sounds was produced using songs recorded in the field with an Olympus LS-10 digital recorder and a Sennheiser ME62/K6 microphone mounted on a Sony PBR-400 parabolic reflector. Recordings were stored as *.wav* files with a 44.1 kHz sampling rate and 16-bit resolution.

The songs of white-throated thrushes include two syllable categories: broadcast syllables and soft syllables (Vargas-Castro 2015). Soft syllables have lower amplitude and more complex acoustic structure than broadcast syllables (Figure 3.1). I selected 12 syllables in total, including six syllables of each category from five different males recorded in previous breeding seasons (2012 or 2013) from the same geographical region (0-21 km away). Within each syllable category, I chose three syllables with relatively narrow frequency bandwidth and three with relatively wide bandwidth. Syllables were selected based on recording quality, favoring those with lower background noise. Additionally, I generated modified versions of the soft syllables by artificially lowering their frequency by half without changing syllable duration using Adobe Audition 1.0 (Adobe Systems, San Jose, CA, USA) (Figure 3.2). In this way, these artificial syllables virtually became broadcast syllables in terms of frequency range but retained their soft syllable structural design. Hereafter, I will refer to this third syllable category as ‘modified soft’ syllables in our analysis. I then applied specific band-pass filters to each syllable type using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA) to remove noise outside the syllables’ frequency ranges (Table SM1, Supplementary Material). In order to test whether soft song structure, independently of amplitude, is adapted to limit transmission range, I normalized amplitude levels using Adobe Audition 1.0. to give equal peak amplitude for all syllables.

Finally, I assembled a test sound file composed of a sequence of 18 syllables: 6 broadcast, 6 soft and 6 modified soft, which was repeated five times. I included 1.5 s and 2 s of silence between syllables and repetitions, respectively. Also, I added 5 s of silence at the beginning of the test sound file from which I later selected a 2 s period in the experimental field recordings to measure background noise level (avoiding foreground noise). Background noise was assumed to be constant throughout the duration of the test file. In total, the test file contained a series of 90 sounds and a total duration of 40.75 s.

Sound Propagation Experiment

The test sounds were broadcast from an active loudspeaker (Anchor Audio, Minivox; frequency response: 0.1-15 kHz ± 3dB) and re-recorded using a Sennheiser ME62/K6 omnidirectional microphone connected via a microphone preamplifier (Sound Device MP-1; frequency response: 0.02-22 kHz) to a Marantz PMD661 digital recorder. Files were stored as *.wav* files with a 44.1 kHz sampling rate and 16-bit resolution. The test sounds were played at approx. 85 dB SPL measured at 2.5 m, in order to match the natural amplitude of broadcast syllables in white-throated thrushes and comparable to the reported song amplitude in common blackbirds *Turdus merula* (Dabelsteen 1981).

I placed the speaker and microphone at two heights, 1.5 and 4 m, which correspond to positions at which typical singing activity occurs (4 m) and at which soft signaling in response to playback has been observed in the field (1.5 m). Propagated sounds were re-recorded at three horizontal distances (10, 20 and 40 m). The minimum distance between neighboring territories that has been observed is 40 m (Vargas-Castro 2015). Within sites, the order of factors (horizontal distance, speaker height and microphone height) was randomized.

In some cases, where there was high environmental background noise, I played the test file a second time in order to make sure that I would obtain at least three clean renditions of each syllable. A clean rendition refers to a syllable recording that is suitable for acoustic analysis because it was not overlapped by other sounds. If the test file was played a second time, a new background noise level measurement was obtained for these respective renditions.

Acoustic Analysis

Propagated sounds were analyzed using SIGPRO 3.25 and an established protocol (Dabelsteen et al. 1993, Holland et al. 2001, Balsby et al. 2003, Sandoval et al. 2015). The first three clean renditions of each syllable were selected for analysis. In total, I analyzed 1944 sounds in a balanced factorial design (3 sites X 3 horizontal distances X 2 speaker heights X 2 microphone heights X 18 syllable types X 3 renditions). I measured the following sound degradation response variables on each syllable: excess attenuation (loss of amplitude beyond that expected by spherical spreading: 6 dB per doubling of the distance), blur ratio (frequency dependent distortion of amplitude in the signal) and signal-to-noise ratio (amount of energy contained in the sound signal relative to the energy of the background noise). Excess attenuation (EA) is calculated as EA = $-20 \log k - A$, where k is a constant that represents the mean attenuation of the sound channel during transmission and A is the attenuation in dB caused by spherical spreading.

Statistical Analysis

I conducted linear mixed-effects models (LMM) to analyze the effect of multiple factors on acoustic degradation. Mainly, I was interested in comparing the sound transmissions properties of broadcast, soft and modified soft syllables. I conducted three independent LMM, one for each sound degradation response variable: excess attenuation, blur ratio and signal-to-noise ratio. Each LMM had four fixed factors: speaker height (2 levels: 1.5 and 4 m), microphone height (2 levels: 1.5 and 4 m), horizontal distance (3 levels: 10, 20 and 40 m) and syllable mode (3 levels: broadcast, soft and modified soft). Also, I included the site where each experiment was conducted (3 sites) and syllable type (18 types) as random effects in the models. I estimated the main effects and one two-factor interaction (syllable mode X horizontal distance) in our analysis. Later, I conducted post-hoc tests on all pairwise comparisons within main effects and the two-factor interaction term using Tukey's HSD method for multiple comparisons.

Also, I analyzed the effect of frequency structure on sound degradation using multiple linear regressions and three basic spectral traits (minimum frequency, peak frequency and frequency bandwidth) as predictors. First, I calculated overall averages for the three sound degradation responses by syllable type (18 types). Each sound degradation response was analyzed independently. Lastly, I conducted backwards stepwise regression analyses to select the final models and determine which specific spectral traits significantly affect the sound degradation responses.

In order to analyze background noise variation, I performed another LMM on background noise amplitude values collected from the field recordings (Sandoval et al.

2015). Background noise measurements were syllable specific, as they were obtained from the same frequency bandwidth defined by the frequency filters applied to each syllable type. I conducted this analysis using two fixed factors: microphone height (2 levels) and syllable mode (3 levels), as these are the factors expected to affect the recorded background noise level. I also included two random factors in the model: experiment site (3 levels) and syllable type (18 levels). The response variable was the background noise level.

All statistical tests were conducted in R version 3.2.5 (R Development Core Team, Vienna, Austria). LMM were performed using the R package *lmerTest* and the ANOVA degrees of freedom are based on the Kenward-Roger approximation. Tukey's HSD post-hoc tests were conducted using the R package *lsmeans*. Throughout the results, values are reported as mean ± SE.

RESULTS

Sound degradation by song mode

I observed significant variation in sound degradation between broadcast, soft and modified soft syllables in terms of their excess attenuation (LMM main effect: $p<0.001$), blur ratio ($p<0.001$), and signal-to-noise ratio ($p<0.001$) (Table 3.1). With increasing propagation distance, sounds showed higher excess attenuation and blur ratio, as well as lower signal to noise ratio (Figure 3.3). Also, when the speaker was placed at 1.5 m, closer to the ground, sounds showed higher excess attenuation, higher blur ratio and lower signal to noise ratio than when it was placed at 4 m height (Figure 3). In addition, microphone height significantly affected excess attenuation, with lower excess attenuation values when the microphone position was closer to the ground, but I found no statistically significant differences in blur ratio or signal-to-noise ratio that were dependent on microphone height (Figure 3).

The syllable mode X distance interaction explained a significant amount of variation in all sound degradation and attenuation responses (Table 3.1). In terms of excess attenuation, broadcast and modified soft syllables had similar values at 10 and 20 m, but soft song showed more than two and three times greater excess attenuation at those distances respectively (Figure 3.4). At 40 m, modified soft syllables showed higher excess attenuation than broadcast syllables, while soft syllables had significantly higher excess attenuation than both of these two other song modes, reaching more than 5 dB in both cases (Figure 3.4). The blur ratios of broadcast and modified soft song showed similar values at 10 and 20 m, while soft song blur ratio was significantly higher at these distances (Figure 3.4). The blur ratio values observed for soft song at 10 m are matched by broadcast song only when broadcast song has propagated for 40 m. At 40 m, modified soft and soft song showed similar blur ratios that are in turn significantly higher those of broadcast song (Figure 3.4). Additionally, broadcast syllables showed the highest signal to-noise ratio at 10 m, while soft song had the lowest values and values for modified soft song were intermediate (Figure 3.4). At 10 m there is a ~7-10 dB difference between broadcast and modified soft syllables, as well as between modified soft and soft syllables, a difference that remains fairly constant as signal-to-noise ratio decreases with distance for all song modes from 10 to 40 m. In sum, the frequency manipulation of soft syllables (modified soft syllables) recovered similar transmission properties to those of broadcast syllables in terms of excess attenuation and blur ratio at short distances, and intermediate signal-to-noise ratio values between the two syllable modes for all distances. Also, soft song constantly showed higher sound degradation and attenuation that broadcast song at all distances.

Effect of spectral traits on sound degradation

Spectral traits that characterize the acoustic structure of the syllables explained a considerable amount of the variation in excess attenuation (multiple linear regression: $p<0.001$), blur ratio ($p<0.001$) and signal-to noise ratio ($p<0.001$) (Table 3.2). Excess attenuation increased as the minimum frequency ($p<0.001$) and peak frequency of the propagated sounds increased ($p<0.05$) (Table 3.2). Variation in blur ratio was mainly affected by bandwidth, with broader bandwidth syllables resulting in higher blur ratios ($p<0.01$) (Table 3.2). Finally, signal-to-noise ratio decreased in syllables with broader bandwidth ($p<0.001$) and higher peak frequency ($p<0.001$) (Table 3.2). Therefore, the effect of the acoustic structure of bird sounds on sound degradation depends on the particular spectral trait that is being analyzed and the respective sound degradation and attenuation response.

Background noise variation

There was significant variation in the background noise level between syllable modes ($F_{2,15}=10.17$, $p<0.01$). Broadcast syllables registered significantly lower levels of environmental noise compared to soft and modified soft syllables (RMS noise amplitude for broadcast 13.69 ± 0.68, modified soft 23.74 ± 1.17, and soft 26.16 ± 1.14). I also observed variation in the background noise level between the two microphone heights ($F_{1,1923}=9.58$, $p<0.01$). When the microphone was closer to the ground (1.5 m), higher levels of background noise were observed (RMS noise amplitude for 1.5 m height 22.99 ± 0.92, and 4 m height 19.40 ± 0.77).

DISCUSSION

Sound degradation by song mode

I found differences in the patterns of sound degradation and attenuation between broadcast and soft song that are dependent on their respective acoustic structure. The acoustic structure of soft syllables favors sound degradation as showed by their higher excess attenuation, higher blur ratios and lower signal-to-noise ratios when compared to broadcast syllables. Therefore, the sound transmission properties of soft syllables are consistent with predictions of the eavesdropping avoidance hypothesis, and suggest that both the acoustic structure and low amplitude of this song mode are adapted to reduce transmission range and avoid eavesdropping by third party receivers.

An earlier sound propagation study, where the natural amplitude of each song mode was used, found that the twitter sounds (soft song) of common blackbirds *Turdus merula* showed higher excess attenuation, higher blur ratio and lower signal-to-noise ratio than the motif sounds (broadcast song) after propagating for a distance of 25 m (Dabelsteen et al. 1993). After normalizing the amplitude of both song modes in the present study, I still observed lower transmission in soft song compared to broadcast song at a distance of only 10 m in white-throated thrushes. Considering the effects of both the acoustic structure, and the lower amplitude, soft song seems to be adapted to degrade very quickly in the environment within a limited propagation range.

In fact, Dabelsteen et al. (1993) estimated that the soft components (twitters) of the full songs of common blackbirds are not transmitted over distances greater than one territory diameter, while the loud components of the songs can travel over 2-4 territories. The patterns of sound degradation reported in this study also suggest that soft syllables are not transmitted between territories, as neighboring male territories are often separated by more than 40 m in white-throated thrushes (Vargas-Castro 2015). These results demonstrate that soft song is a signal adapted for short range communication, which corresponds with the behavioral contexts and functional role that have been reported for soft vocalizations in previous studies, such as signaling aggressive motivation in corncrakes (Rek and Osiejuk 2011) and brownish-flanked bush warblers (Xia et al. 2013), predicting physical attack between males in song sparrows (Searcy et al. 2006, Searcy and Beecher 2009), or courtship in dark-eyed juncos (Reichard et al. 2013) and common blackbirds (Dabelsteen and Pedersen 1988, Dabelsteen et al. 1998).

Effect of spectral traits on sound degradation

Dabelsteen (2005) suggested that higher frequency, broader bandwidth and higher frequency modulation reduce signal transmission range and thus represent adaptations that increase privacy in acoustic signals. Our results confirm the effects of specific spectral traits on increased sound degradation and attenuation, including higher peak frequency and broader frequency bandwidth. I showed that, if under selection, these spectral traits could reduce the intended communication range of the signals. As exemplified by the modified soft syllables, frequency manipulation of soft syllables recovered similar transmission properties to those of broadcast syllables. In general, the sound degradation responses of modified soft syllables were either statistically equivalent to those of broadcast syllables or showed intermediate values between the natural song modes. Therefore, the region of the frequency spectrum occupied by the signals has major effects on their degradation notwithstanding the complexity of the vocalizations (e.g. the contour or shape of the sounds).

The analysis of the effects of specific spectral traits on sound degradation indicated that not all sound degradation responses react in the same way to changes in the basic spectral traits of sound signals that I analyzed, providing some flexibility to the communication system from an evolutionary point of view. For example, our results suggest that individuals could potentially modify the peak frequency of their sounds, while holding bandwidth constant, without significantly changing the blur ratio of their signals, which is important for signal discrimination (Wiley and Richards 1982, Dabelsteen et al. 1993). Signal discrimination is a fundamental stage of the communication process, as it allows individuals to differentiate conspecific vocalizations from those of other species, as well as the acoustic variation comprised among conspecific song repertoires (Lohr et al. 2003).

Nevertheless, there is also considerable inter-dependence between the spectral traits as well. For instance, if there is selection acting on peak frequency, and lower values are favored in a forested habitat because they result in lower excess attenuation and thus greater transmission distance, the signal-to-noise ratio is likely to increase at the same time; such structural change would improve sound detectability (Wiley and Richards 1982, Wiley 2006). Signal detectability is the first requirement during the perception process to achieve effective acoustic communication (Dooling et al. 2000). Hence, multiple spectral traits of sound signals are affected simultaneously either directly or indirectly under a given selective pressure. Overall, the adaptive vale of structural changes that have consequences on the active space of acoustic signals will also depend on other factors besides degradation and attenuation that need to be taken into account, such as signal directionality (Larsen and Dabelsteen 1990), receiver's auditory sensitivity (Brenowitz 1982, Vélez et al. 2015) and environmental noise profiles (Slabbekoorn 2004).

Background noise variation

I observed more background noise in the section of the frequency spectrum occupied by soft syllables compared to broadcast syllables, which makes detection of soft syllables more difficult (Wiley 2006). Biotic environmental noise in tropical forests is commonly dominated by insect sounds (Ryan and Brenowitz 1985, Slabbekoorn 2004). In the region where our study was conducted, cicadas of the genus *Zammara* are an important source of noise, producing loud sounds between approximately 2.7 and 6.5 kHz (Hart et al. 2015). The frequency of this noise band overlaps mainly with soft syllables and probably explains an important part of the observed background noise variation. These results on background noise support the eavesdropping avoidance hypothesis. If eavesdroppers impose selection to reduce transmission range, the high peak frequency and broad bandwidth that characterize soft syllables may represent adaptations to limit signal detectability through greater masking by noise in this forest habitat. The soft calls of corncrakes have been proposed as another example of soft signals undergoing masking by noise and thus reduced detectability from potential eavesdroppers (Rek 2013, Searcy and Yasukawa 2016). In the case of the corncrakes however, the mechanism involves low-frequency signals (~0.13-0.6 kHz) in open habitats (Rek 2013), where environmental noise is more affected by wind and typically characterized by low frequency (<2 kHz) (Ryan and Brenowitz 1985, Bradbury and Vehrencamp 2011).

Our analysis showed that soft syllables have features that lead to relatively greater excess attenuation, degradation and masking by environmental noise, reducing the potential communication range in a pattern that is consistent with selection to avoid eavesdropping by unintended receivers. Optimal structural design for sound signal transmission is subject to interactions among communication range, environmental noise profiles, habitat acoustic properties, and phylogenetic and morphological constraints (Morton 1975, Wiley and Richards 1982, Ryan and Brenowitz 1985, Dabelsteen 2005, Brumm and Naguib 2009). Here I showed how the acoustic structure of soft signals limits transmission distance during propagation through the environment. Future research on the acoustic structure of soft signals using a comparative approach should provide further insights on the evolution of this complex behavior.

Table 3.1. ANOVA table of the linear mixed-effects models showing the main effects and interaction term on the sound degradation and attenuation responses.

	Excess attenuation			**Blur ratio**			**Signal-to-Noise ratio**		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Syllable mode	120.92	2, 15	<0.001	21.01	2, 15	<0.001	51.80	2, 15	<0.001
Distance	1964.28	2, 1916	<0.001	1062.76	2, 1916	<0.001	6739.40	2, 1916	<0.001
Speaker height	83.52	1, 1916	<0.001	14.64	1, 1916	<0.001	88.40	1, 1916	<0.001
Microphone height	6.70	1, 1916	<0.01	0.94	1, 1916	0.33	1.90	1, 1916	0.16
Syllable mode X Distance	25.96	4, 1916	<0.001	21.12	4, 1916	<0.001	22.40	4, 1916	<0.001

Table 3.2. Estimated coefficients (SE) and final models of three spectral traits (log10) on sound degradation and attenuation responses using multiple linear regressions and backward stepwise analysis. Statistical significance denoted by p-values <0.05 (*), <0.01 (**) or <0.001 (***).

	Minimum frequency	**Bandwidth**	**Peak Frequency**	**Intercept**	**Model**
Excess attenuation	7.87 (1.64)***	2.03 (1.02)	4.87 (1.87)*	-0.96 (0.59)	$F_{3,14}$=83.39***, r^2=0.94
Blur ratio		0.07 (0.02)**	0.06 (0.03)	0.14 (0.01)***	$F_{2,15}$=55.00***, r^2=0.86
Signal-to-noise ratio		-11.30 (2.65)***	-18.14 (4.04)***	46.76 (1.54)***	$F_{2,15}$=143.40***, r^2=0.94

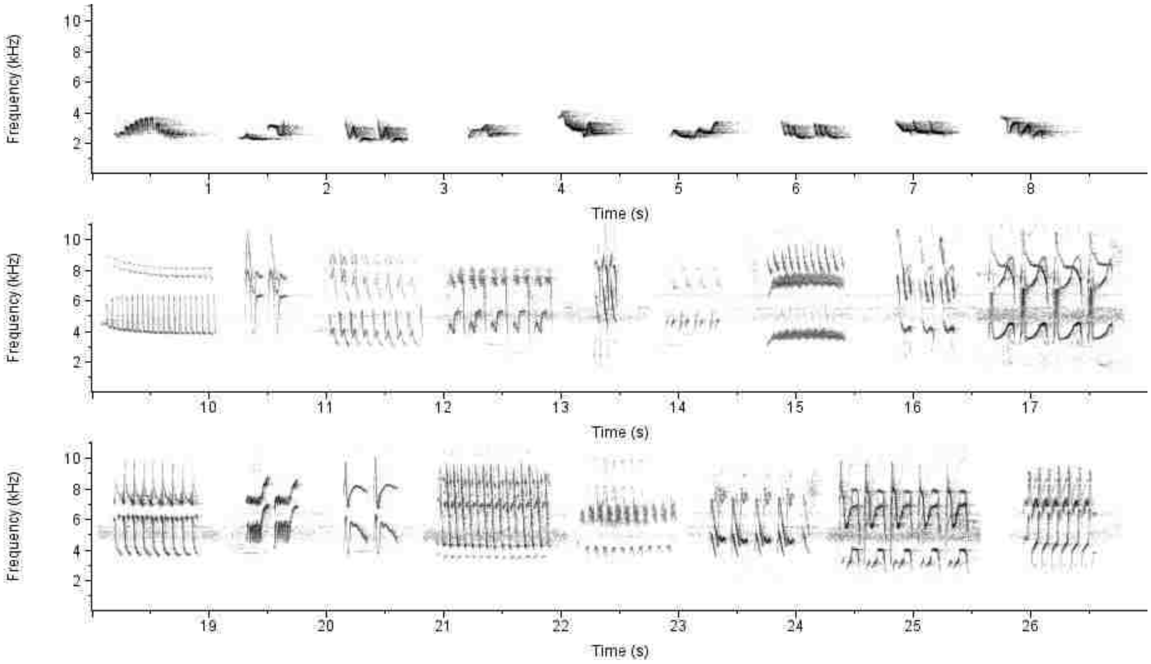

Figure 3.1. Song syllables of a male white-throated thrush, including broadcast syllables (upper row) and soft syllables (center and lower rows) of a partial repertoire of one male. The temporal pattern and organization of the syllables depicted here is not natural. Color intensity corresponds to sound amplitude, with louder sounds being darker.

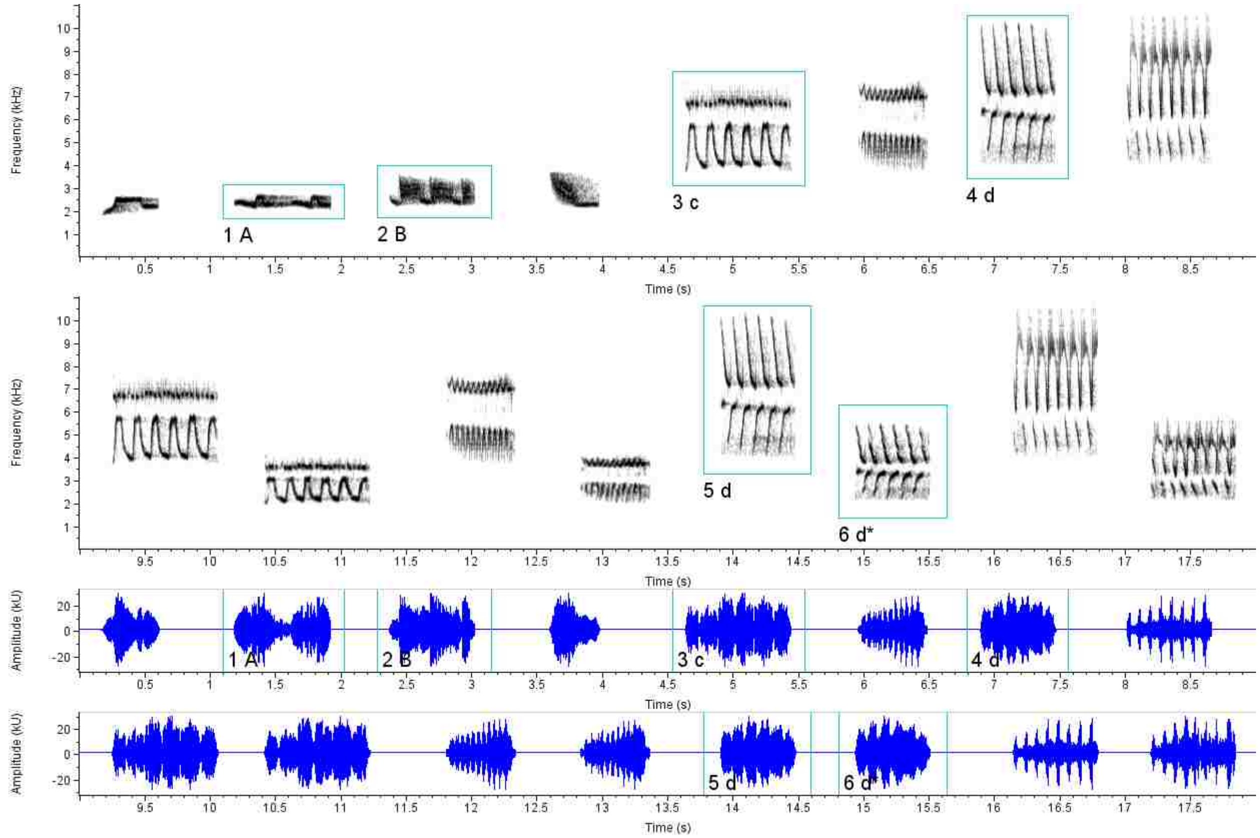

Figure 3.2. Examples of the syllables used in the sound propagation stimulus showing 4 broadcast syllables followed by 4 soft syllables (upper spectrogram), and 4 soft syllables each followed by its respective modified soft syllable version (lower spectrogram). Broadcast syllable 1A has narrower bandwidth compared to 2B. Soft syllable 3c has narrower bandwidth compared to 4d. Syllable 6d* is a modified soft syllable, obtained by lowering syllable 5d's frequency by half. Waveforms (below) illustrate overall equal peak amplitude among syllable categories.

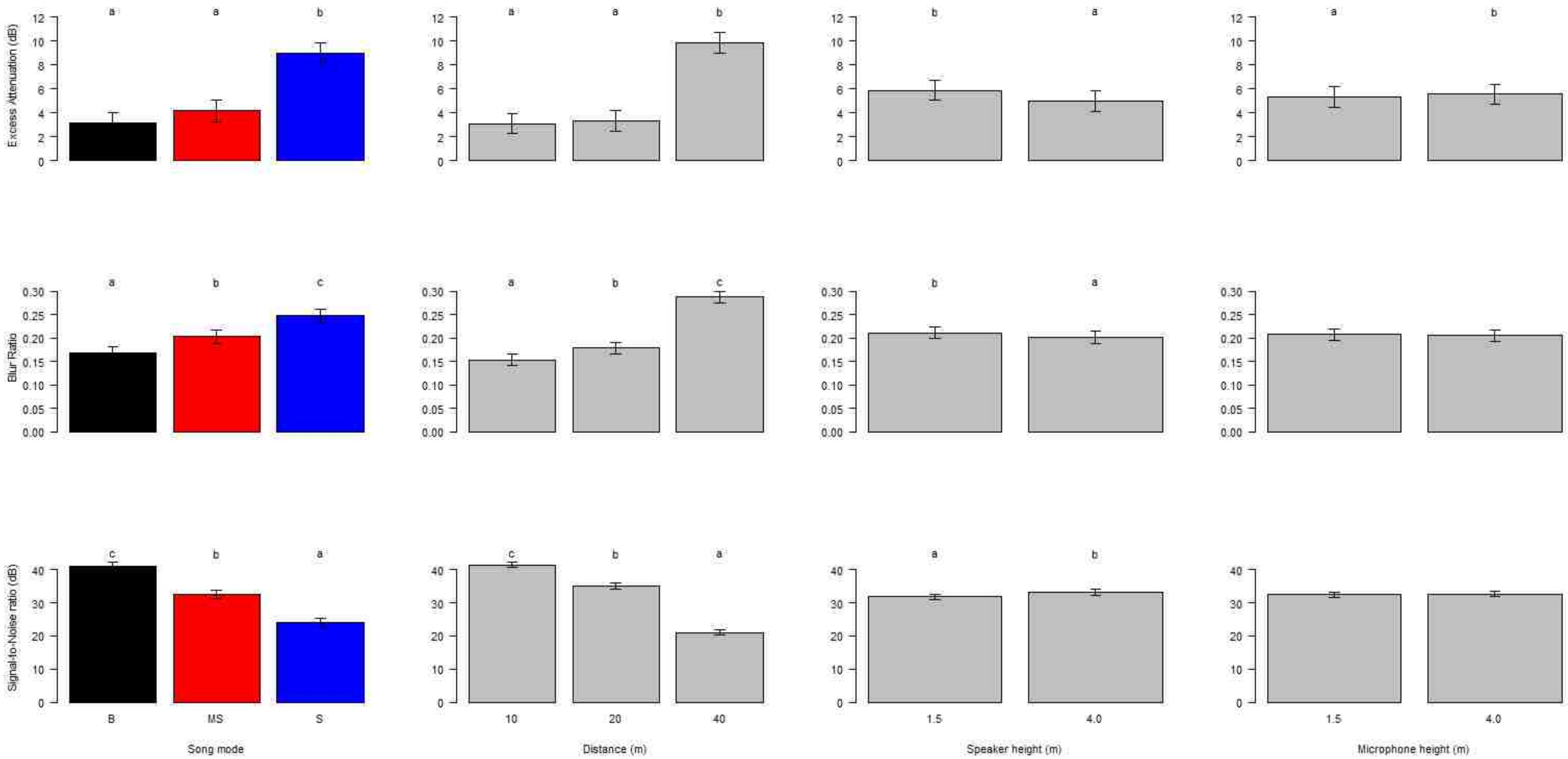

Figure 3.3. Mean variation in sound degradation and attenuation responses (rows) according to song mode, horizontal distance, speaker height and microphone height used in the sound propagation experiment. Song mode colors indicate broadcast (black), modified soft (red) and soft song (blue). Statistically significant differences of the post-hoc tests are shown with different lowercase letters above the bars. Error bars are SE.

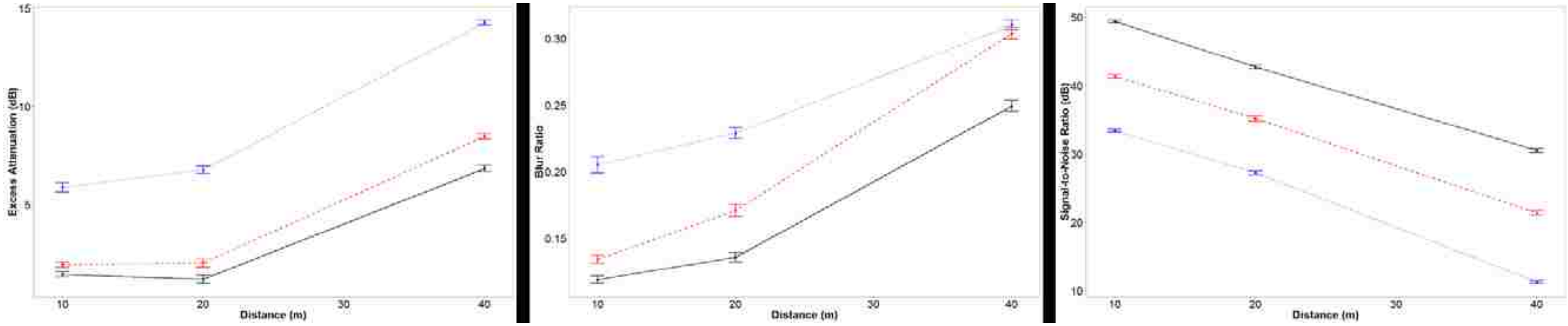

Figure 3.4. Mean variation in sound degradation and attenuation responses according to the two-factor interaction between song mode and horizontal distance used in the sound propagation experiment. Lines are color coded based on song mode as broadcast (solid black), modified soft (dashed red) and soft song (dotted blue). Error bars indicate SE.

Chapter 4

Comparative analysis of habitat and morphology for two song modes of Turdus thrushes: testing the acoustic adaptation hypothesis

OVERVIEW

The ‘acoustic adaptation hypothesis’ proposes that the acoustic properties of animal sounds are shaped by selection dependent on habitat structure (Morton 1975). As sounds propagate through the environment, different structural characteristics of particular habitats interact with the physical properties of acoustic signals. For example, in closed habitats such as forests, dense vegetation acts as a barrier to sound propagation. Acoustic signals are reflected from the surface of trees, branches and foliage, causing reverberations and amplitude attenuation of the sound signal (Morton 1975, Wiley and Richards 1978, Badyaev and Leaf 1997). Since the capacity of sound waves to travel around objects increases with sound wavelength, long distance communication in the forest is best achieved by using signals whose wavelength is longer than the average diameter of the environmental obstacles (i.e. using low frequencies) (Konishi 1970). In addition, reverberations may alter the initial signals as delayed echoes can fill silent intervals between sound elements, especially if the elements are close to each other in time, blurring the distinction between separate sound elements and therefore obscuring rapid amplitude modulation patterns (Brown and Handford 1996, Badyaev and Leaf 1997, Brown and Handford 2000).

Other environmental factors such as wind and temperature gradients increase atmospheric turbulence and affect sound transmission in open habitats. Wind and temperature gradients are more heterogeneous and dynamic over space and time in open habitats than in closed habitats, causing irregular fluctuations in the amplitude of acoustic signals that may affect the receivers' ability for signal discrimination (Wiley and Richards 1978). Brown and Handford (2000) proposed that the temporal instability of irregular amplitude fluctuations favors acoustic signals that improve the consistency of transmission rather than average transmission quality. A sound propagation experiment that they conducted showed that in open habitats sounds with rapid amplitude modulation (trills) propagate as well as sounds with slow amplitude modulation (whistles) on average, but the transmission quality of the former is more consistent. Even though 'closed' and 'open' habitat categories represent two extremes of a continuous gradient in habitat structural complexity, this classification is useful to understand environmental influences on acoustic signal design within the context of the acoustic adaptation hypothesis (Barker 2008).

Since different habitat types pose different selective pressures on sound signals, it is expected that the acoustic properties of animal signals will be adapted to prevent early degradation in their respective environments in order to promote efficient transmission to the intended receivers. A number of studies have shown that bird songs of species that live in forested habitats generally have lower frequency, narrower bandwidth, lower frequency modulation, longer elements, and longer inter-element intervals, providing empirical support for the acoustic adaptation hypothesis (Morton 1975, Badyaev and Leaf 1997, Tubaro and Lijtmaer 2006, Boncoraglio and Saino 2007). However, this hypothesis assumes that signals are used for long range communication and therefore are designed to be propagated far in the environment (Morton 1975), such as in territorial advertisement (Konishi 1970). Adaptations that increase propagation distance are not expected to be important if the acoustic signals are used for short range communication. Thus, signals used in short range communication are not expected to be correlated with habitat structure.

Turdus thrushes are a large genus of passerines distributed worldwide that occupy habitats ranging from dense forests to habitats with sparse or no tree cover (Sibley and Monroe 1990, Clement 2001, Voelker et al. 2007). In *Turdus*, the singing behavior of males is characterized by two different song modes: broadcast (loud) songs and soft songs (Dabelsteen 1984, Lampe 1991, Ishizuka 2006, Johnson 2006, Vargas-Castro et al. 2012, Vargas-Castro 2015). Broadcast songs are used in long range communication, traveling long distances between male territories. Soft songs are mainly used during short range interactions when con-specifics approach each other (to within 10 m or less), usually in aggressive or courtship contexts. These song modes have different acoustic characteristics. Therefore, in this group of birds with two different song modes, the acoustic adaptation predicts that the acoustic properties of broadcast songs should be correlated with habitat structure characteristics while no relationship between habitat structure and the acoustic properties of soft song is expected.

The acoustic structure of bird songs may also be shaped by morphological effects. For example, there is substantial evidence showing a negative relationship between body mass and the frequency of bird vocalizations (Ryan and Brenowitz 1985, Badyaev and Leaf 1997, Tubaro and Mahler 1998, Palacios and Tubaro 2000, Bertelli and Tubaro 2002, Seddon 2005). In addition, beak size and morphology have been associated with song frequency (Palacios and Tubaro 2000, Podos 2001) and the temporal pattern of songs

(Podos 2001, Seddon 2005). Thus body mass and beak size and morphology are important morphological factors that may explain differences in the acoustic properties of the songs of *Turdus*, regardless of their habitat type. These morphological effects on the frequency and temporal patterns of songs are expected in both song modes, since these effects are independent of whether songs are used for long or short range communication.

When a large number of species are compared, each data point is not independent due to phylogenetic relationships (Harvey and Purvis 1991). For example, two species may have songs with similar acoustic properties because they are closely related to each other in terms of their evolutionary history, even if they have contrasting habitat types or body size. This lack of independence can be controlled by incorporating phylogenetic information into the analysis of song acoustic properties and habitat structure (Felsenstein 1985, 2008). Voelker et al. (2007) proposed a *Turdus* phylogeny that can be used to account for phylogenetic relationships in this avian group. In sum, the acoustic properties of each song mode may be affected by habitat structure, morphology and phylogeny.

Here, I will measure frequency variables in the broadcast and soft songs of *Turdus* thrushes to test for associations between the acoustic properties of each song mode, morphology and habitat structure. Considering the effect of morphological adaptations is independent of the transmission range of each song mode, I predict that the acoustic properties of both song modes will be associated with morphological traits. Second, according to the acoustic adaptation hypothesis, I expect to find associations between acoustic features and habitat structure for broadcast songs but not for soft songs.

METHODS

Study species and song recordings

Turdus thrushes are a large and widely distributed genus of passerine birds consisting of 65 species distributed throughout North, Central and South America, Africa and Eurasia (Sibley and Monroe 1990, Clement 2001, Voelker et al. 2007). They occupy a wide range of habitat types, including temperate and tropical zones, from dense forests to habitats with sparse or no tree cover. They are mostly ground-feeders but there are also forest species that have become almost totally arboreal and forage in trees (Clement 2001).

Song recordings were obtained from sound collections including the Macaulay Library (Cornell University, USA), the Animal Sound Archive (Museum für Naturkunde, Germany), a personal collection for *T. assimilis* and *T. grayi*, and the internet-based birdsong sharing community "xeno-canto" (www.xeno-canto.org).

Frequency variables

The overall temporal pattern of songs in *Turdus* shows two types of organization: two-part and mixed (Figure 4.1). 'Two part-songs' have a sequence of broadcast syllables followed by a sequence of soft syllables (e.g. common blackbirds *T. merula*, redwings *T. iliacus* and eyebrowed thrushes *T. obscurus*). Together, both parts constitute 'full songs', but each part may be produced individually as well, such as in the 'twitter song' of common blackbirds, which is produced during short-range conspecific interactions and is only composed of soft syllables (Dabelsteen et al. 1998). 'Mixed songs' are composed of syllable sequences that are highly variable in sequence length (e.g. clay-colored thrushes *T. grayi*, white-throated thrushes *T. assimilis* and Hauxwell's thrushes *T. hauxwelli*). In species with mixed songs, one song mode comprises most of the syllable sequence but syllables of the other song mode are embedded, although less frequently, into different parts of the syllable sequence as well. In mixed song, the dominant song mode (more frequently produced) is determined by the behavioral context of the singing bird. For example, broadcast syllables are relatively more common in the songs of clay-colored thrushes (Vargas-Castro et al. 2012) and white-throated thrushes (Vargas-Castro 2015) during spontaneous singing, whereas soft syllables become the dominant song mode during short-range con-specific interactions.

For each of 20 species, 22-111 syllables of each song mode (broadcast mean = 70, soft mean = 47) were additively obtained from recordings of 3-8 (mean = 5) different individuals. Three frequency variables were measured on each syllable: peak frequency (frequency with highest amplitude), minimum frequency and frequency bandwidth. These frequency measurements were obtained from spectrograms produced in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY), using robust signal measurements (Frequency 5% for minimum frequency and IQR bandwidth). Robust signal measurements take into account the energy that is stored in a selected spectrogram section; therefore small changes in the borders of the selection have little effect on the computed measurement values (Charif et al. 2010). An additional set of 6 species was added from Oblanca and Tubaro (2012) for the estimation of peak frequency values in broadcast song.

Habitat classification

Habitat type data for each species were collected from Birdlife International's website (www.birdlife.org) using the 'forest dependency' categories. 'Low forest dependency' species represent open habitat species, while 'high forest dependency' represent species that live in closed habitats and 'medium forest dependency' those occupying partially open habitats. Closed habitat refers to forests and woodlands, including boreal forest, temperate forest, subtropical/tropical dry forest, subtropical/tropical moist lowland forest, subtropical/tropical swamp forest and subtropical/tropical montane forest. Open habitat refers to habitats with sparse or no tree cover, including savannas, shrublands, grassland and artificial terrestrial areas (pastures, agricultural fields, rural gardens).

Body size, bill size and morphology data

Body mass (g) data for all 26 species were obtained from Dunning (2008). Two measurements of bill length (mm) (skull to upper mandible tip) and (anterior end of the nares to upper mandible tip), bill depth (mm) and width (mm) at the anterior end of the nares were obtained for 3-7 individuals (mean = 5 individuals) for 45 species at the ornithological collection of the American Museum of Natural History. This dataset was used to conduct a PCA and estimate a compound beak variable (beak PC1) describing beak size (Figure 4.3).

Comparative method and statistical analysis

I ran phylogenetic generalized least squares models (PGLS) to investigate correlated evolution of morphological and ecological traits with song frequency responses while controlling for the phylogenetic non-independence of the comparative data (Nunn 2011). Maximum likelihood methods were used to estimate the parameter lambda and scale the variance-covariance matrix accordingly (Freckleton et al. 2002, Revell 2010). I constructed a phylogenetic tree for the 26 species (Figure 4.2) based on the *Turdus* phylogeny proposed by Voelker et al. (2007). As branch lengths were unknown I assumed equal branches and assigned them a value of 1 (Nunn 2011). The effect of body size on beak size was controlled by regressing beak PC1 on body mass and using the residuals of that linear model as a new variable to run further analyses related to beak size. Statistical procedures were conducted in R version 3.2.5, using the software packages ‘caper’, ‘ape’, and ‘phytools’. All statistical tests were performed using log-transformed values for mass and song frequency variables.

RESULTS

PCA based on 45 species and four beak size variables resulted in one principal component (beak PC1) explaining 94% of the beak size variation among *Turdus* thrushes (Figure 4.3). Species body size explained a large proportion of their beak morphology, as shown by the significant regression of beak PC1 on body mass ($F_{1,22} = 87.07$, $R^2 = 0.80$, $p < 0.001$) (Figure 4.4). Using the estimated coefficients (intercept = -9.14, $p < 0.001$; slope

= 0.11, $p < 0.001$) of this linear model, I estimated the beak PC1 fitted values for two additional species for which no beak morphology data were available: *Turdus chiguanco* and *T. dissimilis* (estimated beak PC1 = 1.58 and -1.71, respectively).

Results for all phylogenetic generalized least square models are summarized in Table 4.2. The peak frequency of broadcast songs decreased as species body mass increased ($F_{1,24} = 4.68$, $p < 0.05$) (Figure 4.5). Also, broadcast song bandwidth decreased as beak size increased (PGLS model: beak PC1 slope = -0.05, lambda = 0.09, $F_{1,18} = 4.74$, $p < 0.05$), a relationship that remained after controlling for body size (Figure 4.5) (Table 4.2). None of the acoustic frequency variables of broadcast song showed correlated evolution with forest dependency (Figure 4.5).

In the case of soft song, species with larger beak size had lower peak frequency (PGLS model: beak PC1 slope = -0.04, lambda = 0.07, $F_{1,18} = 8.88$, $p < 0.01$) as well as lower minimum frequency (PGLS model: beak PC1 slope = -0.05, lambda = 0.00, $F_{1,18} = 9.63$, $p < 0.01$). Both of these morphological associations with the acoustic structure of soft song remained significant after controlling for species body size (Figure 4.6) (Table 4.2). In contrast to broadcast song, forest dependency was correlated with minimum frequency and bandwidth in soft song (Table 4.2). The effect of forest dependency on soft song minimum frequency, which was also correlated with beak size (Table 4.2), remained significant after running an additional model that included both predictors (PGLS model: beak (residuals) slope = -0.11, $p < 0.01$; forest dependency high-low slope -0.04, $p = 0.60$; forest dependency high-medium slope = -0.31, $p < 0.01$; full model $F_{3,16} = 8.54$, lambda = 0.00, $R^2 = 0.62$, $p < 0.01$). Therefore, species with high forest dependency had higher minimum frequency than species with medium forest dependency (Figure 4.6).

DISCUSSION

I found correlated evolution of morphological and ecological traits with song in *Turdus* thrushes. Body size and beak size where each one correlated with the acoustic structure of broadcast or soft songs, but each song mode has evolved different correlated responses with these morphological traits. Contrary to my second prediction, habitat showed correlated evolution with soft song but not with broadcast song. However, the observed response was in the opposite direction as that predicted by the acoustic adaptation hypothesis. This is the first study to show evidence of correlated evolution of morphology and habitat structure with soft song.

Morphological effects

Morphology is known to be an important factor shaping the acoustic structure of animal sounds (Searcy and Nowicki 2005). One pattern supported by numerous studies is the decrease in the frequency of bird vocalizations as body mass increases (Ryan and Brenowitz 1985, Badyaev and Leaf 1997, Tubaro and Mahler 1998, Palacios and Tubaro 2000, Bertelli and Tubaro 2002, Seddon 2005), although *Corvus* provides a counter example (Laiolo and Rolando 2003). In songbirds for example, the size of the vibrating membranes of the syrinx, the vocal organ, is correlated with body mass, with larger individuals having larger membranes that produce lower frequency sounds (Ryan and Brenowitz 1985, Nowicki and Marler 1988). The allometry of the syrinx can thus explain the negative relationship between species body mass and peak frequency observed in this study among different species of *Turdus*. In addition, Oblanca and Tubaro (2012) had previously analyzed broadcast song and its relation to body mass in a different group of South American thrushes, further supporting this pattern.

I also found correlated evolution of beak size and song frequency variables in both song modes. The relationship between bandwidth and beak morphology has been investigated in emberizids (Podos 2001, Podos and Nowicki 2004, Huber and Podos 2006) and woodcreepers (Palacios and Tubaro 2000, Derryberry et al. 2012). Bandwidth typically shows a negative correlation with beak size in these avian groups (Palacios and Tubaro 2000, Huber and Podos 2006), which is consistent with the results obtained for broadcast song in *Turdus* thrushes.

Moreover, I observed that species with relatively smaller beaks have soft song with higher pitch and higher minimum frequency. A negative relationship between beak size and song frequency was also found by Palacios and Tubaro (2000) in woodcreepers. Even though their study was based on broadcast songs, the mechanism they provided to explain this pattern applies to soft song as well. Considering that the vocal tract has resonating properties that affect sound frequency (Nowicki and Marler 1988), they argued that longer beaks add proportionally more to the length of the tube formed by the trachea and buccal cavities, reducing its resonating frequency relative to smaller beaks (Palacios and Tubaro 2000). Consistent with this idea, *Turdus* species with relatively larger beaks may be unable to produce sounds with a pitch as high as species with smaller beaks.

Habitat effects

The effects of forest dependency on the acoustic frequency variables analyzed in both song modes did not meet my initial prediction. In the context of the acoustic adaptation hypothesis, broadcast songs are expected to be correlated with habitat. Broadcast songs function in long range communication and therefore are expected to be under selection derived from habitat acoustics (Morton 1975). I found no direct evidence to support the acoustic adaptation hypothesis in the broadcast songs of the *Turdus* thrushes. However, the pattern observed for soft songs in relation to habitat structure is compatible with this hypothesis.

Morton (1975) identified an 'acoustic window' or range of frequencies (1.6-2.5 kHz) in forest habitats where animal vocalizations have lower sound attenuation compared to other frequencies outside this range. A number of studies have provided empirical support for the acoustic adaptation hypothesis, showing that bird songs of species occupying forested habitats generally have properties matching the acoustic window, such as lower frequency and narrower bandwidth relative to those of open habitats (Morton 1975, Badyaev and Leaf 1997, Tubaro and Lijtmaer 2006, Boncoraglio and Saino 2007). In this study, species with high forest dependency had broadcast songs with peak frequencies (mean = 2.75 kHz) and minimum frequencies (mean = 2.35 kHz) nearby or contained within the acoustic window, respectively.

The mechanism proposed by the acoustic adaptation hypothesis explains why acoustic signals in closed habitats are expected to be constrained within certain frequency boundaries, but it does not argue that acoustic signals in open habitats are actively selected to depart from that range. Species in open habitats may use other frequencies due to the lack of selection constraining signal frequency for effective sound propagation. Similarly, if improved sound propagation is not an important factor for effective communication, as for short range signals, then habitat-induced selection based on sound attenuation and degradation in forest habitats is not expected to constrain those acoustic signals. I propose this is the case for soft song in species with high forest dependency. Peak frequency and minimum frequency were much higher than expected by the acoustic window. Overall, these results would provide evidence against the acoustic adaptation hypothesis, if found in broadcast songs, but in soft song there is no reason to expect active selection constraining their frequency towards the acoustic window. Instead it could be argued, that there may be selection in closed habitats favoring higher frequencies, which are more susceptible to sound degradation, in order to avoid eavesdropping by third party receivers (Chapter 3) (Dabelsteen 2005). It might prove useful to segregate medium forest dependency species into either high or low categories to give more power to the analysis, or perhaps translate forest dependency into a numerical variable using measurements like ‘vegetation index’ (Medina-García et al. 2015) to further explore this evolutionary correlation between habitat structure and soft song frequency in future analyses.

Thrushes, as is true of many songbirds, learn their songs through imitation of adult conspecifics (Marler 1970). Some authors have discouraged the analysis of songs in comparative studies of songbirds, mainly due to the learning capabilities of many oscine species and the consequent difficulty in assigning genetic versus cultural sources of phenotypic variation in acoustic behavior (McCracken and Sheldon 1997, Seddon 2005). On the other hand, song learning may facilitate matching between habitat and song characteristics (Slater 1989). Hansen (1979) suggested that juvenile males will be most prone to learn the conspecific song models that have suffered the least degradation during transmission through particular habitats, because these will be the most clearly heard models for copying. A sound propagation study in Carolina wrens *Thryothorus ludovicianus* supported this idea by showing that songs native to the test habitat underwent less environmental induced degradation compared to foreign conspecific songs (Gish and Morton 1981). Thus, the cultural evolution process provides a mechanism for how songs can acquire characteristics that favor transmission in a given environment.

In conclusion, I observed correlated evolution of morphological traits and song frequency variables in both song modes. Body mass had a significant negative effect on broadcast peak frequency, while beak morphology was a significant predictor of bandwidth in broadcast song and soft song frequency. It is interesting to note that even though the interspecific variation in beak morphology in *Turdus* thrushes is smaller compared to other avian groups that have undergone adaptive radiation, such as woodcreepers and Darwin's finches (Podos 2001, Derryberry et al. 2012), there is correlated evolution of beak morphology and acoustic traits. Thus, it is reasonable to assume that beak morphology has played a role over the evolutionary trajectory of acoustic signal diversification in this speciose, and acoustically rich, avian group. Finally, there was no correlated evolution of forest dependency with broadcast song and, contrary to predictions based on acoustic adaptation, soft song did show a correlation with forest dependency.

Table 4.1. Acoustic frequency variables by species according to song mode and forest dependency level

			Broadcast song			Soft song		
Species	**Common Name**	**Forest dependency**	**Peak Frequency**	**Minimum Frequency**	**Bandwidth**	**Peak Frequency**	**Minimum Frequency**	**Bandwidth**
T. poliocephalus	Island Thrush	high	3.07	2.58	0.33	4.43	3.25	1.08
T. obscurus	Eyebrowed Thrush	high	2.72	2.36	0.42	5.53	4.02	1.22
T. boulboul	Grey-winged Blackbird	high	2.61	2.29	0.24	4.06	2.88	1.1
T. dissimilis	Black-breasted Thrush	high	2.53	2.08	0.35	4.91	3.86	1.37
T. leucops	Pale-eyed Thrush	high	3.58	3.13	0.33	6.25	5.08	1.32
T. hauxwelli	Hauxwell's Thrush	high	2.19	1.95	0.15	4.9	3.68	1.42
T. infuscatus	Black Thrush	high	2.58	2.06	0.43	5.62	4.48	0.97
T. fuscater	Great Thrush	low	2.66	2.38	0.23	4.98	3.93	1.03
T. chiguanco	Chiguanco Thrush	low	3.04	2.69	0.28	4.22	3.64	1.26
T. ignobilis	Black-billed Thrush	low	3.00	2.36	0.46	4.31	3.43	1.1
T. amaurochalinus	Creamy-bellied Thrush	low	2.52	2.06	0.34	3.29	2.61	0.94
T. nudigenis	Spectacled Thrush	low	2.27	1.82	0.31	3.69	3.06	0.95
T. grayi	Clay-coloured Thrush	low	2.39	2.10	0.27	4.94	4.01	1.16
T. rufiventris	Rufous-bellied Thrush	low	2.21	2.00	0.21	5.31	3.27	1.67
T. falcklandii	Austral Thrush	low	3.03	2.58	0.37	3.37	2.74	0.76
T. philomelos	Song Thrush	low	2.97	2.54	0.33	5.81	4.62	1.05
T. albicollis	White-necked Thrush	medium	1.90	1.72	0.14	4.33	2.62	1.63
T. assimilis	White-throated Thrush	medium	2.72	2.22	0.38	4.91	3.64	1.33
T. migratorius	American Robin	medium	2.97	2.29	0.46	4.63	2.94	1.71
T. merula	Eurasian Blackbird	medium	2.29	2.01	0.23	3.74	2.85	1.11
T. nigriceps	Slaty Thrush	medium	4.18	---	---	---	---	---
T. serranus	Glossy-black Thrush	medium	3.50	---	---	---	---	---
T. leucomelas	Pale-breasted Thrush	medium	2.46	---	---	---	---	---
T. obsoletus	Pale-vented Thrush	medium	2.26	---	---	---	---	---
T. fumigatus	Cocoa Thrush	medium	2.21	---	---	---	---	---
T. flavipes	Yellow-legged Thrush	medium	3.72	---	---	---	---	---

Table 4.2. Phylogenetic GLS model results according to predictor and acoustic variable response. All acoustic variables and body mass were log transformed. Beak (res) corresponds to beak size after controlling for body mass. Forest dependency is a discrete predictor with three levels, ‘high’ corresponds to the base level

Mode	Predictor	Response	Coefficient	p-value	Lambda	F	df	R^2	Model p-value
Broadcast	Body mass	Peak Frequency	-0.300	0.041	0.849	**4.679**	**1, 24**	**0.163**	**0.041**
	Beak (res)	Peak Frequency	-0.045	ns	0.000	2.632	1, 24	0.099	ns
	Forest high-low	Peak Frequency	-0.035	ns	0.718	0.094	2, 23	0.008	ns
	Forest high-medium	Peak Frequency	-0.002	ns					
	Body mass	Minimum Frequency	-0.054	ns	0.840	0.155	1, 18	0.009	ns
	Beak (res)	Minimum Frequency	-0.037	ns	0.000	1.863	1, 18	0.094	ns
	Forest high-low	Minimum Frequency	0.026	ns	0.714	1.241	2, 17	0.127	ns
	Forest high-medium	Minimum Frequency	-0.100	ns					
	Body mass	Bandwidth	-0.396	ns	0.243	1.740	1, 18	0.088	ns
	Beak (res)	Bandwidth	-0.122	0.032	0.000	**5.412**	**1, 18**	**0.231**	**0.032**
	Forest high-low	Bandwidth	0.007	ns	0.266	0.115	2, 17	0.013	ns
	Forest high-medium	Bandwidth	-0.074	ns					
Soft	Body mass	Peak Frequency	-0.374	0.058	0.303	4.116	1, 18	0.186	0.058
	Beak (res)	Peak Frequency	-0.080	0.035	0.000	**5.187**	**1, 18**	**0.224**	**0.035**
	Forest high-low	Peak Frequency	-0.189	0.093	0.698	2.837	2, 17	0.250	0.086
	Forest high-medium	Peak Frequency	-0.232	0.041					
	Body mass	Minimum Frequency	-0.371	ns	0.314	2.833	1, 18	0.136	ns
	Beak (res)	Minimum Frequency	-0.114	0.008	0.000	**8.980**	**1, 18**	**0.333**	**0.008**
	Forest high-low	Minimum Frequency	-0.159	ns	0.671	**5.132**	**2, 17**	**0.377**	**0.018**
	Forest high-medium	Minimum Frequency	-0.354	0.005					
	Body mass	Bandwidth	-0.167	ns	0.000	0.505	1, 18	0.270	ns
	Beak (res)	Bandwidth	0.039	ns	0.000	0.842	1, 18	0.045	ns
	Forest high-low	Bandwidth	-0.112	ns	0.000	**4.649**	**2, 17**	**0.354**	**0.025**
	Forest high-medium	Bandwidth	0.206	0.080					

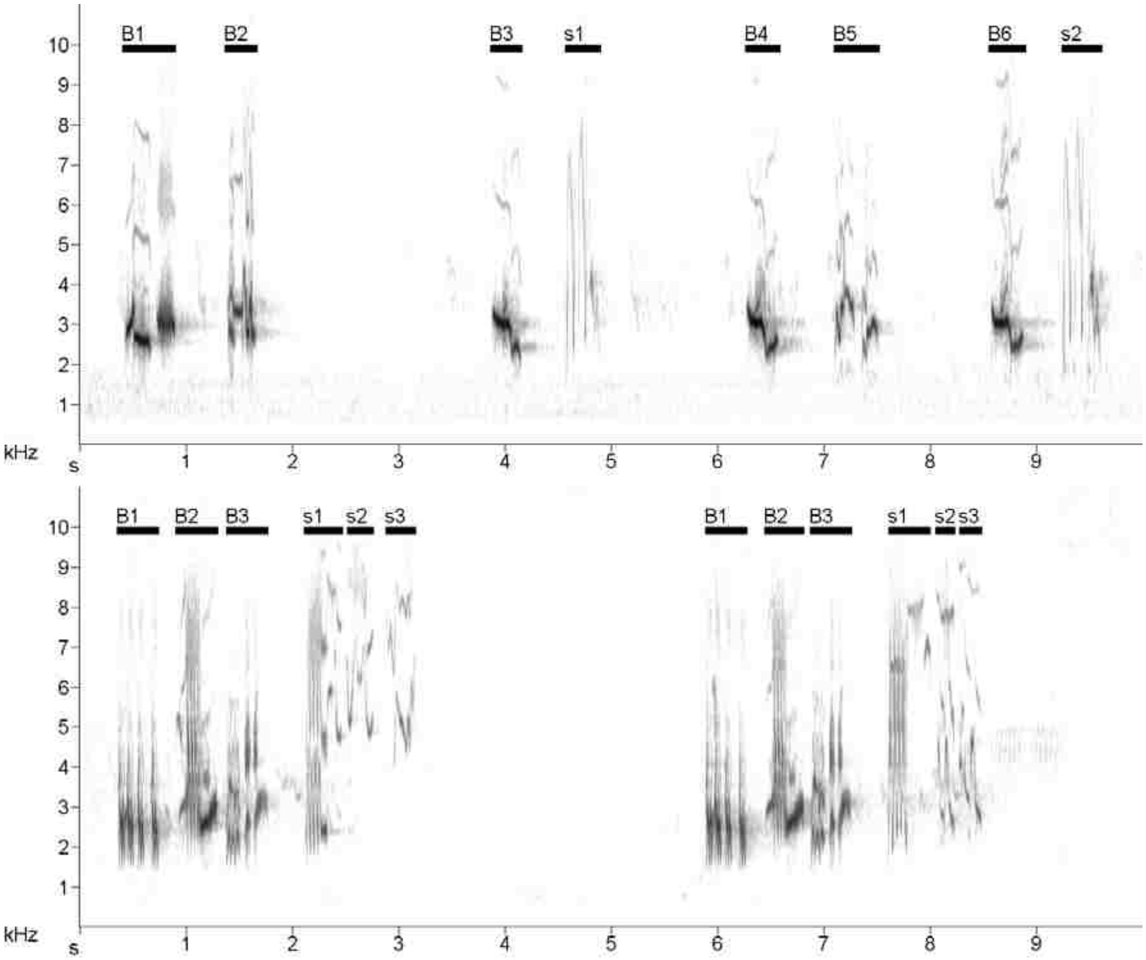

Figure 4.1. Song syllables of the Austral Thrush *Turdus falcklandii* (upper panel), a South American species with low forest dependency and mixed songs. Songs of the Eyebrowed Thrush *Turdus obscurus* (lower panel), a Eurasian species with high forest dependency and two-part songs

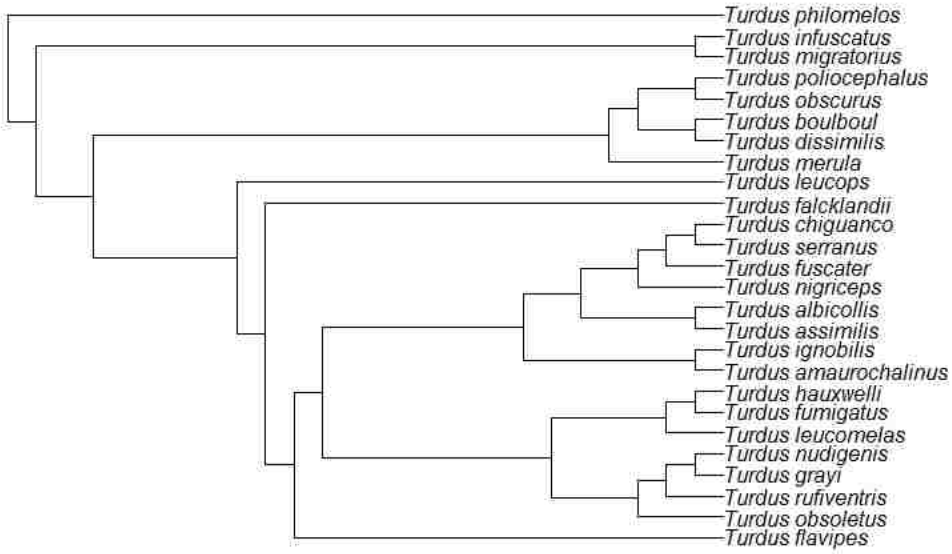

Figure 4.2. Phylogenetic tree showing the relationships between the 26 species of *Turdus* thrushes analyzed in the present study. The tree was constructed based on the *Turdus* phylogeny proposed by Voelker et al. (2007), which used mitochondrial (mtDNA) sequence data from the ND3, ND2, and cytochrome b genes and included 60 of the 65 extant species currently recognized in the genus.

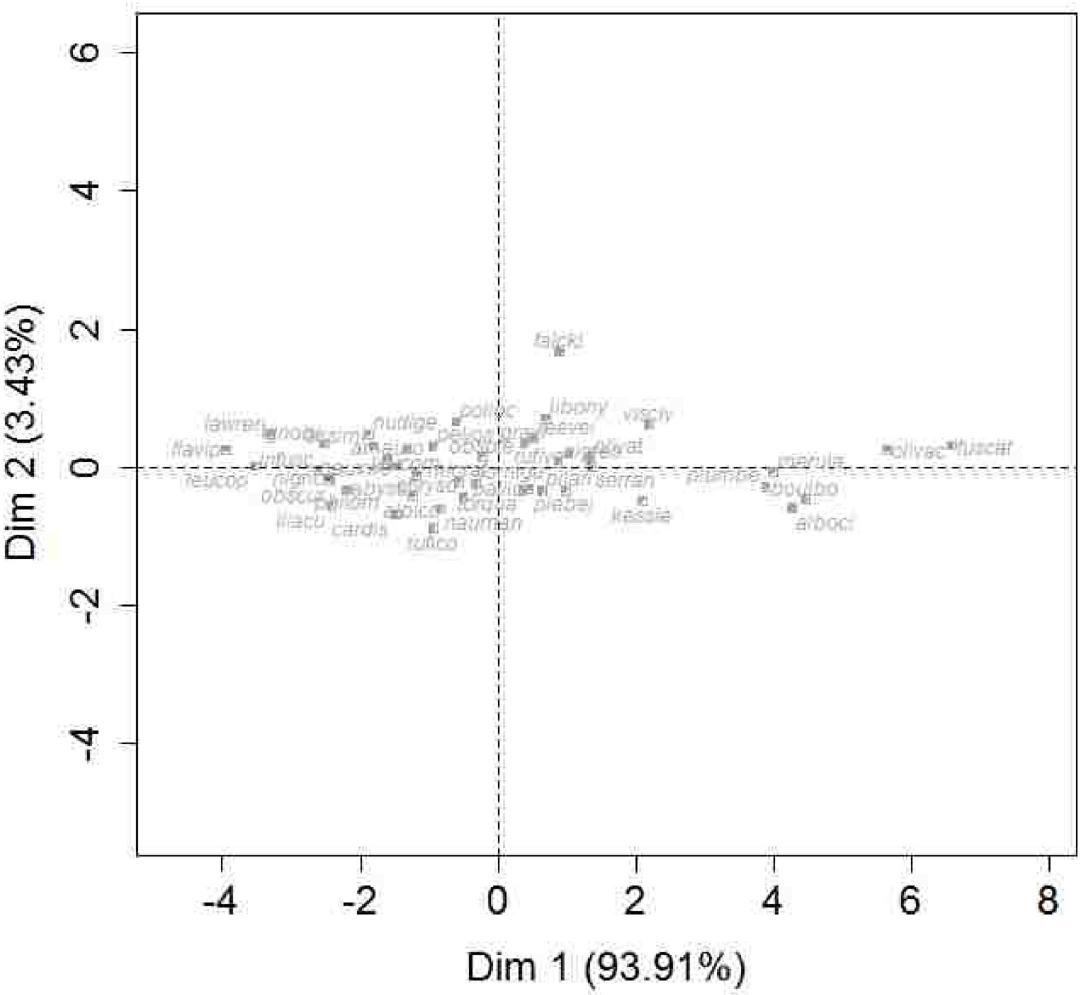

Figure 4.3. PCA diagram showing the segregation of 45 *Turdus* species according to the first two principal components estimated using four beak size measurements that including beak depth, beak width, beak length 1 (skull to upper mandible tip) and beak length 2 (anterior end of the nares to upper mandible tip). The first principal component (beak PC1) was used in subsequent analyses.

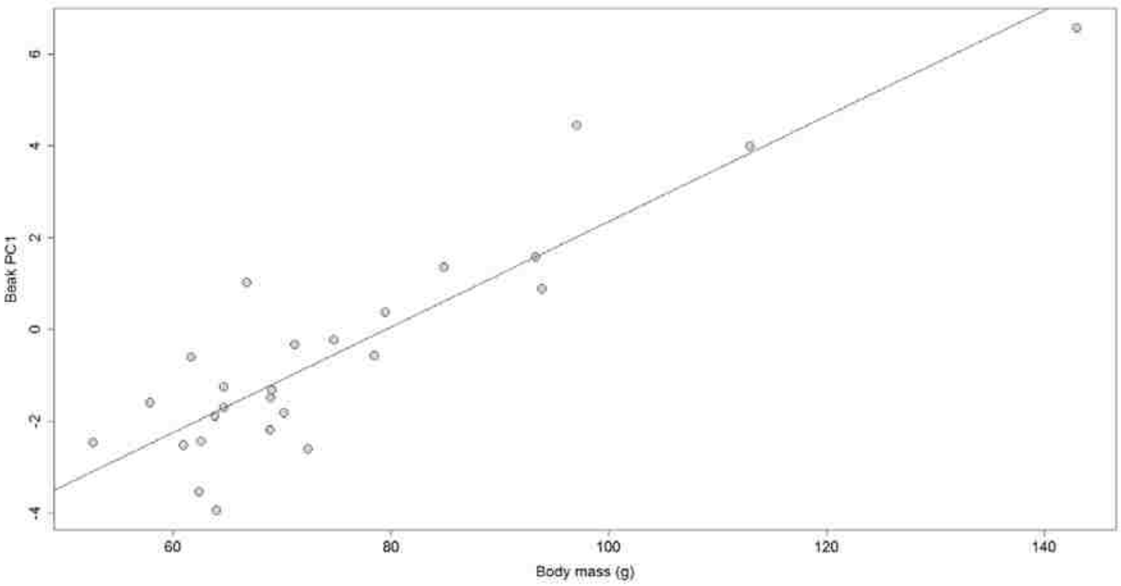

Figure 4.4. Linear regression of beak size (principal component 1) on body mass for 26 species of *Turdus* thrushes. This dataset includes two species in which there was no beak size data available, *Turdus chiguanco* and *T. dissimilis*, for which respective beak PC1 values were estimated using linear model coefficients and can be seen overlapping the fitted line.

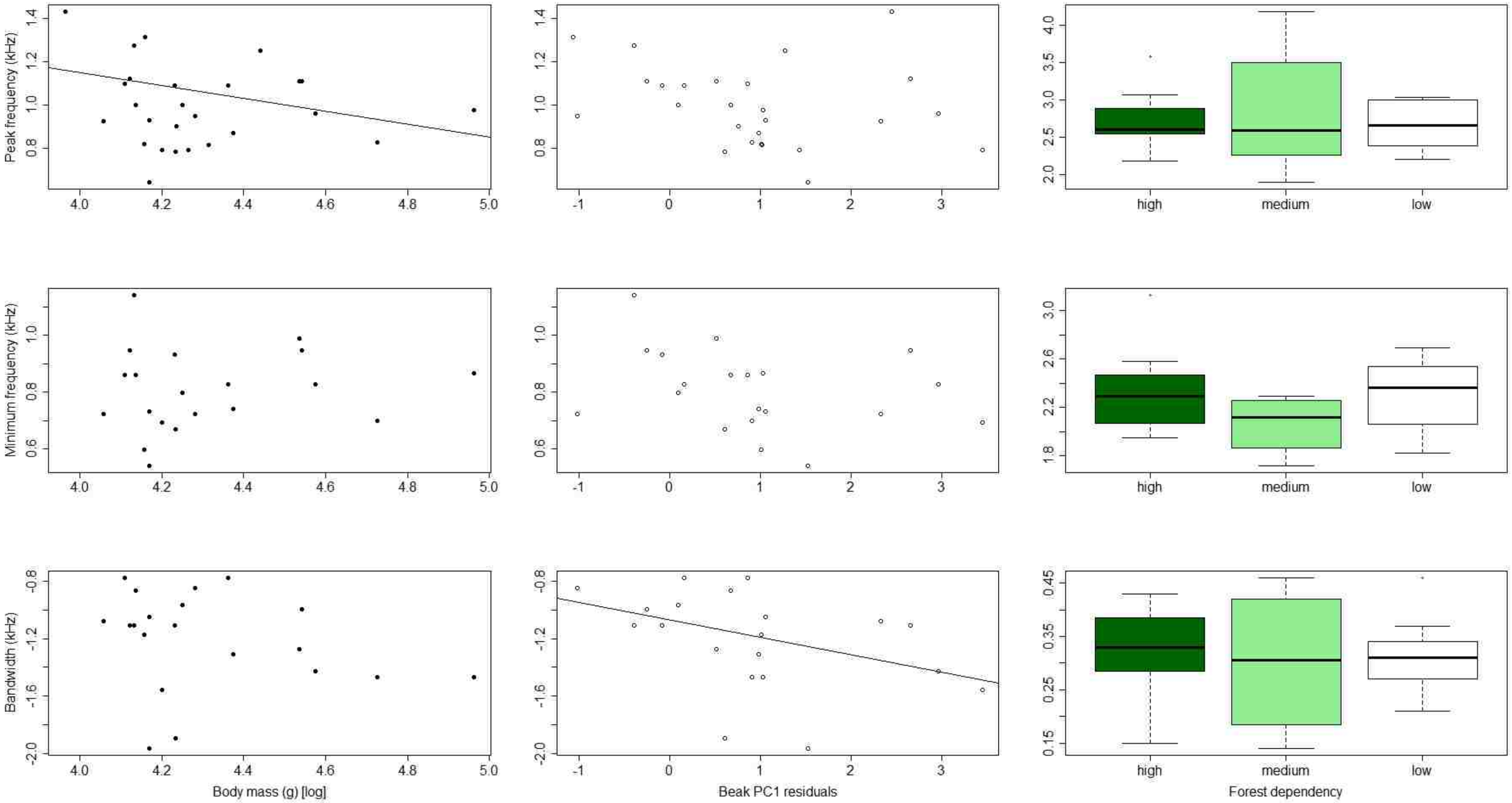

Figure 4.5. Broadcast song frequency variables according to morphological predictors (body and beak size) and forest dependency. Frequency variables are log transformed except for the forest dependency column. Species with high forest dependency inhabit closed habitats, while low forest dependency species occupy open habitats. Regression lines are shown for statistically significant models (see Table 4.1).

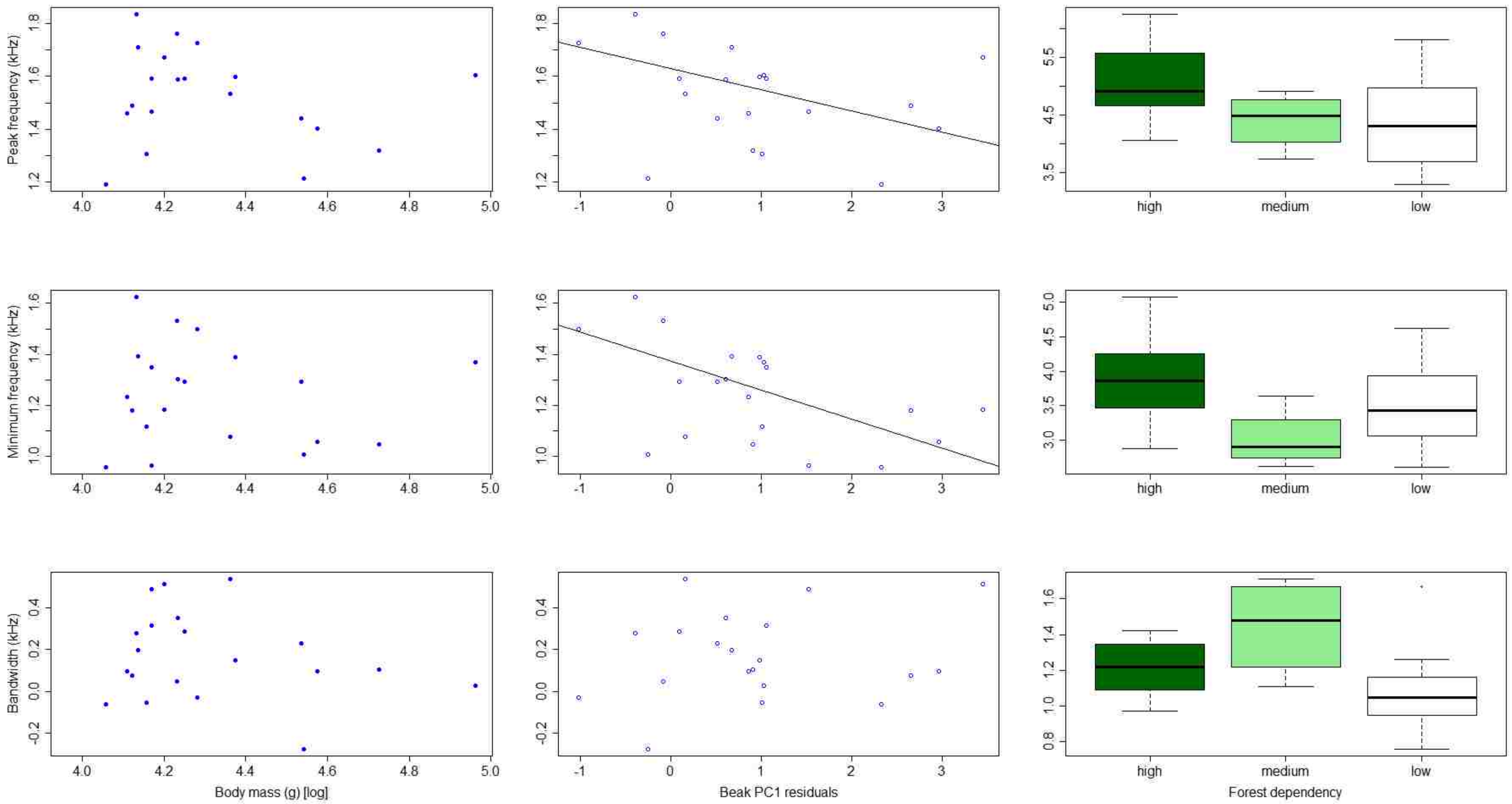

Figure 4.6. Soft song frequency variables according to morphological predictors (body and beak size) and forest dependency. Frequency variables are log transformed except for the forest dependency column. Species with high forest dependency inhabit closed habitats, while low forest dependency species occupy open habitats. Regression lines are shown for statistically significant models. Forest dependency models significantly explained variation in minimum frequency and bandwidth (see Table 4.1).

CONCLUSION

The low levels of syllable sharing between males in both song modes suggest that invention plays a greater role than imitation during song development. A large proportion of the broadcast repertoires in other *Turdus* species are also unique to particular males, and hand-rearing experiments support invention (or improvisation) of broadcast songs (Rasmussen and Dabelsteen 2002, Johnson 2006, Vargas-Castro et al. 2012). Also, most of the soft song syllables analyzed here in white-throated thrushes were unique to the repertoires of particular males. These findings suggest that invention seems to be a widespread mechanism of song acquisition in *Turdus* species, which possibly extends to the acquisition of soft songs as well.

Moreover, the observed spatial pattern of song sharing differs between song modes in white-throated thrushes, implying that individuals are adding song types to their repertoires by means of two different strategies, one that acquires shared broadcast songs and one that acquires shared soft songs. In the last, no geographical pattern was observed. Thus, soft signaling invites a more inclusive reconsideration of the relationship between spatial patterns of song sharing and song learning strategies (Slater 1989, Wilson et al. 2000). For example, a fourth pattern could be added when song sharing exists but remains uniform with geographic distance, which would apply to soft song. The generalization of this pattern however, is pending on future research. Nonetheless, it would be valuable to acknowledge that different song learning strategies can potentially operate simultaneously as birds develop their song.

In addition, this dissertation provides the first analyses of soft song signal design within the context of two important hypotheses that explain the properties of animal sounds: the ‘eavesdropping avoidance’ and the ‘acoustic adaptation’ hypotheses. It was found that the acoustic structure of soft syllables favors sound degradation and attenuation, which is consistent with predictions of the eavesdropping avoidance hypothesis. Therefore, the acoustic structure of soft signals, besides their low amplitude, reduce transmission range and is compatible with the idea that soft song is a signal adapted to avoid detection by third party receivers.

The comparative approach showed that each song mode in *Turdus* thrushes has evolved different correlated responses with body size and beak morphology. Soft song frequency was particularly affected by beak size. Therefore, selection acting on this morphological trait may influence the evolution of low amplitude signals in this group as it has been shown for the high amplitude signaling of Darwin’s finches (Podos 2001). In terms of habitat effects, no correlation between habitat and broadcast song was found, but the acoustic adaptation mechanism often only has a weak effect (Boncoraglio and Saino 2007). Interestingly, the observed response for soft song was in the opposite direction as that predicted by the hypothesis. Even though no correlation was expected for soft song, because it is a signal adapted to reduce transmission range (Chapter 3), perhaps there is selection in closed habitats species favoring sound degradation, and therefore higher frequencies, which is also congruent with the hypothesized functional role of avoiding eavesdropping by third party receivers.

This dissertation integrates behavioral, ecological and evolutionary processes in the analysis of multiple factors that shape the acoustic traits of soft signals. It is a modest contribution to our understanding of this intriguing behavior. I hope this research inspires future work on soft song, and low-amplitude signaling in general, where many questions remain to be explored in this fertile field within the study of animal sounds.

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APPENDICES

Table SM1. Frequency band-pass filters and duration of the syllables used in the sound propagation experiment. Syllable mode is denoted by B, S and MS which represent broadcast, soft and modified soft syllables respectively.

Syllable mode	Low frequency (Hz)	High frequency (Hz)	Duration (s)
B 1	1885.0	2775.0	0.541
B 2	1785.0	2520.0	0.443
B 3	2095.0	2630.0	0.739
B 4	2175.0	3585.0	0.655
B 5	2150.0	3605.0	0.382
B 6	1935.0	3430.0	0.658
S 7	2585.0	9820.0	0.392
S 8	3640.0	7600.0	0.811
S 9	3700.0	7605.0	0.529
S 10	3965.0	10385.0	0.575
S 11	3970.0	10820.0	0.650
S 12	4065.0	7470.0	0.448
MS 13	1292.5	4910.0	0.392
MS 14	1820.0	3800.0	0.811
MS 15	1850.0	3802.5	0.529
MS 16	1982.5	5192.5	0.575
MS 17	1985.0	5410.0	0.650
MS 18	2032.5	3735.0	0.448