

# EVOLUTION OF VOCAL SIGNALS IN A NEOTROPICAL AVIAN LINEAGE

A Dissertation

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## Table of Contents

Acknowledgments . . . . .	ii
List of Tables . . . . .	v
List of Figures . . . . .	vi
Abstract . . . . .	vii
Chapter 1. Introduction and Literature Review . . . . .	1
Chapter 2. Individual Song Variation in <i>Synallaxis</i> , with Emphasis on <i>S. frontalis</i> . . . . .	12
Chapter 3. Geographic Variation in Vocalizations of the <i>Synallaxis azarae</i> Complex . . . . .	31
Chapter 4. Patterns of Vocal Character Evolution in <i>Synallaxis</i> . . . . .	53
Chapter 5. Summary and Conclusions . . . . .	73
Literature Cited . . . . .	77
Appendix A. Species Accounts . . . . .	89
Appendix B. Recordings Used in Chapter 3 . . . . .	140
Appendix C. Character Matrix for Chapter 4 . . . . .	147
Appendix D. Character Maps . . . . .	150
Vita . . . . .	172



## List of Tables

2.1. <i>F</i> -values and ranges of means for note measurements of <i>Synallaxis frontalis</i> song . . .	17
2.2. Correlations between note duration and frequency variables in <i>Synallaxis frontalis</i> . .	18
2.3. Note duration measurements before and after playback . . . . .	21
2.4. Note frequency measurements before and after playback . . . . .	22
3.1. Nomenclature and distribution of <i>Synallaxis azarae/courseni</i> . . . . .	36
3.2. ANOVA on vocal characters of <i>Synallaxis azarae</i> and <i>S. frontalis</i> . . . . .	40
3.3. Vocal character differences among subspecies of <i>Synallaxis azarae</i> . . . . .	41
4.1. <i>Synallaxis</i> vocal characters and character states . . . . .	62
4.2. Summary of state changes and homoplasy indices for each vocal character . . . . .	63
4.3. Homoplasy indices for three vocal character categories . . . . .	63

## List of Figures

2.1. Peak correlations for notes within and among individuals of <i>Synallaxis frontalis</i> . . . .	17
2.2. The 3-dimensional “song space” of <i>Synallaxis frontalis</i> . . . . .	19
2.3. Song similarity as a function of distance between sampling localities . . . . .	20
2.4. Song plasticity in multivariate space . . . . .	23
3.1. Measurements of single vocal characters in <i>Synallaxis azarae/courseni</i> . . . . .	39
3.2. Number of non-overlapping characters among subspecies of <i>Synallaxis azarae</i> . . . .	42
3.3. Linear discriminant analysis of <i>Synallaxis azarae/courseni</i> . . . . .	43
3.4. Loadings on principal components for <i>Synallaxis azarae/courseni</i> vocal data . . . . .	44
3.5. Linear discriminant analysis of <i>Synallaxis azarae/courseni</i> with <i>S. frontalis</i> . . . . .	45
4.1. Molecular phylogeny of <i>Synallaxis</i> showing vocal character state changes . . . . .	65
4.2. DNA sequence divergence vs. number of vocal character differences . . . . .	66
4.3. An alternate song of <i>Synallaxis albescens</i> and the song of <i>S. hypospodia</i> . . . . .	72

## Abstract

In this dissertation I explored variation in vocalizations of the avian genus *Synallaxis* (Passeriformes: Furnariidae) and the use of vocal characters to determine phylogenetic relationships at the species level. Vocalizations of suboscine passerines have recently gained favor as a proxy for genetic material in systematic studies; however, individual and geographic variation are both widespread in suboscines, complicating the definition and analysis of vocal characters. This is particularly true for species that have simple, phylogenetically conserved vocalizations. Moreover, the use of vocal characters in suboscine systematics depends on the confident assessment of homologous vocalizations, as well as a thorough understanding of their role in the behavioral processes fundamental to reproductive isolation and speciation. My research was based upon a collection of approximately 1200 *Synallaxis* recordings, representing every species and most subspecies in the genus. I identified presumably homologous vocalizations (“songs”) and analyzed variation within and among individuals, populations, and species. Song playback induced statistically significant changes in character measurements within individuals, although individual diagnosability was generally high even in classifications based on few measurements. Geographic variation was pronounced in a widespread, polytypic Andean species (*S. azarae*) but nonexistent in a related monotypic lowland form (*S. frontalis*). In comparisons both within and among species, a high degree of vocal convergence within a limited multivariate space and between geographic and elevational extremes obscured potentially significant patterns of variation in other characters, and underscore the need for large sample sizes and complete geographic sampling in suboscine vocal studies. Little phylogenetic information was recovered when vocal characters were mapped onto a molecular phylogeny of *Synallaxis*. Only one clade showed a strong pattern of phylogenetic conservatism, and there was no relationship overall between the number of vocal differences and

genetic distance. The low incidence of autapomorphies and low consistency index for syntactical vocal characters suggest that vocalizations are constrained by morphology and prone to convergence in distantly related species. My results demonstrate substantial variation in suboscine vocalizations and suggest that vocal characters may not be reliable indicators of phylogenetic relationships at broad taxonomic scales, particularly among behaviorally and ecologically diverse taxa.

## **Chapter 1. Introduction and Literature Review**

### **1.1. Songs and Calls – Clarifying Terminology**

The study of bird song encompasses a wide range of scientific disciplines, from physics to neurobiology to ecology and systematics (for reviews see Kroodsma and Miller 1996; Marler and Slabbekoorn 2004; Catchpole and Slater 2008; Zeigler and Marler 2008). Although a general definition of song is elusive and may never be established (Spector 1994), the classic view holds that bird songs are “long, complex vocalizations produced by males in the breeding season” (Catchpole and Slater 2008). For most species studied, this definition refers to a species-specific stereotyped vocalization used by males to attract mates and defend territories, and there is little to no disagreement regarding its characterization or function. With song so clearly defined, the prevailing tendency among researchers has been to classify all other vocalizations as “calls”, for which Catchpole and Slater’s definition is most succinct: “. . . ‘calls’ tend to be shorter, simpler and produced by both sexes throughout the year . . . [and] usually occur in particular contexts which can be related to specific functions such as flight, threat, alarm and so on” (Catchpole and Slater 2008).

Hailman (1989), in a detailed analysis of vocalizations of the Paridae, found that all species in the family had at least two vocalizations that could be considered “song” despite failing to conform to the classic definition in both structural and functional terms; for example, certain vocalizations appeared to be used in courtship despite being less complex than other vocalizations in a species’ repertoire. He advocated the recognition of multiple types of vocalizations that together could serve the same functions as a single complex song, and proposed a relaxation of the strictly dichotomous terminology of “songs” and “calls”. He also

pointed out the link between song function and migratory habit: many species with a clearly definable, complex song (and thus most models in vocal studies) were migratory species breeding in the Nearctic. These species have short breeding seasons, short-term pair bonds, low annual adult survivorship, and a high frequency of extra-pair copulations during the breeding season (Morton 1996; Stutchbury and Morton 2001), all of which impose extraordinary selection pressures for reproductive success, long thought to drive the evolution of song complexity in birds (but see Kroodsma 2004; Byers and Kroodsma 2009). As more species are studied, the emerging consensus is that evolution of vocal signals is influenced by many factors, and that a dichotomous categorization of bird vocalizations underestimates the diversity of their functions.

## **1.2. Oscines vs. Suboscines, Temperate vs. Tropical**

The vast majority of vocal studies have focused on a handful of species of so-called “songbirds”, or oscine passerines, in which the neural circuitry associated with song learning and development is highly advanced (Zeigler and Marler 2008 and references therein). Oscines produce sound by manipulating both sides of the syrinx independently and can thus produce two sounds simultaneously (Ames 1971; Raikow 1986). They represent the pinnacle of vocal complexity in birds not only in terms of sheer phonological diversity, but also individual repertoire size (Kroodsma and Parker 1977), geographic variation within species (Baptista 1975), frequency range within songs (Greenewalt 1968), and propensity for mimicry (Kelley et al. 2008).

Considerably less attention has been given to vocal evolution in suboscine passerines (Chesser 2004); in fact, the body of literature on vocalizations of the Zebra Finch (*Taeniopygia guttata*) alone vastly exceeds the volume and scope of all suboscine vocal studies combined. Suboscines comprise roughly one-fifth of all passerine species; they occur mainly in the New World tropics, with one family (Tyrannidae) breeding into Nearctic latitudes and another

(Eurylaimidae) found in the Palearctic. The pioneering work of Kroodsma and colleagues (Kroodsma 1984, 1985, 1989; Kroodsma and Konishi 1991) presented strong evidence for innate song development in three species of tyrant-flycatchers (Tyrannidae); furthermore, all suboscines studied so far appear to lack the specialized forebrain song control system thought to promote vocal complexity in oscines (Brenowitz and Kroodsma 1996; Doupe and Kuhl 2008). Based largely on the results of Kroodsma's work, the notion that song is entirely innate in all suboscines has gained wide acceptance in the literature (e.g., Morton and Derrickson 1996; Krabbe and Schulenberg 1997; Isler et al. 1998) and is reinforced by the general lack of intraspecific geographic variation in song relative to oscines (Lanyon 1978; Payne and Budde 1979; Johnson 1980; Lindell 1998). Further evidence of a strong genetic basis for song development comes from Isler et al. (2005), who demonstrated parallel patterns of vocal and genetic variation within a suboscine species.

The acceptance of a rigidly innate basis for song acquisition as a shared characteristic of all suboscines, and the corollary that vocalizations can serve as a proxy for genetic material, have led to an explosion of publications proposing the elevation of vocally diagnosable populations to species rank, often without genetic data (Whitney 1994; Bierregaard et al. 1997; Krabbe and Schulenberg 1997; Isler et al. 1998, 1999, 2001a, 2001b, 2002, 2007a, 2007b, 2008; Krabbe et al. 1999; Zimmer and Whittaker 2000; Zimmer 2002, 2008; Isler and Isler 2003; Nyári 2007; Zimmer et al. 2008). From the standpoint of the Phylogenetic Species Concept (Cracraft 1983), the formal recognition of vocally diagnosable populations is justified; in fact, vocal diversity may underestimate genetic diversity (Tobias et al. 2008). However, the rush to describe new "species" using vocal data has outpaced understanding of the vocalizations' functions, which are only beginning to be explored (Morton 1996; Seddon and Tobias 2006). Indeed, very few suboscines have been studied in sufficient detail that their full repertoires are known. Our

interpretation of suboscine vocalizations has been influenced strongly by the history of the science of birdsong, which was developed in the temperate zone using oscine passerines as models. As a result, despite recent advances, the classic view persists (Hailman 1989) that a single complex vocalization fulfills the dual function of mate attraction and territory defense. This is particularly problematic for the study of tropical suboscines, and currently only circumstantial evidence supports that what we define as suboscine “song” plays any role in promoting reproductive isolation or lack thereof.

Defining suboscine song in terms of function is difficult due to the ecological diversity of tropical birds and the tremendous variety of social systems found in the tropics (Stutchbury and Morton 2001). For lekking species, song is generally considered synonymous with vocalizations given during displays to attract females (Snow 1982; Trainer and McDonald 1993). However, this breeding system is restricted to a relatively small number of suboscine species. Most tropical suboscines that have been studied are sedentary, occur at relatively low densities, form long-term pair bonds, and have low reproductive rates and high annual adult survivorship (Skutch 1969, Terborgh et al. 1990; Greenberg and Gradwohl 1986, 1997; Morton and Stutchbury 2000; Stutchbury and Morton 2001). The selective pressures thought to influence the development of complex songs in the temperate zone are thus potentially much reduced in the tropics. Even so, most species of tropical suboscines are highly vocal, and vocal signals certainly play significant roles in the maintenance of pair bonds and territory integrity (Seddon and Tobias 2006). For this reason, the tendency persists to characterize particular vocalizations as songs (e.g., Seddon and Tobias 2007).

Suboscine song is easier to characterize from a structural perspective: it is generally considered to be the most complex vocalization in a species’ repertoire, provided that the syllables are arranged in a stereotyped pattern and that the vocalization is given at more-or-less



regular (and frequent) intervals. Song is perhaps easiest to recognize in the families Formicariidae and Grallariidae, in which the singing behavior of their species fits most ornithologists' conception of song, invariably involving repetition of a stereotyped complex vocalization at regular intervals by one bird. Indeed, the behavioral homogeneity across each of these families facilitates the identification of homologous vocalizations in comparative studies (DeQueiroz and Wimberger 1993). Similarly, the complex dawn songs of most species of Tyrannidae (Fitzpatrick et al. 2004) are almost certainly homologous; although they tend to be given only during a short period each day, they are structurally consistent with "song" as classically defined. For many other suboscines, particularly the Thamnophilidae and Furnariidae, the song is considered to be the most frequently heard multi-note vocalization, usually given by both members of a pair, often as an antiphonal duet (Remsen 2003; Zimmer and Isler 2003). Willis (1967) coined the term "loudsong" for these vocalizations in the Thamnophilidae, and they have been the sampling unit for studies of vocal evolution in that family (Isler et al. 1998; Seddon 2005). Although variation in loudsongs has proven useful in documenting discrete populations, the tendency is strong to infer that such variation plays a prominent role in reproductive isolation and speciation, as suggested for birds in general (Martens 1996; Slabbekoorn and Smith 2002). More detailed studies focusing on single species have revealed that the characterization of one vocalization as the "song" may obscure the biological significance of other vocalizations. Smith and Smith (1996) identified 12 distinct vocalizations in *Myiarchus crinitus* (Tyrannidae), each associated with particular behaviors, and eight of which were only given in close interactions. In the Thamnophilidae, a study of *Cercomacra tyrannina* found that birds sang a different song following the removal of mates from territories (Morton 1996). Isler et al. (2007a) found that call notes, not loudsongs, distinguished a pair of syntopic taxa in *Hypocnemis cantator*. Thorough documentation of

suboscine repertoires is essential before the biological and evolutionary significance of any vocalizations can be investigated.

The Furnariidae is perhaps the most ecologically varied family of birds in the world, and they display a wide range of vocal behaviors (Remsen 2003). Despite this, furnariid vocalizations remain largely unstudied. The purpose of this dissertation is to document the extent of vocal variation within and among species in a large furnariid genus, to examine vocalizations in a phylogenetic context, to compare furnariid vocal behavior to that of other suboscine families, and to investigate the implications of geographic variation and phenotypic plasticity for the use of vocal characters in suboscine systematics.

### **1.3. The Genus *Synallaxis***

The genus *Synallaxis* Vieillot, as currently recognized (Remsen et al. 2009), consists of 33 species of relatively small-bodied, morphologically similar furnariids that occupy forest undergrowth and scrub habitats from southern Mexico to central Argentina (Remsen 2003). Most species have a fairly short, straight bill, short wings, large feet, and long, graduated or decomposed rectrices. Historical classifications used plumage similarity to infer relationships among members in the genus (Cory and Hellmayr 1925; Peters 1951). The largest diagnosable group is the “rufous-capped” assemblage, comprising 15 species united by a contrasting rufous crown and rufous shoulders. Most species have a semiconcealed throat patch that is often displayed during agonistic interactions. Variation in contour plumage coloration is considerable within the rufous-capped group, ranging from pale brown to dark gray. The “rufous” group comprises five species (*S. unirufa*, *castanea*, *fuscorufa*, *ruhilans*, and *cherriei*) that are mostly to entirely rufous with a distinctive black throat patch of variable size. The “plain” group comprises five species (*S. gujanensis*, *maranonica*, *albilora*, *cinerascens*, and *propinqua*) that are mostly dull gray-brown with contrasting rufous shoulders (although *S. propinqua* is included

in this group, it is morphologically distinct from the other species, having a longer bill and whiter ventral plumage). The *Poecilurus* group (*S. scutata*, *kollari*, and *candei*) has been recognized as a separate genus (see Ridgely and Tudor 1994) characterized by rufous-orange plumage and a strong facial pattern; however, it has recently been subsumed under *Synallaxis* on the basis of similarities in voice and nest architecture (Remsen 2003; Remsen et al. 2009). The remaining five species of *Synallaxis* (*S. erythrothorax*, *stictothorax*, *tithys*, *cinnamomea*, and *zimmeri*) are phenotypically distinct, and their relationships to others in the genus are unclear (Remsen 2003).

## **1.4. Vocal Diversity in *Synallaxis***

### **1.4.1. Methods**

Although descriptions of *Synallaxis* vocalizations can be found in any field guide to Neotropical birds (e.g., Hilty and Brown 1986; Ridgely and Tudor 1994; Schulenberg et al. 2007), there are only two published studies in the primary literature. Vaurie and Schwartz (1972) presented the first overview of vocal diversity in the genus. They described the “song” of *Synallaxis* as “a constant repetition of a stereotyped phrase that consists of two or three figures<sup>1</sup> in the majority of species studied” (Vaurie and Schwartz 1972). They also described the common occurrence of introductory and terminal notes in longer *Synallaxis* songs, and presented spectrographs to support the recognition of *S. unirufa* and *S. castanea* as separate species (Vaurie 1971). Most significantly, they were the first to describe unusual, complex vocalizations in *S. unirufa*, which they hypothesized were related to breeding behavior. Lindell (1998) described limited geographic variation in the song of *Synallaxis albescens*; her paper was one of the first to document such variation within a suboscine species. The results of these studies suggest that both geographic variation and repertoire size may be more extensive in suboscines than

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<sup>1</sup> Vaurie and Schwartz (1972) define “figure” as a “sound which produces a single, complete and distinct impression – usually represented on a spectrogram as an uninterrupted trace”. It is synonymous with “note”, which is the term I use in this dissertation.

previously thought, yet there have been few attempts to document either (but see Smith and Smith 1996; Isler et al. 2007a).

I obtained approximately 1200 *Synallaxis* recordings from the Macaulay Library of Natural Sounds at the Cornell Lab of Ornithology (MLNS), the Banco de Sónidos Animales at the Instituto Alexander von Humboldt in Bogotá, Colombia (BSA), the online resource Xeno-Canto ([www.xeno-canto.org](http://www.xeno-canto.org); XC), and the personal archives of several colleagues (see Acknowledgments). All species and most subspecies of *Synallaxis* were included in the sample. To create the species accounts in Appendix A, I listened to every recording and classified it according to vocalization type. I identified as many vocalization types as possible and created spectrographs of each vocalization, provided that recordings were of sufficient quality. I generated spectrographs using Raven Pro 1.3 ([www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)) with the following settings: Window type = Hann; window size = 256 samples; 3-dB filter bandwidth = 248 Hz; window overlap = 50%; hop size = 128 samples; DFT size = 256 Hz; grid spacing = 172 Hz. In general, spectrographs of vocalizations less than 1.4 seconds in length were scaled to fit on half of a page, whereas longer vocalizations were scaled to the entire width of a page (see Appendix A).

I identified songs for most species based on published voice descriptions and my own field experience with the genus. For species with large geographic ranges, I attempted to include recordings from throughout the range. I did not document intraspecific variation in call notes unless there were substantial qualitative differences that appeared to be restricted to a portion of a species' range. In general, call notes were much more similar than songs across species.

#### **1.4.2. Overview**

Separate accounts documenting vocal diversity in all species of *Synallaxis* are presented in Appendix A. Most species of *Synallaxis* have a distinct song frequently given as an

antiphonal duet by members of a pair; although simple in structure, these songs appear to be functionally homologous to the loudsongs of the *Thamnophilidae* (Zimmer and Isler 2003). In general, geographic variation in song occurs within most species of *Synallaxis* with large ranges. Although some variation appears to be clinal (e.g., *S. cinnamomea*), there are diagnosable vocal groups within several species. *S. stictothorax chinchipensis*, *S. albescens australis*, *S. brachyura cauae*, and *S. rutilans omissa* are all vocally distinct from other populations. *Synallaxis scutata scutata* and *S. s. whitii* are also distinguishable vocally, as are *S. e. erythrothorax* and *S. e. pacifica*. Striking vocal differences exist between populations of *S. gujanensis* from north and south of the Amazon River.

*Synallaxis* spinetails differ from thamnophilids in many aspects of vocal behavior. For example, songs given in response to playback sometimes include drastic rearrangements of notes, as well as insertion of notes never given in normal song. By contrast, thamnophilids tend simply to repeat the normal song at a faster rate when subjected to playback (Isler et al. 1998; BJO pers. obs.). Whereas loudsongs are described for virtually all thamnophilids, songs are rudimentary or practically nonexistent in several species of *Synallaxis* – notably *S. cabanisi*, *infuscata*, and *whitneyi*. These species produce a single note that is often doubled or tripled and repeated at irregular intervals – never as a stereotyped, multi-noted song. Although more complex songs may remain to be discovered in these species, vocal diversity in the group appears to be minimal, and suggests that complex vocal signals may be more important for some species than others.

On the other hand, the occurrence of complex alternate songs is widespread in *Synallaxis*. At least 13 species produce one or more alternate songs, which are usually longer and contain a greater variety of notes than the typical song. Several species have been recorded giving these songs in rapid series at dawn in a manner suggestive of dawn singing in the *Tyrannidae*.

The singing behavior of *Synallaxis* species appears to vary substantially within the genus. Although many species participate in asynchronous duets, others seem to do so only rarely. The frequency of singing itself may vary among species as well. Whereas the songs of some *Synallaxis* species are common sounds in the Neotropics, other species appear to be quite furtive – particularly *S. macconnelli* and *S. moesta*, whose songs are often given at low volume. This may be indicative of a fundamental difference in song function within the genus – The loudest and most frequent singers (e.g., *S. albescens*, *S. frontalis*, and *S. gujanensis*) often ascend into higher vegetation to deliver their songs, suggesting that songs are designed to be long-distance signals (and thus perhaps more important for territory advertising). On the other hand, the less vocal species rarely venture out of dense undergrowth, and thus their vocalizations may serve primarily as short-distance signals between mates. There also appears to be a positive correlation between propensity to vocalize and repertoire size, although this could be an artifact of sampling, because birds that vocalize often are more likely to be recorded.

In terms of singing behavior, the most unusual members of the genus are *Synallaxis stictothorax* and *S. propinqua*, both of which have a wide vocal repertoire that bears little resemblance to that of other *Synallaxis* species. Both species have a set of characteristic calls that seem to function as contact notes between members of a pair or family group. However, the “song” appears to be a distinctive duetting vocalization that starts explosively and trails off, with one bird typically finishing the duet (see species accounts). Qualitatively, these duet vocalizations are more similar to those of other furnariid genera (e.g., *Certhiaxis*) than to *Synallaxis*.

The variety of vocalizations and singing behaviors within *Synallaxis* illustrates the inherent difficulty in identifying homologous vocalizations in such a diverse family of birds as the Furnariidae. In contrast to the loudsongs of thamnophilids, which are nearly universal in

general structure and pattern of delivery, furnariid vocal signals and associated singing behaviors show a high degree of variability even within one genus. In subsequent chapters, I focus on variation in typical songs as defined in the species accounts (Appendix A). Controlled field experiments are needed to determine the functions of these vocalizations. Also needed are more detailed studies of species or genera in other suboscine families to determine the extent of their repertoires.

## **Chapter 2. Individual Song Variation in *Synallaxis*, with Emphasis on *S. frontalis***

### **2.1. Introduction**

Individual variation in song has been documented in multiple oscine passerine species (reviewed in Stoddard 1996) and, more recently, in suboscines as well (Bard et al. 2002; Lovell and Lein 2004; Wiley 2005). These findings are typically interpreted as evidence for the ability of birds to discriminate between songs of multiple individuals. However, the evidence for song discrimination in suboscines comes exclusively from members of one family (Tyrannidae) breeding in the temperate zone, whereas most studies of individual variation have focused on lekking species in another family (Cotingidae; Fitzsimmons et al. 2008). In both groups, strong selection for individual differences is expected. Temperate-zone breeders have relatively short breeding seasons, high adult mortality, dense territories, and a high frequency of extra-pair copulations (Stutchbury and Morton 2001); therefore, the ability to discriminate between the songs of neighbors and strangers allows a territory holder to monitor the whereabouts of neighbors and thereby maximize its own fitness. Most cotingids are polygynous and sing to attract mates at leks – conditions well known to foster strong sexual selection for individual traits (Andersson 1994; Snow 2004). The documentation of individual song differences in different social contexts within the suboscines supports the idea, now generally accepted, that suboscine song is more complex than has been recognized historically. However, the causal mechanisms promoting individual variation remain unknown for most species. Temperate-zone breeding and lekking are atypical mating systems in suboscines, most of which are sedentary tropical species that form larger, more stable territories, occur at lower densities, spend less time singing, and form longer pair bonds than their temperate-zone counterparts (Stutchbury and Morton 2001).



Bard et al. (2002) found diagnosable song differences among individuals in a population of *Hylophylax naevioides* (Thamnophilidae) in Panama, but no evidence for discrimination of neighbors' and strangers' song in playback trials. Their study is the only published documentation of individual song variation in a monogamous, sedentary tropical suboscine, and their results suggest that individual song differences may occur in the absence of obvious selective pressures. However, clarifying the significance of small song differences depends on an understanding of the extent of variation at larger spatial scales, as well as the factors influencing song variability within an individual.

In this study, I assessed individual variation in the song of a sedentary tropical suboscine, *Synallaxis frontalis* (Furnariidae), and examined song plasticity by comparing recordings of individuals of several *Synallaxis* species made before and after playback of that individual's own song. Many species of *Synallaxis* (including *S. frontalis*) sing simple, two-parted songs that are presumed to be homologous to the more complex "loudsongs" of another suboscine family, the Thamnophilidae (Willis 1967; Isler et al. 1998). The goals of this study were to assess individual diagnosability in *S. frontalis* song and to determine whether behavioral context could affect song characteristics and classifications based on vocal characters.

## **2.2. Methods**

*Synallaxis frontalis* occurs in dry forest and scrub habitats from eastern Brazil south to central Argentina and west to the Bolivian Andes, where it occurs locally up to 2500 m (Remsen 2003). The species' song is a two-noted signal with strong harmonic structure, and is typically 0.5-1.0 sec in length (see species account in Appendix A). Although relatively high-pitched, it is similar structurally to the songs of many other *Synallaxis* species and is given under similar behavioral circumstances. The song is sometimes given as an antiphonal duet by mated pairs.

Recordings of *S. frontalis* songs were obtained as digital sound files from the Macaulay

Library, Cornell Lab of Ornithology, from online resources ([www.xeno-canto.org](http://www.xeno-canto.org)), and from the personal archives of several colleagues (see Acknowledgments). All recordings used in the analyses featured a high signal-to-noise ratio and an uninterrupted series of at least 10 songs from the same individual. I used Raven Pro 1.3 ([www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)) to generate waveforms and spectrographs of 10 songs from each of 20 individuals. Spectrograph settings for time and frequency measurements are given in the Methods section of Chapter 3. Because there are no described subspecies of *S. frontalis* (Remsen 2003), I divided samples into five geographic groups, as follows: an Eastern group, representing localities in eastern Brazil from the state of Ceará south and west through Minas Gerais; a Chaco group (Paraguay and the province of Chaco, Argentina); a Southern group (Rio Grande do Sul, Brazil; and the provinces of Corrientes and Entre Rios, Argentina); a Bolivian group (Andes from deptos. La Paz to Santa Cruz); and a Southern Andean group (province of Jujuy, Argentina).

For each song, I measured the duration and peak frequency (frequency with maximum amplitude) of first (N1) and second (N2) notes. Because simple time and frequency measures may fail to discriminate differences in note shapes among individuals, I used spectrographic cross-correlation (SPCC) to compare notes at each position within and among individuals. SPCC compares two spectrographs by sliding them across each other in time and generating a coefficient of similarity based on the normalized covariance of the time-frequency-amplitude matrices at successive time offsets (Clark et al. 1987; Beeman 1998; Seddon 2005); a correlation value of 1 indicates that two signals are similar, whereas values approaching zero indicate increasing dissimilarity. For each song, I correlated notes at the N1 and N2 positions separately, both to allow greater resolution of the contribution of each note to overall song variation, and to minimize the effect of note reverberation on correlation values (reverberation causes notes to appear longer than they actually are). For correlations, I saved spectrograph traces of individual

notes as separate files using a window size of 512 Hz to provide a compromise between frequency and time resolution; I also used a band-pass filter to remove frequencies outside the fundamental and lower harmonic range of *S. frontalis* song (1-7 kHz). Four recordings were excluded from the correlation analyses because they were either compressed (.mp3) files or were sampled at a rate other than 44.1 kHz.

For 16 recordings of *S. frontalis*, I performed correlations of all possible combinations of notes at each position (N1 and N2); I then extracted the highest (peak) value from each correlation matrix and calculated the mean value of peak correlations for N1 and N2 within and among individuals. I averaged the values of N1 and N2 mean peak correlations for each pair of individuals to generate a single measure of similarity between individuals. To test the hypothesis that song similarity was inversely related to geographic distance between sampling localities, I measured map distances using the measurement function in Google Earth, and plotted geographic distance against the mean of N1 and N2 mean peak correlation values for each song.

For the analysis of playback effects, I analyzed 19 recordings representing nine species,<sup>2</sup> all of which have a two-parted song type similar in pattern to *S. frontalis*. I selected recordings that included a series of at least five songs (up to a maximum of 20) recorded without the use of tape playback, followed by an equal number of songs recorded from the same individual after playback of the natural recording. Playback is a common technique used by recordists to lure birds into view and, often, to obtain a higher-quality recording of a bird's song. Birds generally sing at an increased rate in response to playback, and use of the technique is relatively easy to infer when listening to a recording; nevertheless, I only analyzed recordings in which the use of playback was ascertainable through recordists' announcements or notes. For each song series, I

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<sup>2</sup> Northern and southern vocal types of *S. gujanensis* are here considered separate species. See species account in Appendix A.

measured the same duration and frequency measurements as for *S. frontalis* and performed SPCC on notes at the same position within each set of songs. I then compared note duration and frequency measurements for each individual before and after playback using a paired t-test design. Because I did not pool data from multiple individuals to assess treatment effects, I assumed that all songs in a set were independent to allow an adequate number of degrees of freedom for analysis. I used Levene's test (Levene 1960) to compare variances of song measures before and after playback; when variances were significantly different and the assumptions of the t-test could not be met, I used a Welch ANOVA to test differences in group means given unequal variances (Welch 1951). Although the ANOVA was not a repeated measures design, *P*-values were similar to those obtained in paired t-tests. Although the pooled distributions of note measures were approximately normal, sample sizes for some comparisons were small, so I also performed a nonparametric (Wilcoxon signed-rank) test on all comparisons. All statistical analyses were performed in JMP 7.0 (SAS Institute, Cary, NC).

As an alternative test of the effect of playback on song variability, I compared mean correlation values within sets of songs before and after playback. Higher correlation values indicated greater consistency among songs in a set, whereas lower mean correlation values reflected higher variability.

## **2.3. Results**

### **2.3.1. Individual Variation in *S. frontalis***

All four measurements were significantly more variable between than within individuals, although *F*-values for note durations were an order of magnitude greater than those for frequency measurements (Table 2.1).

Mean peak correlation values were significantly greater within than between individuals for N1 ( $F_{1,30} = 82.8, P < 0.0001$ ) and N2 ( $F_{1,30} = 167, P < 0.0001$ ; Fig. 2.1), and values for N1 and

TABLE 2.1.  $F$ -values and ranges of means for note measurements of *S. frontalis* song (all  $P < 0.001$ ). D1 and D2 = duration of first and second notes; F1 and F2 = frequency with maximum amplitude in first and second notes, respectively.

Measure	$F_{18,171}$	Range of means
D1	107	0.075-0.117 s
D2	340	0.148-0.219 s
F1	19.7	2597-5797 Hz
F2	21.1	2382-5379 Hz

N2 were significantly correlated ( $r = 0.25$ ;  $P = 0.002$ ).

Note length and frequency variables were all weakly to moderately correlated (Table 2.2). The first two principal components explained 79% of the variance in the data. Positive loadings on PC 1 were associated with frequency of both N1 and N2, whereas negative loadings corresponded to N2 duration. Positive loadings on the second PC were associated with N1 duration. The discriminant function on all four PCs classified 90% of songs to the correct individual, but revealed high variability within geographic groups (Fig. 2.2).

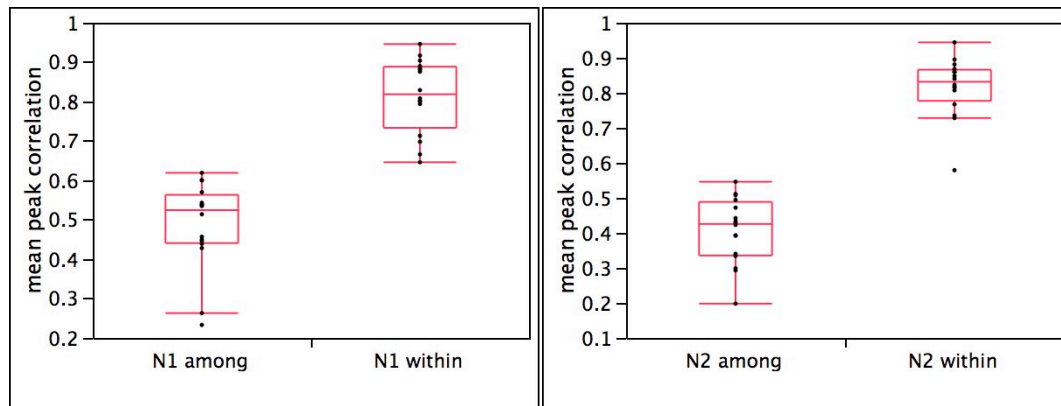


FIG. 2.1. Mean peak correlations for first (N1) and second (N2) notes within and among individuals of *S. frontalis*. Lines through each quartile box plot indicate median correlation values for each group.

There was no overall effect of geographic distance between sampling localities on the mean peak correlation value of notes ( $r = 0.045$ ;  $F_{1,76} = 0.157$ ;  $P = 0.69$ ; Fig. 2.3).

### 2.3.2. Effects of Playback

Playback affected the durations of one or both notes in 17 of 19 comparisons (Table 2.3,

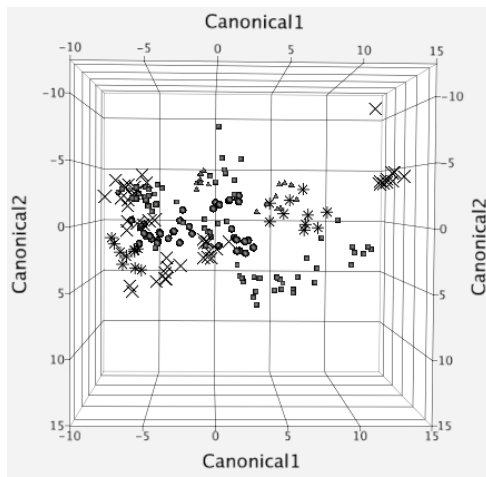
TABLE 2.2. Correlations ( $r$ ) between note duration and frequency variables.

	D1	F1	D2	F2
D1	1			
F1	-0.1210	1		
D2	0.3914	-0.4496	1	
F2	-0.2062	0.5791	-0.5566	1

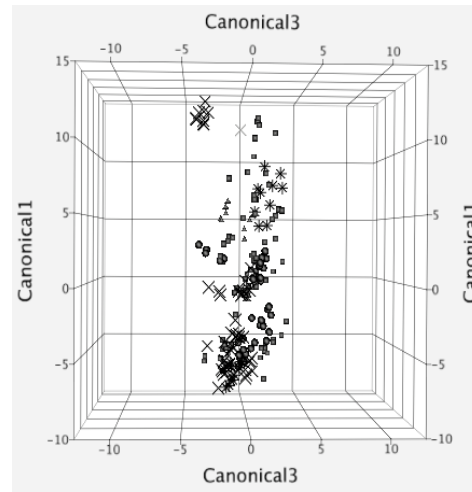
2.4); in several comparisons, ranges of values did not overlap. Although the direction of response was not consistent among individuals or within species, note durations increased in 12 of 15 and 11 of 14 statistically significant comparisons for N1 and N2, respectively. The Wilcoxon signed-rank and paired t-tests agreed on statistical significance ( $P < 0.05$ ) for all sample sizes of six or greater. Note frequencies were highly variable within individuals, and there was no effect of playback on mean emphasized frequencies in 10 of 19 comparisons (Table 2.4). Among statistically significant comparisons, there was an equal tendency for frequencies to be higher vs. lower after playback. Only four comparisons showed significant frequency differences in both N1 and N2. Variance estimates for both frequency and duration measures were affected by playback; among statistically significant comparisons, variances tended to increase for note durations, although there were exceptions, and many comparisons were not significant (Table 2.3). By contrast, variance in frequencies tended to decrease substantially; some standard deviations were an order of magnitude lower in playback samples (Table 2.4).

Data from *S. maranonica* and the southern vocal type of *S. gujanensis* were removed from multivariate analyses because they clustered far from all other samples in multivariate space. Linear discriminant analysis on principal components derived from the remaining pre-playback samples revealed a three-dimensional song space similar to that of *S. frontalis*, indicating a general similarity in note durations and frequencies across species (Fig. 2.4A). The discriminant function correctly classified 91% of songs to the correct individual; however,

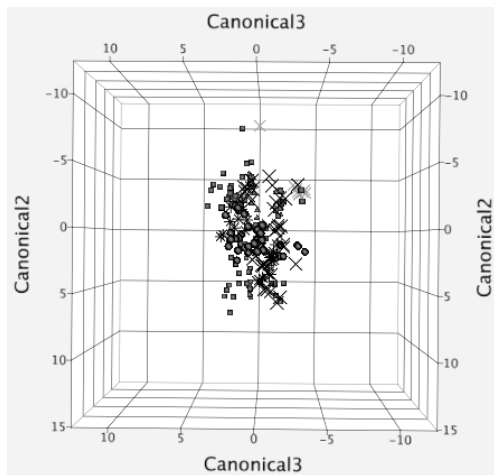
eleven of the 19 misclassifications were across species. Repeating the analysis with playback samples (Fig. 2.4B) slightly increased the percentage of correctly classified songs (93%) and



(A)



(B)



(C)

FIG. 2.2. The 3-dimensional “song space” of *S. frontalis* based on principal components derived from note duration and frequency data from 200 songs and 20 individuals. Representatives of the five geographic groups are coded as follows: Eastern group (\*); Chaco group (circles); Southern group (X); Bolivian group (squares); and Southern Andean group (triangles). There was much variation within each group and thus no discernable geographic variation in the song of *S. frontalis*.

reduced the number of cross-species misclassifications (4 of 15 samples). However, the frequency of within-species misclassifications increased after playback; at least one song was

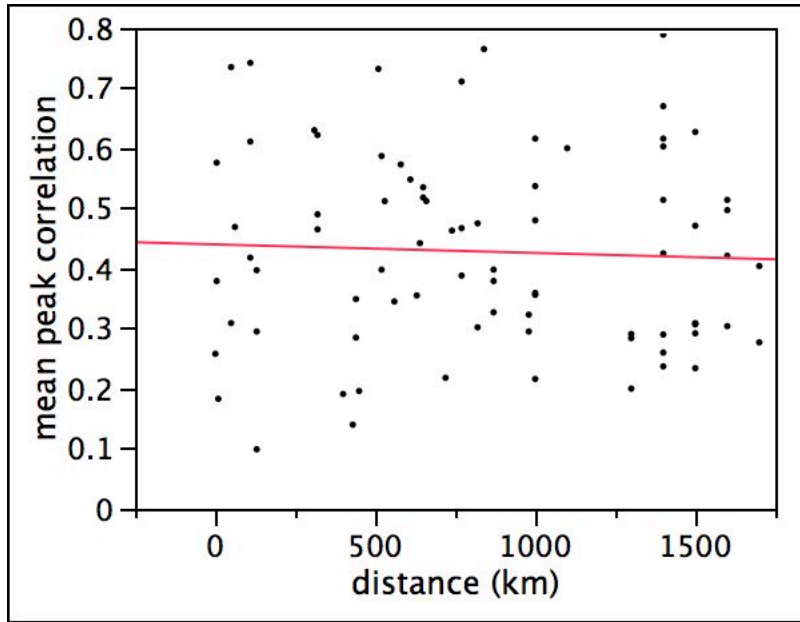


FIG. 2.3. Song similarity (mean of mean peak correlation values for N1 and N2) as a function of geographic distance between sampling localities.

incorrectly classified for every species with more than one individual in the analysis (*S.*

*albescens*, *S. azarae*, *S. frontalis*, *S. cinnamomea*, and *S. gujanensis*).

Mean correlation values varied significantly between pre-playback and playback samples in 13 and 11 comparisons for N1 and N2, respectively. A weak trend toward higher correlation (i.e., reduced variability among notes after playback) was not significant (all  $\chi^2 < 0.41$ ;  $P > 0.1$ , 1 d.f.).

In summary, songs given after playback tended to contain notes similar in frequency (and more consistent in that domain) but longer than those given before playback. Although playback affected one or more note measures in all but one comparison, the effect was not consistent within or among species.

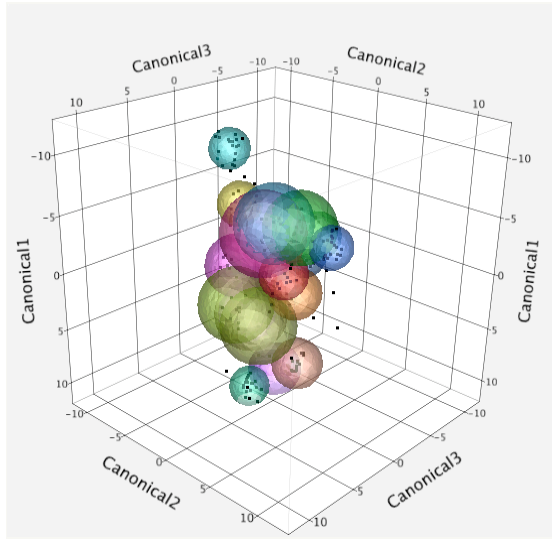


TABLE 2.3. Means and standard deviations of note durations from the same individual before and after playback. Asterisks indicate significant differences in the variance of each group; p-values are derived from the Welch ANOVA test of group means given unequal variance. All other group variances were not significantly different, and *P*-values are from paired t-tests. Lambda ( $\lambda$ ) indicates that comparisons were not significant ( $P>0.05$ ) in Wilcoxon signed-rank tests.

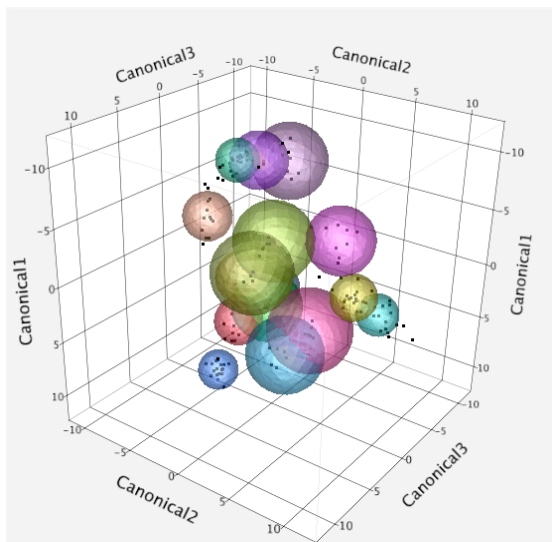
Catalog #	Species	N	Mean (s.d.) D1 before playback	Mean (s.d.) D1 after playback	<i>P</i>	Mean (s.d.) D2 before playback	Mean (s.d.) D2 after playback	<i>P</i>
MLNS 20019	<i>albescens</i>	15	0.095 (0.007)	0.107 (0.007)	0.0015	0.201 (0.004)	0.202 (0.005)	0.26
MLNS 66123	<i>albescens</i>	7	0.115 (0.003)	0.108 (0.003)	0.006	0.195 (0.005)	0.193 (0.002)	0.22
MLNS 112203	<i>albescens</i>	20	0.121 (0.004)	0.133 (0.003)	<0.0001	0.162 (0.007)	0.176 (0.005)	<0.0001*
MLNS 127736	<i>albescens</i>	12	0.089 (0.006)	0.099 (0.004)	0.0001	0.178 (0.005)	0.172 (0.005)	0.009
MLNS 18058	<i>azarae</i>	20	0.057 (0.002)	0.065 (0.002)	<0.0001	0.110 (0.003)	0.121 (0.003)	<0.0001
MLNS 21583	<i>azarae</i>	11	0.054 (0.002)	0.059 (0.002)	<0.0001	0.148 (0.003)	0.165 (0.002)	<0.0001
MLNS 44249	<i>cinnamomea</i>	17	0.100 (0.007)	0.095 (0.003)	0.03*	0.242 (0.010)	0.259 (0.006)	<0.0001
MLNS 66158	<i>cinnamomea</i>	20	0.098 (0.004)	0.095 (0.003)	0.007	0.334 (0.010)	0.315 (0.040)	0.04*
MLNS 66164	<i>cinnamomea</i>	8	0.073 (0.002)	0.075 (0.005)	0.32*	0.238 (0.006)	0.257 (0.010)	0.002*
MLNS 19259	<i>frontalis</i>	6	0.082 (0.004)	0.088 (0.002)	0.02 ( $\lambda$ )	0.148 (0.002)	0.153 (0.003)	0.02
MLNS 84497	<i>frontalis</i>	7	0.109 (0.004)	0.116 (0.003)	0.006	0.211 (0.009)	0.227 (0.006)	0.02
MLNS 85652	<i>frontalis</i>	5	0.105 (0.002)	0.113 (0.002)	0.0002 ( $\lambda$ )	0.204 (0.010)	0.219 (0.003)	0.03 ( $\lambda$ )
KZ uncat.	<i>frontalis</i>	6	0.082 (0.002)	0.093 (0.003)	0.0002	0.146 (0.004)	0.156 (0.002)	<0.0001
MLNS 30059	<i>gujanensis</i> (S)	5	0.246 (0.003)	0.252 (0.007)	0.22	0.142 (0.005)	0.152 (0.005)	0.06
MLNS 66129	<i>gujanensis</i> (N)	15	0.106 (0.003)	0.105 (0.005)	0.60*	0.204 (0.009)	0.205 (0.010)	0.83
MLNS 117073	<i>gujanensis</i> (N)	18	0.098 (0.003)	0.106 (0.002)	<0.0001	0.186 (0.007)	0.201 (0.006)	<0.0001
MLNS 68281	<i>maranonica</i>	17	0.442 (0.020)	0.462 (0.010)	0.002	0.505 (0.080)	0.547 (0.060)	0.08
MLNS 66251	<i>rutilans</i>	6	0.063 (0.002)	0.060 (0.006)	0.35*	0.203 (0.007)	0.189 (0.006)	0.01
MLNS 66133	<i>unirufa</i>	13	0.079 (0.003)	0.092 (0.007)	<0.0001*	0.086 (0.005)	0.097 (0.005)	0.0005

TABLE 2.4. Means and standard deviations of note frequencies from the same individual before and after playback. Asterisks indicate significant differences in the variance of each group; p-values are derived from the Welch ANOVA test of group means given unequal variance. All other group variances were not significantly different, and *P*-values are from paired t-tests. Lambda ( $\lambda$ ) indicates that comparisons were not significant ( $P>0.05$ ) in Wilcoxon signed-rank tests.

Catalog #	Species	N	Mean (s.d.) F1 before playback	Mean (s.d.) F1 after playback	<i>P</i>	Mean (s.d.) F2 before playback	Mean (s.d.) F2 after playback	<i>P</i>
MLNS 20019	<i>albescens</i>	15	3503 (79.4)	3566 (352)	0.27	4361 (543)	4596 (348)	0.19*
MLNS 66123	<i>albescens</i>	7	3759 (174)	3839 (94.0)	0.44	3827 (327)	3649 (47.8)	0.20*
MLNS 112203	<i>albescens</i>	20	3299 (76.9)	3325 (137)	0.47*	3908 (179)	4126 (172)	0.0002
MLNS 127736	<i>albescens</i>	12	3090 (614)	3607 (279)	0.02	3420 (756)	3966 (46.6)	0.03*
MLNS 18058	<i>azarae</i>	20	3923 (155)	3962 (143)	0.41	4106 (337)	3999 (285)	0.36
MLNS 21583	<i>azarae</i>	11	2721 (717)	3571 (448)	0.003	3022 (920)	3802 (796)	0.07
MLNS 44249	<i>cinnamomea</i>	17	4803 (91.8)	4788 (130)	0.72	3572 (70.9)	3468 (172)	0.03*
MLNS 66158	<i>cinnamomea</i>	20	4479 (209)	4303 (146)	0.002*	3322 (101)	3131 (146)	<0.0001*
MLNS 66164	<i>cinnamomea</i>	8	4059 (806)	4285 (120)	0.47	3349 (627)	3586 (134)	0.37
MLNS 19259	<i>frontalis</i>	6	4953 (223)	4744 (143)	0.20	4163 (52.5)	4020 (494)	0.48
MLNS 84497	<i>frontalis</i>	7	4276 (73.7)	4344 (16.3)	0.05*	4116 (541)	4128 (514)	0.95
MLNS 85652	<i>frontalis</i>	5	4470 (56.1)	4565 (30.4)	0.04 ( $\lambda$ )	4152 (560)	3523 (36.3)	0.07*
KZ uncat.	<i>frontalis</i>	6	4206 (1100)	4888 (146)	0.19*	4508 (1010)	4946 (129)	0.35
MLNS 30059	<i>gujanensis</i> (S)	5	3161 (99.0)	3118 (141)	0.53	3755 (280)	3764 (203)	0.97
MLNS 66129	<i>gujanensis</i> (N)	15	2862 (32.1)	2776 (79.4)	0.001*	2658 (494)	2667 (445)	0.96
MLNS 117073	<i>gujanensis</i> (N)	18	3096 (132)	3189 (89.1)	0.03	2510 (41.2)	2577 (16.5)	<0.0001*
MLNS 68281	<i>maranonica</i>	17	4038 (375)	4079 (482)	0.77	3595 (486)	3734 (509)	0.35
MLNS 66251	<i>rutilans</i>	6	3453 (468)	3237 (142)	0.34	3324 (578)	2763 (42.3)	0.06*
MLNS 66133	<i>unirufa</i>	13	3290 (77.6)	3025 (111)	<0.0001	3329 (103)	3091 (99.7)	<0.0001



(A)



(B)

FIG. 2.4. Song plasticity in multivariate space. The graphs are based on note duration and frequency data from the same individuals before (A) and after (B) playback of their own song. Spheres represent 95% confidence regions around the multivariate mean for each individual. Reduced variance in frequency measures after playback results in higher loadings of frequency variables, greater dimensionality, and fewer cross-species misclassifications, but negatively affects individual diagnosability within species.

## 2.4. Discussion

### 2.4.1. Variation within *S. frontalis*

In this study, I compared songs of *S. frontalis* from across the range of the species. Songs were much more variable among than within individuals, as expected given the geographic breadth of sampling and relatively small sample size. In multidimensional space, the first two principal components explained almost 80% of the variance in the data, suggesting that single measures of duration and frequency can be used in lieu of multiple spectrograph measurements. This has important implications for comparative studies of simple vocal signals and especially for comparison of spectrographs of differing quality. Using fewer measurements reduces the potential for correlated measurement errors within spectrographs and compounded error on the part of the investigator. Although greater dimensionality may have been revealed by the use of more variables, the degree of correlation between temporal and frequency domains suggests that additional variables in each domain would be highly correlated and would thus contribute little to overall song variation.

In the discriminant analysis of *S. frontalis* song, variation among individuals obscured any pattern of geographic variation. None of the five geographic groups were diagnosable in multivariate space. This finding corroborates a previous analysis of *S. frontalis* that used more variables and a larger sample size but fewer songs per individual (see Chapter 3). In that analysis, a clear pattern of geographic variation in a related species (*S. azarae*) collapsed when samples from *S. frontalis* were added to the dataset, suggesting that statistically significant patterns of geographic variation in *S. azarae* likely have little biological significance. I predict a similar result from the addition of more *S. frontalis* songs to the dataset presented here; specifically, individual diagnosability should decrease with sample size. The multidimensional “song space” in Figure 2.3 was defined using samples from the geographic and elevational

extremes of the species' range; given the demonstrated roles of such isolation in suboscine song divergence (Seddon and Tobias 2007; Chapter 3) and speciation in general (Mayr 1942; Price 2007), as well as the qualitative similarity of *S. frontalis* song over its range, it is likely that additional samples would fall within the existing song space rather than expand it substantially. This prediction is supported by the lack of geographic structure in the data.

Song similarities derived from SPCC data corroborated the multivariate analyses with regard to geographic variation. As expected, correlations were significantly higher within than among individuals, although it is possible that correlations among individuals were affected by differences in quality and background noise level among recordings, which would drive down correlation values between similar notes. Even so, the spread of the data in Figure 2.3 and the relatively weak correlation ( $r=0.25$ ) between N1 and N2 correlation values strongly suggest no relationship between geographic distance and song similarity. In this regard, *S. frontalis* conforms to the classical view that suboscine vocalizations show little intraspecific variation (Lanyon 1978; Johnson 1980).

Peak emphasized frequencies were considerably more variable than note durations, as emphasized by the differences in *F*-values for each domain (Table 2.1). The range of means for each note was 3 kHz or greater – more than half the range for the genus as a whole (BJO *unpublished data*). Differences in frequency were caused either by differences in energy distribution across a note or by concentration of sound energy on different harmonic bands, both of which were variable within an individual. Differential emphasis within notes would lead to high variance in peak frequency measurements for modulated notes such as those produced by *S. frontalis*. Because harmonic bands were separated by 800-1000 Hz, changes in harmonic emphasis within a song bout would cause substantial frequency variation as well. In general, most frequency variation appeared to be the result of changes within notes; although occasional

changes in harmonic emphasis were noted, the energy in most songs was concentrated in the first harmonic band. This is the general case for most species of *Synallaxis* (see spectrographs in Appendix A).

Bard et al. (2002) found evidence for individual song distinctiveness in a population of *Hylophylax naevioides* (Thamnophilidae). In their study, 73% of male songs and 94% of female songs were classified to the correct individual (N=25 and 5 for males and females, respectively) based on four weakly correlated frequency and temporal measures. The lower overall diagnosability in their study suggests a negative relationship with sample size, although the difference can also be explained as an expected effect of analyses at a small geographic scale. I found no evidence for geographic variation in *S. frontalis*, but it may be an important component of individual variation in other suboscine species, particularly those restricted to forest understory or with topographically complex ranges.

In summary, *S. frontalis* songs were individually diagnosable with a high degree of certainty using relatively few measurements of note duration and frequency, but geographic groups were not diagnosable, and multiple cases of convergent note phenotypes were noted between individuals separated by considerable geographic distances. The relatively narrow 3-dimensional space defined by overall duration and frequency measures would not be likely to expand significantly with the addition of more variables or samples, due to the highly correlated nature of variables in simple vocal signals and the geographic and elevational distribution of samples used in this analysis. This implies that adding more samples would simply fill in the existing song space and result in a higher misclassification rate.

#### **2.4.2. Effects of Song Playback**

Song playback is a potent stimulus for territorial birds, and it is widely used by researchers to determine territory boundaries, to test neighbor-stranger discrimination, or simply

to stimulate singing behavior. Recordings made after playback are often used in vocal analyses because spectrographs made from such recordings tend to be clearer than those made without a playback stimulus; moreover, many researchers do not discriminate between natural and playback recordings because many recordists do not mention when they use the technique. In response to playback, birds often approach a recordist while continuing to sing; the result is a higher-quality recording because the bird can often be seen and pinpointed with the microphone, allowing a reduction in input volume and an increased signal-to-noise ratio. These recordings are often incorporated into vocal analyses because they sound similar to the natural song; however, to my knowledge, there are no studies explicitly comparing songs from the same individual before and after playback. Songs given after playback are more likely to represent the close-range intraspecific interactions for which vocal signals presumably function; context-dependent differences in song structure may shed light on which features of song are most relevant to such interactions.

In eight species of *Synallaxis*, I found that playback significantly affected mean note length, frequency, or both in all comparisons, and significantly affected the variance of those measures in 14 of 19 comparisons; the reduction in frequency variation, in particular, was substantial. Discriminant functions based on pre-playback and playback songs differed significantly. The apparent expansion of the multivariate space in the playback analysis was due largely to reduced variance in frequency measurements, which resulted in higher loadings of those variables on the principal components used to derive the canonical axes (Fig. 2.4). Although this increased the separation of samples representing different species, it decreased individual diagnosability within species, because the trend for increasing note length was common across multiple species and variance estimates on mean durations either increased slightly or did not change significantly after playback.

The overall song space in the multispecies comparison was similar to that generated for *S. frontalis* after the two species with the longest note lengths (*S. maranonica* and the southern form of *S. gujanensis*) were removed from the analysis. Although sample sizes were small, the data again suggest that adding more individuals to the analysis would disproportionately increase the misclassification rate, particularly within species. Misclassification would be expected to result not from the analysis of too few variables, but rather from the inherent simplicity of the vocalizations themselves, their general similarity (even across species), and the highly correlated nature of variables between and (especially) within the temporal and frequency domains.

In summary, my analysis demonstrates statistically significant changes in song components as a result of playback stimulus and implies some degree of motor control over the structure of vocalizations, which is particularly noteworthy considering that suboscines are not known to possess the forebrain structures that control song production in oscines. However, the changes were slight, and from the standpoint of vocal character analysis at the species level, the use of playback recordings is not likely to confound results, although it may be an important source of variation in vocal data.

The functions of songs are not well known for tropical suboscines, but the available evidence suggests that they function primarily in territory defense in the *Thamnophilidae* (e.g., Morton and Derrickson 1996; Bard et al. 2002) and play a relatively minor role in mate attraction (Morton 1996). In the absence of intense sexual selection on vocalizations, small vocal differences among individuals, although quantifiable, may not be significant to the birds themselves (Wiley 2005). In playback experiments, Bard et al. (2002) found no evidence of discrimination between neighbors' and strangers' songs among territorial *Hylophylax naevioides* despite a high level of individual distinctiveness. Although neighbor-recognition experiments have not been done for any species in the *Furnariidae*, anecdotal evidence suggests that members



of the family are broadly responsive to playback of similar-sounding songs, and responses across genera have been noted (Zimmer and Whittaker 2000). Therefore, I expect that the results of playback experiments with furnariids would be similar to those of Bard et al. (2002).

Interspecific interactions have been demonstrated to mediate signal divergence in at least one avian lineage (deKort et al. 2002) and are likely to affect song characteristics in species-rich tropical communities, where interspecific territoriality is common (Terborgh et al. 1990). If interspecific territoriality reduces the magnitude of vocal differences between species, it may serve as an important control on the extent of individual variation. Although published examples from the Furnariidae are scarce (but see Zimmer and Whittaker 2000), some evidence suggests that songs of *Synallaxis azarae* are more similar to those of *S. frontalis* where the two species overlap in Bolivia (BJO unpublished data; see Chapter 3). A strong role for vocalizations in an interspecific context would trivialize the importance of small structural differences within species. For this reason, caution is warranted in interpreting the results of studies documenting individual variation in suboscines. Most of the vocal literature treats suboscines as a group defined by an inability to learn songs, whereas most variation in oscine song is attributed to cultural influences. Recent demonstrations of song learning in the bellbirds (Cotingidae; Saranathan et al. 2007) and some nonpasserines (e.g. Trochilidae, Psittacidae; Baptista and Schuchmann 1990; Gaunt et al. 1994; Pepperberg 1994) have prompted a search for evidence of learning in other suboscine lineages, starting with the documentation of individual differences as a necessary prerequisite. The underlying assumption in these studies is that learning may be more common than is currently believed, and if present, is likely responsible for intraspecific song variation in most species. If song learning exists in suboscines, its influence on variation should differ among lineages, given the behavioral and ecological diversity of suboscines. Some recent explanations for individual variation (e.g. neighbor recognition, sexual selection) are only

applicable to a small subset of suboscines, and should not be considered representative of the entire suborder. Detailed behavioral and neurological studies are needed to identify the mechanisms promoting individual variation in suboscines.

## Chapter 3. Geographic Variation in Vocalizations of the *Synallaxis azarae* Complex

### 3.1. Introduction

Several recent studies have presented evidence challenging the traditional view that suboscine passerines have little geographic variation in the structure of their songs (e.g., Lindell 1998; Isler et al. 2005, 2007a,b; Seddon and Tobias 2007). Lindell (1998) was one of the first studies to quantify such variation by demonstrating vocal differences among Venezuelan populations of *Synallaxis albescens*. Isler et al. (2005) found congruent patterns of genetic and vocal variation in *Thamnophilus caerulescens*, providing the first evidence that vocal characters can be used as a proxy for determining patterns of population genetic structure within a suboscine species. This view is consistent with the lack of evidence for vocal learning in the majority of suboscines that have been tested (Kroodsma 1984; Kroodsma and Konishi 1991) and the corollary hypothesis that vocal differences reflect genetic divergence among populations. Rheindt et al. (2008) provided further support for this hypothesis, demonstrating that vocalizations were less conserved than plumage patterns in *Zimmerius* tyrannulets and were more concordant with patterns of DNA sequence divergence. These findings suggest that quantitative comparison of vocalizations can be a useful technique for assessing the degree of genetic divergence among populations of suboscine birds, and can inform taxonomic revisions (Remsen 2005).

Isler et al. (1998) introduced an empirical framework for definition and use of vocal characters in studies of the suboscine family Thamnophilidae. They analyzed vocal differences between syntopic, closely related species and determined that a minimum of three non-overlapping characters separated each pair of species known to be reproductively isolated. This

guideline has been used to support proposals for species-level taxonomic changes for many thamnophilid populations since that time (Isler et al. 1999, 2001, 2007a, 2007b, 2008). Although a similar framework has yet to be proposed for other families, recent taxonomic revisions have emphasized the importance of vocal differences in other suboscine lineages (Krabbe and Schulenberg 1997; Zimmer 1997, 2002, 2008; Zimmer and Whittaker 2000; Alvarez and Whitney 2001; Nyári 2007; Rheindt et al. 2008).

The Furnariidae comprises some 300 species distributed from southern Mexico throughout Central and South America, where at least one species can be found in virtually all terrestrial habitats (Remsen 2003). The family has been largely neglected in studies of suboscine vocalizations, despite being highly vocal and exceptionally diverse from an ecological standpoint. However, furnariid vocalizations appear to be under strong phylogenetic constraint (Remsen 2003) and are relatively simple, which complicates comparisons between species, particularly those that are closely related or similar vocally. Simple signals present few features that may be coded or measured as vocal characters. If intraspecific vocal variation exists within two widespread species, then variation within each species might obscure significant genetic differences between them, thereby rendering vocalizations less effective as a tool for discerning species limits. In this study, I assess this possibility by analyzing variation within and among three furnariid species with similar, structurally simple primary vocalizations.

### **3.2. The *Synallaxis azarae* Complex**

*Synallaxis azarae*, *courseni*, and *frontalis* form a superspecies that occupies a vast range in South America (Remsen 2003). *S. azarae* occurs from western Venezuela and Colombia south to northern Argentina. In most parts of its range, it is common in humid forest undergrowth and secondary habitats along the eastern Andean slope, primarily between 1500-3500 m; however, populations in southwestern Ecuador and northwestern Peru (*S. a. ochracea*)

occur in dry forest as low as 600 m on the western slope. *S. azarae* occurs at similarly low elevations at the southern extreme of its range (*S. a. samaipatae* and *superciliosa*), where it remains restricted to pockets of humid forest (Remsen et al. 1988; Remsen 2003). *S. courseni* is endemic to *Polylepis* forest and scrub in the Apurímac valley of Peru (Blake 1971; Schulenberg et al. 2007). *S. frontalis* inhabits dry forest, scrub, and riparian habitats from eastern Brazil south to southern Brazil and Uruguay, and west through Paraguay to Argentina and Bolivia. Although the vast majority of its range is in the lowlands, *frontalis* occurs locally up to 2500 meters in Bolivia (Remsen 2003). *S. azarae* and *frontalis* are sympatric in central and southern Bolivia and northern Argentina, where they tend to segregate by habitat, with *frontalis* occurring in drier habitats, often at lower elevations than *azarae*, although overlap in their elevational distributions is extensive (N. Krabbe *pers. comm.*).

The primary vocalization of *S. azarae* and *S. courseni* is a two-noted song, approximately 0.5 seconds in length, and variously transcribed as “pip-squéek!” (Hilty and Brown 1986), “ka-kwééek” (Remsen et al. 1988; Ridgely and Tudor 1994), or “kheet-wee?” (Fjeldså and Krabbe 1990). Both notes have a positive slope, with strong “hooks” on the ends. The song is usually given in long sequences, often as an asynchronous duet by members of a pair. Although the vocalization is short, it is given in the same behavioral context as the “loudsongs” of the *Thamnophilidae* (Isler et al. 1998; Seddon 2005) and other *furnariids* (BJO *pers. obs.*). The songs of *azarae* and *courseni* are generally considered indistinguishable to the human ear (Ridgely and Tudor 1994; Schulenberg et al. 2007). The song of *S. frontalis* is similar in temporal pattern to that of *azarae*, but the slope of the first note is negative, the second note is strongly modulated, and the mean frequencies of each note are higher than the corresponding notes in the song of *azarae*. The songs of the two species are easily distinguishable in the field (Herzog et al. 1999). See species accounts in Appendix A for spectrographs of songs.

*Synallaxis azarae* is highly polytypic and provides a classic example of the “leap-frog” pattern of variation, with nine subspecies forming a chain of alternating light and dark populations along the Andes (Zimmer 1936; Remsen 1984, 2003; Table 3.1). The various *S. azarae* taxa were originally diagnosed based on plumage characters, especially the color (darkness) of the underparts, the extent of the frontal band, the color of the crown, back, and tail, and the extent of the eyebrow. Considerable variation in all these characters, even within subspecies, was noted as early as Chapman (1926). The species’ range is characterized by extreme topographic complexity, with numerous barriers to gene flow resulting in high rates of speciation and endemism in the Andes (Vuilleumier 1980; Remsen 1984; Cracraft 1985; Stotz et al. 1996; Rahbek and Graves 2001). Although all populations from Venezuela to Argentina are currently recognized as one species (Remsen et al. 2008), the two southernmost subspecies were long considered to comprise a separate species, *S. superciliosa* (Cory and Hellmayr 1925; Bond and de Schauensee 1941; Peters 1951; Remsen et al. 1988). Vaurie (1971, 1980) considered the northern populations (*elegantior*, *media*, *ochracea*, and *fruticicola*) to comprise a third species, *S. elegantior*, although Vaurie’s taxonomy was not followed by subsequent authors (with the exception of Fjeldså and Krabbe (1990)).

*Synallaxis frontalis* is considerably less variable phenotypically than *S. azarae* – both Vaurie (1980) and Remsen (2003) considered it monotypic, with plumage characters showing gradual clinal variation across its range. Although the degree of intraspecific genetic variation is unknown for either species, topographical differences between the species’ ranges and striking differences in the degree of plumage variation suggest that *S. azarae* should show considerably more population genetic structure than *S. frontalis*. If vocal differences reflect genetic differences in this lineage, then this hypothesis should be testable using vocal data.

For this study, I analyzed variation in vocal characters across the ranges of *Synallaxis*

*azarae* (including *courseni*) and *S. frontalis* using single-character and multivariate approaches. The goals were to determine the extent and pattern of geographic variation in each species; to test the hypothesis that vocalizations of a polytypic Andean species (*S. azarae*) should show more geographic structure than those of a monotypic, lowland congener (*S. frontalis*); and to investigate vocal differences between *S. azarae* and *S. courseni*.

### 3.3. Methods

Recordings of *Synallaxis azarae*, *courseni*, and *frontalis* were obtained from the Macaulay Library at the Cornell Laboratory of Ornithology, as well as from online resources and personal collections (see Acknowledgments). Recordings selected for analysis had to meet the following criteria: 1) they featured a series of at least five two-noted songs, as described above; 2) recording quality was good, i.e., the recordings did not feature faint or distorted signals; 3) they did not feature members of a pair overlapping excessively with each others' vocalizations; and 4) they did not contain alarm notes or other calls indicative of unusually motivated individuals. I assigned samples to subspecies according to the distributions given by Peters (1951) and Remsen (2003; Table 3.1). I selected 81 recordings of *S. azarae/courseni* for analysis, representing all described subspecies. Populations and sample sizes were as follows: *elegantior* (5); *media* (18); *ochracea* (7); *fruticicola* (10); *infumata* (6); *urubambae* (7); nominate *azarae* (9); *samaipatae* (5); *superciliosa* (8); and *S. courseni* (6).

For *S. frontalis*, I selected 35 recordings for analysis. Because there are no described subspecies of *frontalis*, I classified recordings into five geographic groups based on the distribution of samples – an Eastern group, representing localities in eastern Brazil from the state of Ceará south and west through Minas Gerais (n=5); a Chaco group (Paraguay and the province of Chaco, Argentina; n=6); a Southern group (Rio Grande do Sul, Brazil; and the provinces of Corrientes and Entre Rios, Argentina; n=6); a Bolivian group (Andes from deptos. La Paz to

TABLE 3.1. Nomenclature and distribution of *Synallaxis azarae/courseni*. Taxonomy follows Remsen (2003); distributions modified from Peters (1951).

Taxon	Ventral coloration	Distribution
<i>S. a. elegantior</i>	pale	Eastern Andes of Colombia and Andes of western Venezuela
<i>S. a. media</i>	dark	Central and western Andes of Colombia; Andes of Ecuador south to approximately S03°30'
<i>S. a. ochracea</i>	pale	West slope and foothills of Andes in SW Ecuador and NW Peru
<i>S. a. fruticicola</i>	intermediate	N Peru in Marañón Valley
<i>S. a. infumata</i>	dark	Central Peru (deptos. San Martín to Junín)
<i>S. courseni</i>	dark	S Peru in Apurímac Valley
<i>S. a. urubambae</i>	dark	SE Peru (depto. Cusco)
<i>S. a. azarae</i>	intermediate	S Peru (depto. Puno) to C Bolivia (depto. Cochabamba)
<i>S. a. samaipatae</i>	pale	S Bolivia (deptos. Santa Cruz, Chuquisaca, and Tarija)
<i>S. a. superciliosa</i>	pale	N Argentina

Santa Cruz; n=13); and a Southern Andean group (province of Jujuy, Argentina; n=5). Given the geographic distribution of samples, five groups was the maximum number that could be created to impart geographic structure to the *frontalis* data while maintaining at least five samples in each group (the minimum number for any *azarae* subspecies). See Appendix B for a list of recordings used in this study.

Spectrographs of two-noted vocalizations were generated using Raven Pro 1.3 ([www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)). For frequency measurements, I used the following settings in RAVEN: Window type = Hann; window size = 800 samples; 3-dB filter bandwidth = 79.3 Hz; window overlap = 92%; hop size = 64 samples; DFT size = 1024 Hz; grid spacing = 43.1 Hz. All measurements were made on the spectrograph traces of fundamental frequencies. For measurements of temporal parameters, I generated a second spectrograph for each song sequence using the following settings: Window type = Hann; window size = 150 samples; 3-dB filter bandwidth = 423 Hz; window overlap = 57.3%; hop size = 64 samples; DFT size = 256 Hz; grid



spacing = 172 Hz.

Because recordings typically consisted of long series of songs, I used a random number generator to select five songs from each recording; therefore, values for character measurements represented averages from five songs from each individual. Seven characters were measured, as follows: length of the first note, second note, and the interval between them (LN1, LN2, and INT, respectively); frequency with maximum amplitude of the first and second notes (PK1 and PK2, respectively); and the slope (change in frequency (kHz) \* sec<sup>-1</sup>) of the ascending or descending portion of each note (SL1 and SL2, respectively). For both notes of *azarae* and the first note of *frontalis*, portions used for the slope measurements corresponded to the center segment of each note, with the “hooks” on the ends of the notes excluded. For the second note of *frontalis*, the slope measurement was taken on the modulated portion near the center of the second note. Slope measurements were taken by manipulating a selection box in RAVEN such that the portion of the spectrogram trace inside the box lay along the diagonal of the box, so as to minimize deviation from the diagonal line. The difference in frequencies (represented by the upper and lower borders of the box) was then divided by the time interval contained by the box. This method controlled for slight variation in note shapes among individuals and minimized the loss of information due to non-linear note shapes. Slope measurements were taken as a quantitative measure of the inflection of each note, independent of note length; high slope values indicated strongly inflected notes.

Measurements were analyzed using JMP 7 (SAS Institute, Cary, NC). A MANOVA was used to test for differences between *azarae* and *frontalis*, and among populations of each species; univariate tests were also conducted to test means among populations for each vocal character. Principal Components Analysis was used to reduce the dimensionality of the data and to assess the contribution of each character to overall patterns of variation. The resulting principal

components were used to derive linear discriminant functions to visualize the separation of populations in multivariate space.

### 3.4. Results

Within *Synallaxis azarae/courseni*, univariate ANOVA revealed significant differences between at least one pair of populations in every vocal character (Fig. 3.1, Table 3.2). By contrast, only one pair of *frontalis* populations differed significantly in any vocal character: the Central and Bolivian groups differed in the slope of the second note (Table 3.2).

In 45 pairwise comparisons between subspecies of *S. azarae*, 41 pairs differed significantly in measurements of at least one vocal character, 26 pairs differed in three or more, and 8 pairs differed in five or six, after correcting for multiple comparisons ( $P < .05$ , Tukey-Kramer HSD test; Table 3.3). Although the number of vocal character differences between subspecies tended to increase with geographic distance between them, all subspecies showed exceptions to this pattern: each was more similar (in terms of the number of character differences) to at least one geographically distant subspecies than it was to a closer one. The most striking examples were *S. a. elegantior*, which differed from distant *S. courseni* in only one character but from parapatric *S. a. media* in three; and *S. a. samaipatae*, which showed no differences from distant *S. a. infumata* but differed from adjacent *S. a. azarae* in two characters. Two parapatric subspecies pairs – *S. a. media/ochracea* and *S. a. fruticicola/infumata* – differed in four and five characters, respectively. *S. courseni* differed from all subspecies of *azarae* by an average of 2.55 vocal characters – fewer than the mean number of significant differences among subspecies of *S. azarae* ( $\mu = 3.05$ ;  $t = -1.103$ ;  $P = 0.14$ ).

In addition to testing for differences among means, I also assessed the amount of overlap in vocal character measurements between *azarae* and *frontalis* and among subspecies of *azarae/courseni*. Mean values for character measurements in *S. frontalis* differed significantly

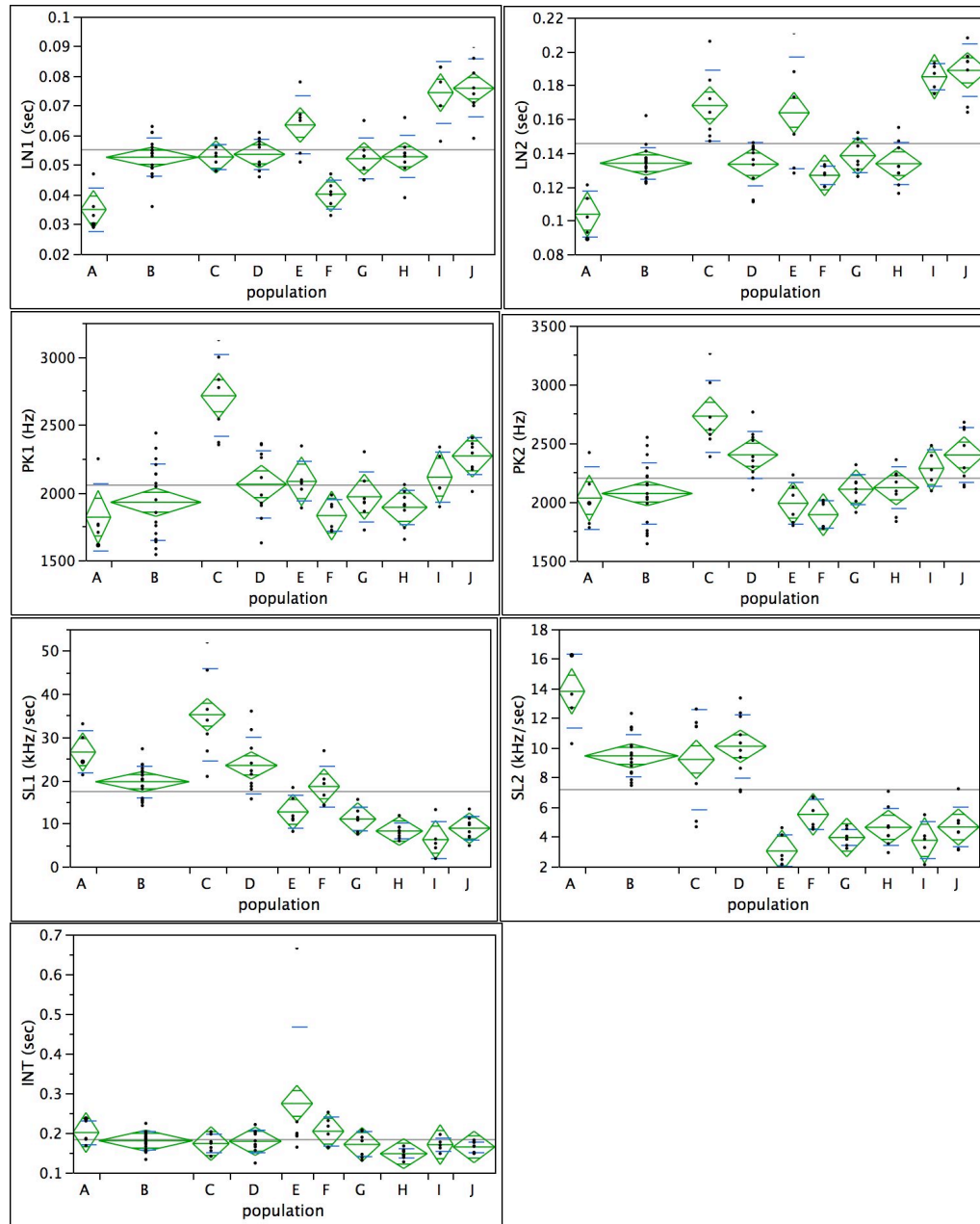


FIG. 3.1. Values for measurements of single vocal characters for ten populations of *Synallaxis azarae/courseni*. Diamonds are centered on the mean for each population; the upper and lower corners of the diamonds represent 95% confidence intervals for the means. Short horizontal lines represent one standard deviation from means; horizontal lines across each graph indicate the overall mean value for each character. Populations are arranged alphabetically from north to south: A = *elegantior*, B = *media*, C = *ochracea*, D = *fruticicola*, E = *infumata*, F = *courseni*, G = *urubambae*, H = *nominate azarae*, I = *samaipatae*, J = *superciliosa*.

from those of *azarae/courseni* for every character (all  $F_{1,108} > 21.55$ ,  $P < 0.001$ ), but the two

species overlapped in all but two characters. Fourteen subspecies pairs within *azarae/courseni*

TABLE 3.2. Results of ANOVA on seven vocal characters for ten subspecies of *Synallaxis azarae/courseni* and five geographic groups of *S. frontalis*.

<i>S. azarae</i>			<i>S. frontalis</i>		
Variable	<i>F</i>	<i>P</i>	Variable	<i>F</i>	<i>P</i>
LN1	20.2	<.0001	LN1	0.832	0.516
LN2	22.5	<.0001	LN2	0.610	0.659
INT	2.5	0.0159	INT	0.392	0.813
PK1	10.5	<.0001	PK1	1.22	0.324
PK2	9.5	<.0001	PK2	1.04	0.404
SL1	24.5	<.0001	SL1	1.31	0.289
SL2	29.3	<.0001	SL2	2.85	0.041

met or exceeded this level of divergence. The number of non-overlapping characters generally increased with geographic distance between subspecies (Fig. 3.2). Both *samaipatae* and *superciliosa* showed no overlap in four characters with *elegantior*, the most distant subspecies geographically, whereas all but two parapatric subspecies pairs overlapped in every character. For multivariate analyses, I excluded all samples of *S. azarae infumata* because several of these samples represented extreme vocal variants that confounded preliminary analyses; excluding them resulted in an insufficient sample size ( $n=4$ ) for comparison to other populations. Using the remaining samples of *S. azarae/courseni*, I derived seven principal components from the seven vocal variables. The resulting discriminant analysis classified 81.8% of samples to their correct population (Fig. 3.3). All 14 misclassifications involved parapatric taxon pairs, and nine misclassified samples represented erroneous placements between *S. a. media* and *fruticicola* or *urubambae* and nominate *azarae*, whereas none involved *S. a. ochracea*. When samples from some populations were combined, the discriminant analysis revealed four 100% diagnosable groups in *S. azarae/courseni*, as follows: a northern group consisting of the subspecies *elegantior*, *media*, and *fruticicola*; a southern group comprising the subspecies *urubambae* and *azarae*, with *S. courseni*; the extreme southern populations *samaipatae* and *superciliosa*; and *S. a. ochracea*. Within the northern and southern groups, differentiation of the geographically

TABLE 3.3. Pairwise comparisons between subspecies of *S. azarae/courseni* showing the number of significantly different vocal character means between each pair (Tukey-Kramer HSD,  $P < 0.05$ ).

	<i>elegantior</i>	<i>media</i>	<i>ochracea</i>	<i>fruticicola</i>	<i>infumata</i>	<i>courseni</i>	<i>urubambae</i>	<i>azarae</i>	<i>samaipatae</i>	<i>superciliosa</i>
<i>elegantior</i>	-									
<i>media</i>	3	-								
<i>ochracea</i>	5	4	-							
<i>fruticicola</i>	3	1	3	-						
<i>infumata</i>	4	3	4	5	-					
<i>courseni</i>	1	2	5	3	2	-				
<i>urubambae</i>	4	2	5	2	1	0	-			
<i>azarae</i>	4	2	4	2	2	2	0	-		
<i>samaipatae</i>	4	4	5	4	0	3	2	2	-	
<i>superciliosa</i>	5	6	4	4	2	5	2	3	0	-

peripheral taxa *S. a. elegantior* and *S. courseni* was suggested by the position of their centroids in the canonical space and by the low incidence of misclassification between these taxa and other samples in their respective groups (Fig. 3.3).

The vocal data showed substantial correlation between variables, especially for note length, frequency, and slope values for first and second notes (i.e., LN1-LN2, PK1-PK2, SL1-SL2). In light of this, for each domain, I reduced the dataset by excluding the variable with the lower  $F$ -value in univariate analyses, retaining LN2, PK1, and SL2 to derive three new principal components. INT was also excluded because it was the least variable character in the dataset, especially after all *S. a. infumata* samples were removed. The first two principal components explained 91.7% of the variance in the data. Positive loadings on the first component were associated with note length and frequency, whereas negative loadings were associated with note

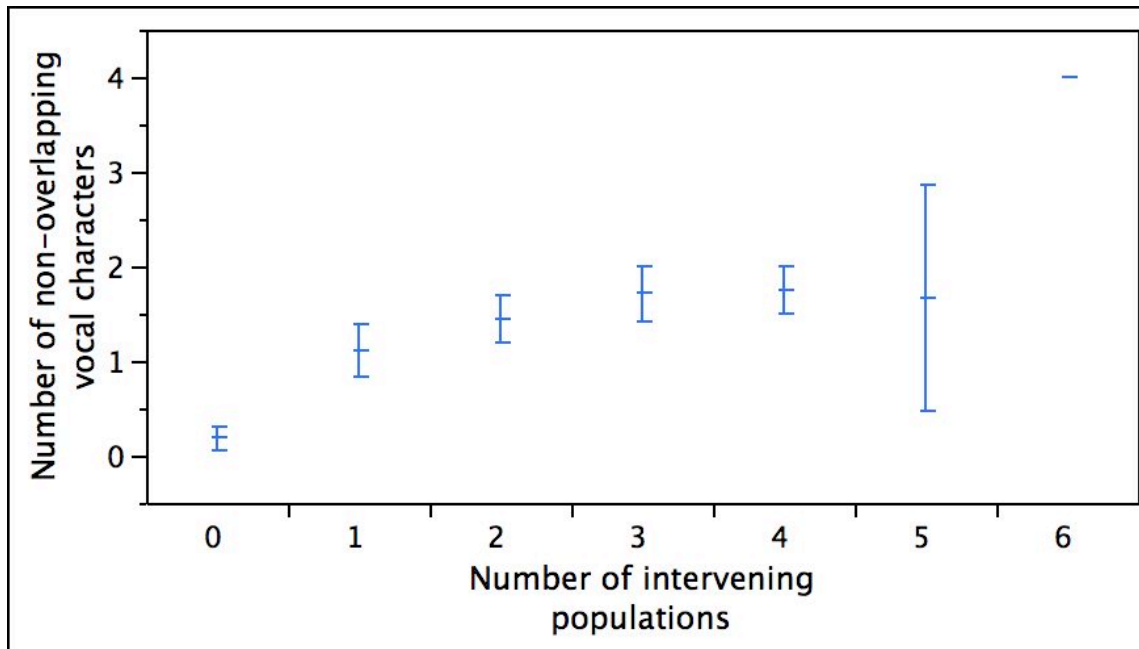


FIG. 3.2. Means and standard errors for the number of non-overlapping vocal characters between subspecies pairs of *S. azarae/courseni* as a function of the number of subspecies separating them. The maximum number of intervening subspecies was six, reflecting the peripheral distribution of *ochracea* and *courseni* relative to other Andean populations.

slope. Positive loadings on the second component were associated with slope and frequency (Fig. 3.4). The resulting discriminant function retained the geographic groups from the previous analysis and correctly classified 97.4% of samples to the correct group. The two misclassified samples were both *S. a. ochracea* misclassified as *samaipatae/superciliosa*. The apparent convergence in signal phenotype between these allopatric populations reflects the fact that they both had higher-pitched and longer songs than parapatric northern and southern groups, respectively, as suggested by the single-character analyses (Fig. 3.1).

Discriminant analysis of the five geographic groups of *S. frontalis* corroborated my finding of minimal variation among groups in the single-character analyses, and MANOVA indicated no significant difference among groups ( $F_{4,30}=0.99$ ;  $P=0.43$ ). Data from *S. frontalis* were thus pooled for comparison to *azarae/courseni*. The addition of vocal data for *S. frontalis* increased the magnitude of correlations between variables, so I generated new principal

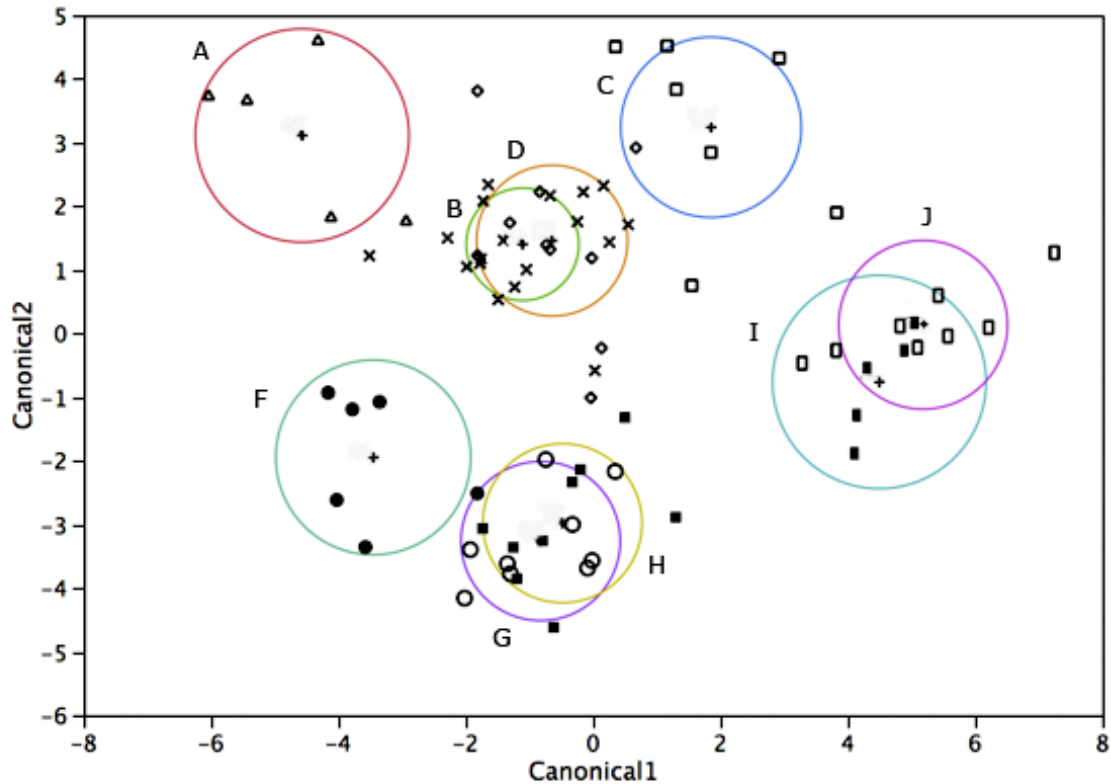


FIG. 3.3. Results of linear discriminant analysis for *S. azarae* and *courseni*, based on principal component scores derived from seven vocal variables. Circles represent 95% confidence regions around the means for each population. Populations are letter-coded for clarity; A=*elegantior* (open triangles), B=*media* (x), C=*ochracea* (open squares), D=*fruticicola* (open diamonds), F=*courseni* (closed circles), G=*urubambae* (open circles), H= nominate *azarae* (closed squares), I=*samaipatae* (closed rectangles) , J=*superciliosa* (open rectangles).

components using the same three variables used for *azarae/courseni*. In the discriminant analysis, *frontalis* was separated unambiguously from all samples of *S. azarae/courseni*, while the separation between northern and southern groups of *azarae/courseni* collapsed (Fig. 3.5). Despite this, *ochracea* and *samaipatae/superciliosa* remained 100% diagnosable from samples representing the main distribution of *azarae* (eastern slope of Andes from Colombia to central Bolivia), although their separation from each other was reduced.

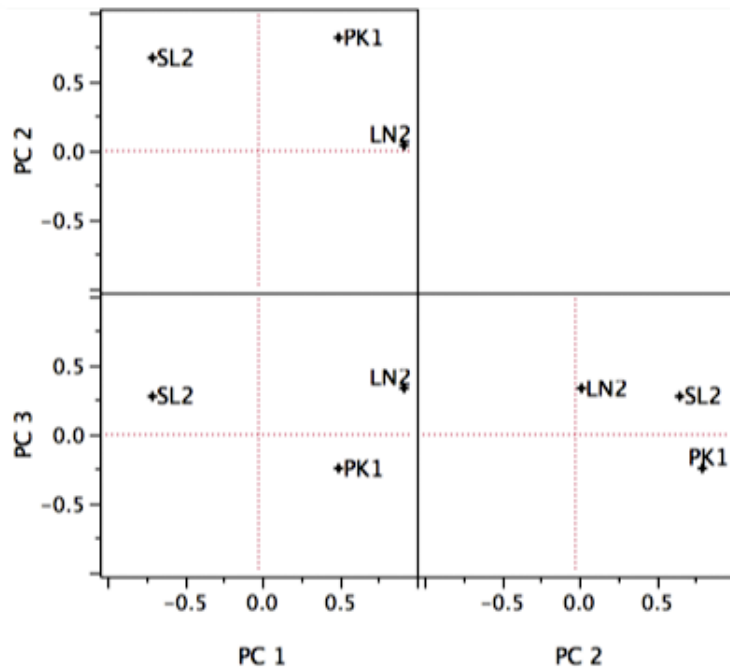


FIG. 3.4. Loadings on PC1-PC3 derived from three vocal variables for *S. azarae/courseni* data.

### 3.5. Discussion

This study provides the first quantitative documentation of vocal variation across the range of an Andean passerine and reveals substantial geographic structure in the vocalizations of a suboscine. The variability is striking, considering that the song of *S. azarae/courseni* is simple in structure and less than one-half second in length, and sounds exceedingly similar throughout the vast range of the species complex. There have been few quantitative assessments of the extent of geographic vocal variation within suboscine species (but see Lindell 1998; Isler et al. 2005), due largely to the historic view that suboscine vocalizations vary minimally, if at all, over geographic distance (e.g. Lanyon 1978; Johnson 1980), and the corollary that differences in songs noticeable to human observers are a requisite for species-level divergence (e.g., Pierpont and Fitzpatrick 1983; Whitney 1994; Isler et al. 1999, 2007a; Zimmer 2002). Qualitative comparison of very different song types, although providing clear evidence of population



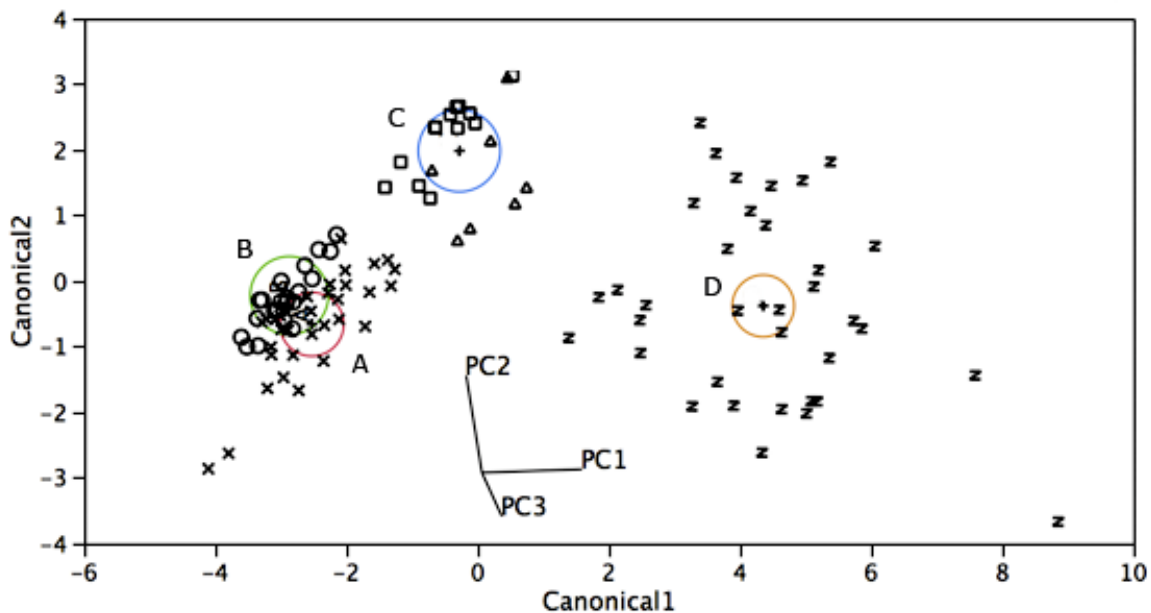


FIG. 3.5. Linear discriminant analysis on combined *S. azarae-courseni-frontalis* data using three principal components derived from three vocal variables, showing clear separation of *S. a. ochracea*, *samaipatae*, and *superciliosa* from other subspecies of *S. azarae*. Groups are as follows: A: northern *S. azarae* populations (*elegantior*, *media*, and *fruticicola*; x); B: southern *azarae* populations (*urubambae*, *azarae*, and *S. courseni*; circles); C: *S. a. ochracea* (triangles) and *samaipatae/superciliosa* (squares); D: *S. frontalis* (z). Biplot rays indicate the relative magnitude of the influence of each component in the canonical space.

divergence, nonetheless obscures the possibility that vocal variation can manifest itself in more subtle but significant ways.

This study tested the relative efficacy of single-character and multivariate analyses in diagnosing vocally distinct groups within *S. azarae/courseni*. In general, although there was a positive correlation between the number of single-character differences between samples and their distance in multivariate space, the multivariate methods outperformed the single-character analyses. This was due largely to substantial variation within populations in the measurements for each vocal character, which created an illusion of vocal similarity when non-overlap was required to differentiate populations. The inadequacy of the single-character approach is

highlighted by the fact that *superciliosa* differed from *elegantior* in four non-overlapping characters but overlapped in every character with *media*, from which it is almost equally isolated geographically, despite clear separation in multivariate space. This particular comparison also reveals the sensitivity of single-character approaches to sample size; *elegantior* and *media* represented the smallest and largest sample sizes, respectively, in this study. The apparent effects of sample size on degree of overlap among populations illustrate a critical shortcoming of many studies of suboscine vocalizations, as pointed out by Isler et al. (2005) and Remsen (2005).

In the multivariate analyses, variation within populations reduced the power of the discriminant function to create diagnosable groupings on all but the broadest geographic scale. *S. a. elegantior* and *S. courseni* showed evidence of divergence from parapatric *S. azarae* populations but still overlapped with them. Whereas the unambiguous separation of *azarae* from *frontalis* reflects a known biological reality, it seems likely that some subspecies of *azarae* could also be diagnosable genetically, considering the level of plumage differentiation within the species and the fact that its range extends over thousands of kilometers of some of the most topographically complex terrain on Earth. Although genetic data are lacking, the geographic structure in the *azarae* vocal data supports this idea. However, the general similarity among groups and the amount of vocal variation within each group effectively confound the ability to hypothesize evolutionary relationships based on vocal similarity.

The discriminant analysis of *azarae/courseni* revealed substantial geographic structure and divergence between *azarae* and *courseni*. I added *frontalis* to the analysis to provide an appropriate phylogenetic context in which to assess the biological significance of intraspecific vocal variation in *azarae/courseni*. When *frontalis* was added to the discriminant analysis, several apparent differences among populations of *azarae* (and between *azarae* and *courseni*) disappeared. This suggests that despite the low incidence of misclassification in the discriminant

analysis of *azarae/courseni*, differences between some populations are biologically trivial and do not represent divergence that is meaningful in the behavioral contexts within which the songs presumably function – namely, species recognition and reproductive isolation. Although empirical evidence is lacking, this impression is supported by observations of playback responses between northern and southern Andean populations of *azarae*, and between *azarae* and *courseni* (Fjeldså and Krabbe 1990; D. F. Lane, pers. comm.). The distribution of *azarae* samples in the expanded discriminant analysis revealed a “core” group representing localities along the eastern slope of the Andes between Colombia and Bolivia, with peripheral populations segregating to a greater or lesser degree. The two most divergent populations – *ochracea* and *samaipatae/superciliosa* – each occupy known areas of endemism for South American birds (Cracraft 1985) and are ecologically distinct from parapatric *azarae* populations.

*Samaipatae/superciliosa* and *ochracea* each consistently varied from other populations in note length, frequency, and degree of inflection, despite their overlap with those populations in each of those characters. It thus appears that the discriminant analysis effectively elucidated the nature of vocal variation at the population level, suggesting a biogeographically plausible hypothesis that can be tested using genetic data. Indeed, vocal and genetic divergence in peripheral populations has been noted recently in another suboscine species (Bates 2000; Seddon and Tobias 2007).

An alternative view, suggested by the comparison of the discriminant analyses of *azarae/courseni* with and without *frontalis*, is that vocal similarity may obscure significant genetic differences among populations. There is certainly some evidence that this is the case, most notably the convergence in vocal phenotype between *S. a. ochracea* and *samaipatae/superciliosa*, and the fact that some vocally indistinguishable populations within *S. azarae* are more different from each other in plumage than are some *Synallaxis* taxa traditionally

ranked as species. Taxa at the geographic extremes of the “core” Andean *azarae* group in Figure 3.5 represent populations that could be considered allopatric in light of the vast distances and numerous biogeographic barriers separating them. The general concordance between vocal and geographic distance in this study suggests that gene flow is an important component of the evolution of song differences among populations, regardless of whether any population is 100% diagnosable. Also suggestive is the fact that peripheral *azarae* populations occupy known areas of species-level endemism, implying a substantial degree of genetic isolation from “core” Andean *azarae* populations. However, many species of *Synallaxis*, including both *azarae* and *frontalis*, are habitat generalists that may not be as influenced by some barriers as species with narrower elevational ranges (in the former case) or those restricted to forest (in the latter).

Isler et al. (1998) proposed an empirically derived framework for assessing the biological significance of vocally divergent populations in the *Thamnophilidae*. Nothing similar has been proposed for any other suboscine family, but results of this study suggest that the benchmark of three non-overlapping differences is too conservative for the *Furnariidae*. *S. azarae* and *S. frontalis* have been recognized as separate species since the late 19<sup>th</sup> century. No hybrids between *azarae* and *frontalis* are known, and all evidence points towards an absence of gene flow between them despite local sympatry. Although mean values for single-character measurements in *S. frontalis* differed significantly from those of *azarae* for every vocal character, the two species overlapped in all but two characters - the slope of the first note (SL1), which was always negative for *frontalis* and positive for *azarae*, and the slope of the second note (SL2), which was much greater for *frontalis*. I chose the abruptly rising segment for the SL2 measurements on *frontalis* because it was the most linear central segment of the note, and because the high SL2 values reflected the sharp frequency modulation that is a key distinguishing feature between the two species in qualitative comparisons. Whether the SL2

measurements on *azarae* and *frontalis* represent homologues is therefore open to question, but it should be noted that the overall rise in frequency over time on the second note of *frontalis* is appreciably higher than that of *azarae*, even if the entire rising portion of the note is used for the measurement (see Fig. 3.2). I have little doubt that using a different metric for SL2 would maintain the significance of the difference between the two species.

Although this study only compared one pair of species, my results nevertheless suggest that under the methodology of Isler et al. (1998), fewer than three non-overlapping characters may be sufficient to diagnose species of *Synallaxis*. On the other hand, applying this criterion to the populations of *azarae* revealed that 14 subspecies pairs differed by two or more non-overlapping characters, whereas some widely separated subspecies pairs showed substantial overlap. In the case of *azarae/frontalis*, single-character comparisons suggested that intraspecific variation could exceed variation between species, despite the fact that the two species were 100% diagnosable in the multivariate analyses. It thus appears that a multivariate approach is more effective than single-character comparisons as a method for delimiting species-level taxa in the Furnariidae using vocal data, especially when the vocalizations are simple in structure and similar between species. Variation in single characters, rather than indicating species-level population divergence or lack thereof, may simply reflect random variation limited by syringeal morphology, which is under rigid phylogenetic constraint (Ames 1971). On the other hand, correlated changes in a number of variables result in true divergence of a signal's phenotype and lead to greater differentiation of populations.

There was some concordance between coarse patterns of plumage variation in *azarae/courseni* and patterns in the vocal data. The palest subspecies (*elegantior*, *ochracea*, and *samaipatae/superciliosa*) were all peripheral populations that segregated vocally to a greater or lesser degree. Additionally, the differentiation between northern and southern groups in the

multivariate analyses parallels the observation that northern birds, although variable, are collectively paler than birds from southern Peru and Bolivia (Chapman 1926; Zimmer 1936). In comparisons between subspecies, however, plumage similarity and vocal similarity do not appear to be correlated. *Elegantior* and *courseni*, for example, are very different from each other in plumage, yet they are similar vocally. On the other hand, *ochracea* and *samaipatae/superciliosa* each show phenotypic evidence of intergradation with adjacent *azarae* populations (Remsen et al. 1988; BJO pers. obs.) despite being highly divergent from them vocally. A quantitative analysis of plumage characters and molecular data is needed.

Bioacoustic adaptation to different habitats is well known in birds (Morton 1975; Wiley and Richards 1978), and my results suggest that it may play an important role in vocal diversification in *Synallaxis*. Songs of *S. a. ochracea* and *samaipatae/superciliosa* were significantly higher-pitched than those of parapatric *azarae* populations, and the mean frequency of the song of *S. frontalis* was significantly higher than the corresponding notes of *S. azarae*. This pattern is consistent with adaptation to the relatively open habitats that these populations inhabit. *S. a. ochracea* occurs in dry forest on the western slope of the Andes, a very different habitat structurally than that found on the humid eastern slopes. *S. frontalis* replaces *azarae* in dry forest, chaco, and scrub habitats of southern South America. Although the data suggest that adaptation to different habitats may mediate vocal divergence, interspecific territoriality may also play a role. Spectrographs of *S. azarae* show increasing similarity to those of *S. frontalis* in their area of sympatry, a pattern also seen in the multivariate analysis (Fig. 3.5; see Appendix A). Signal convergence in sympatry has not been reported in suboscine passerines, but is known to occur in other avian lineages (e.g., deKort et al. 2002, Haavie et al. 2004). Further study of *S. azarae* and *S. frontalis* in their zone of sympatry is needed.

An empirical assessment of the importance of small vocal differences to furnariid

populations in terms of mate choice and gene flow is badly needed under the conceptual framework of the Biological Species Concept (Mayr 1942; Johnson et al. 1999), as is an evaluation of the importance of vocal behavior relative to other potential premating isolating mechanisms (Raposo and Höfling 2003). Seddon (2005) found evidence for song divergence as a consequence of sympatry in the *Thamnophilidae*, up to 40 species of which may be found at some lowland forest localities in South America. By comparison, *furnariids* occupy a greater range of habitats, and the overall degree of sympatry is lower. If species recognition is an important factor driving vocal diversification in suboscines, there should be less vocal diversification and more vocal homoplasy among *furnariids*, particularly the non-dendrocolaptines, than *thamnophilids*. This appears to be the case, but the hypothesis remains to be rigorously tested using quantitative data. Even so, convergence in signal phenotype appears substantial in some lineages, especially those of open habitats. *Furnariids* are notoriously indiscriminant in response to tape playback; in field trials, playback responses across species and even genera have been noted (e.g., Zimmer and Whittaker 2000), suggesting that song may play a more significant role in interspecific territoriality (Cody 1974) than mating. Studies that emphasize the importance of mate recognition in the context of vocal evolution tend to overlook the fact that little is known about the breeding behavior of many Neotropical birds (Stutchbury and Morton 2001), particularly the proximate cues that trigger mating. The *Furnariidae* is an extremely diverse family from a behavioral standpoint; despite their generally drab plumage, they perform a variety of visual displays and have the greatest diversity of nest-building behaviors of any bird family (Zyskowski and Prum 1999; Remsen 2003). The evolution of these behaviors should be considered in light of phylogenetic conservatism in *furnariid* vocalizations to further determine which factors influence vocal evolution in this family.

In summary, a growing body of evidence suggests that vocal differences reflect genetic

divergence in suboscines, but the details of that relationship are not clear. Specifically, the continuous nature of genetic and vocal variation has only been addressed in one study that compared the two variables simultaneously (Isler et al. 2005). Analyses based on single vocal characters do not adequately consider the correlated character changes that drive divergence in signal phenotype. This is an important consideration in suboscine birds, particularly furnariids. That phylogeny is a strong component of variation in suboscine vocalizations is evident to any ornithologist familiar with them; considering its size, vocal diversity in the Furnariidae is relatively limited, and the true function of vocalizations is poorly known for some species (Remsen 2003). Vocal characters that vary geographically present a problem for the elucidation of evolutionary relationships among taxa, particularly when vocalizations are simple and contain few characters that can be defined and measured. My data corroborate previous studies that suggest a relationship between vocal and genetic divergence, but there is clearly a limit to the accuracy of vocal data as a proxy for genetic data. Although data from this study are suggestive, defining the limitations of vocal data in suboscine systematics will require more comparative analyses of vocal and genetic variation with thorough geographic and taxon sampling.



## Chapter 4. Patterns of Vocal Character Evolution in *Synallaxis*

### 4.1. Introduction

Vocal characters have been used in phylogenetic studies of birds for decades (e.g., Lanyon 1969; Payne 1986; McCracken and Sheldon 1997; Isler et al. 1998; Päckert et al. 2003; Farnsworth and Lovette 2008). Recently, there has been much emphasis on the importance of vocalizations in suboscine systematics (e.g., Bierregaard et al. 1997; Isler et al. 1999, 2001, 2007a,b; Isler and Isler 2003; Nyári 2007), based on the presumed genetic basis for song acquisition in suboscines (Kroodsma 1984; Kroodsma and Konishi 1991), congruence between patterns of molecular and vocal variation (Isler et al. 2005; Rheindt et al. 2008), and a general consensus that song is an important means by which birds recognize conspecifics and potential mates (Seddon 2005).

Most studies of bird vocalizations focus on songs, which are typically defined as complex, species-specific vocalizations intended to both attract mates and defend territories (Catchpole and Slater 2008). As previous authors have noted, bird song is prone to variation on multiple spatial scales (e.g. Nottebohm 1969; Baptista 1977; Liu et al. 2008), especially in oscine passerines, which have a substantial learned component to their songs (Nottebohm 1972; Payne 1986). In addition to cultural variation, bird song characters are known to be influenced by properties of the signaling environment (Morton 1975; Ryan and Brenowitz 1985; Wiley 1991), as well as by morphological attributes such as body size (Bertelli and Tubaro 2002) and bill size and shape (Palacios and Tubaro 2000; Podos and Nowicki 2004; Seddon 2005). Nevertheless, nearly all researchers agree that some level of phylogenetic signal exists in vocalizations, because closely related bird species often sound similar to one another.

Despite the definition and use of vocal characters in recent taxonomic studies, there have been relatively few attempts to map them onto molecular phylogenies, in part because vocal characters are generally considered to be prone to rapid evolution and homoplasy, particularly in oscines (Irwin 2000). McCracken and Sheldon (1997) found that some vocal traits were phylogenetically informative in herons. Price and Lanyon (2002, 2004) found a high level of phylogenetic conservatism in vocalizations of oropendolas (*Psarocolius*; Icteridae), but Price et al. (2007) found considerably more lability in vocal traits in another genus (*Icterus*) within the same family. Farnsworth and Lovette (2008) demonstrated significant phylogenetic effects on variation in flight calls of wood-warblers (Parulidae). On the other hand, Joseph et al. (2004) found limited congruence between mtDNA and vocal characters in the suboscine genus *Myiarchus* (Tyrannidae), and several recently described suboscine species sound very different from their presumed closest relatives (e.g., Pierpont and Fitzpatrick 1983; Bierregaard et al. 1997; Zimmer 2008). The evidence thus indicates that the amount of phylogenetic information contained in vocal characters is variable and suggests that they may be unreliable indicators of phylogenetic relationships (Raposo and Höfling 2003). At the very least, patterns of vocal variation should be examined within a phylogenetic framework for a given group of taxa before they are used to support changes to species-level taxonomy in that group (Remsen 2005).

One way to circumvent some of the problems inherent in the multidimensional nature of song variation is to study song evolution in the suboscine passerines (Chesser 2004; Seddon 2005), in which learning is thought to play a reduced role in song development (Kroodsma 1984; Kroodsma and Konishi 1991; Krabbe and Schulenberg 1997). Suboscines have relatively simple songs with less individual and geographic variation than is typically observed in oscine species (Lanyon 1978; Payne 1986), and aspects of their vocalizations are considered to have a strong genetic basis (Isler et al. 1998; Remsen 2003; Zimmer and Isler 2003). The magnitude of

phylogenetic effects relative to other influences on song structure should be easier to assess if analyses are limited to groups of related suboscines that are similar in ecology and morphology, thereby partially controlling for the influences of these variables on signal structure.

The Furnariidae is a family of suboscine passerines distributed throughout the Neotropics and into the temperate latitudes of South America. The family is known for its remarkable ecological and behavioral diversity (Remsen 2003). The Furnariidae has been largely ignored in the recent literature on suboscine vocalizations, much of which has focused on the *Thamnophilidae* and *Cotingidae* (Isler et al. 1998, 1999, 2001, 2005, 2007a,b; Seddon 2005; Saranathan et al. 2007; Fitzsimmons et al. 2008). This is probably due to the fact that, although the majority of furnariids are highly vocal, their behavioral diversity precludes confident identification of homologies in singing behavior between (and sometimes within) genera. This is in marked contrast to the *Thamnophilidae*, virtually all of which have a clearly identifiable “loudsong” (Willis 1967; Isler et al. 1998) that is almost certainly homologous, and the *Cotingidae*, in which vocalizations are an integral part of ritualized displays that function in mate attraction, often at leks (Snow 2004). Although identification of homologous vocalizations in the *Furnariidae* is generally difficult, the task is simplified when the taxonomic scope is reduced, and vocal analyses in the family to date have been limited to: assessing intraspecific song variation (Lindell 1998); elevating vocally distinct taxa to species rank, with the implicit assumption that the distinct populations are each others’ closest relatives (Zimmer and Whittaker 2000; Zimmer 2002, 2008); or, more recently, using vocalizations as one line of evidence to resolve the placement of enigmatic taxa (Krabbe 2008; Zimmer et al. 2008). No studies have attempted to quantify empirically the number of vocal differences between closely related taxa in the *Furnariidae*, as was done for the *Thamnophilidae* by Isler et al. (1998), or to examine vocal differences in the context of an independently derived phylogeny.

In this study, I mapped vocal characters onto a molecular phylogeny of *Synallaxis*, the largest and most widespread genus in the Furnariidae. Under current taxonomy (Renssen et al. 2008), *Synallaxis* consists of 33 species distributed in lowland and montane habitats from southern Mexico to north-central Argentina (Renssen 2003). Although variation is substantial within the genus in both vocalizations and plumage, morphological and behavioral variation is slight – most species average between 10 and 20 grams, with a few averaging slightly larger (Renssen 2003), and all share a relatively short, straight bill, short wings, and relatively large feet; many also have conspicuously “decomposed” rectrices. As a rule, *Synallaxis* inhabit low, dense undergrowth, either within forest or, more commonly, along forest edges, in scrub habitats, or in cleared and cultivated areas. The songs of most species are short, stereotyped vocalizations, sometimes given as antiphonal duets by members of a pair. As far as is known, *Synallaxis* are sedentary and maintain small territories and long-term pair bonds, as has been demonstrated in the Thamnophilidae (Greenberg and Gradwohl 1986; Morton 1996; Morton and Stutchbury 2000; Stutchbury and Morton 2001; but see Fedy and Stutchbury 2004). Accordingly, their vocalizations presumably function primarily as short-distance signals used for mate contact and territory defense, rather than as long-distance advertising songs (Seddon and Tobias 2006). In this context, variation in the sound transmission properties of different environments, such as forest vs. non-forest (Morton 1975; Wiley and Richards 1978; Brown and Handford 2000) should have less influence on signal structure, both because the signals do not need to travel far to be effective, and because the microhabitat in which *Synallaxis* vocalize is less variable structurally than larger-scale patterns would suggest. *Synallaxis* is therefore a good model to examine the evolution of vocalizations in a phylogenetic context while minimizing the effects of differences in morphology and habitat, both of which are capable of shaping the structure of avian vocal signals (Wiley 1991; Podos et al. 2004).

## 4.2. Methods

A molecular phylogeny of *Synallaxis* was generated using 2075 base pairs of mitochondrial DNA representing the COII (687 b.p.), ND3 (347 b.p.), and ND2 (1041 b.p.) genes (Brumfield et al. unpublished data). The 45 taxa in the phylogeny included all but three species of *Synallaxis* (*S. fusciorufa*, *infuscata*, and *whitneyi*). Also included were representatives from several genera hypothesized to share a close relationship to *Synallaxis* (Remsen et al. 2009). For the following seven taxa, the mitochondrial data were supplemented with sequences from the nuclear genes RAG1 (2875 b.p.) and RAG2 (1149 b.p.) (Moyle et al. in press): *Synallaxis stictothorax*, *albescens*, and *scutata*; *Siptornopsis hypochondriacus*; *Gyalophylax hellmayri*; *Schoeniophylax phryganophilus*; and *Certhiaxis cinnamomea*. Addition of the two RAG genes helped resolve basal nodes within the phylogeny. A maximum-likelihood tree was generated using RAxML (Stamatakis 2006). The analysis was partitioned in four sets: mitochondrial sequences by codon position (1, 2 and 3), and RAG genes together.

Recordings of *Synallaxis* vocalizations were obtained as digital sound files from the Macaulay Library, Cornell Lab of Ornithology; and the Banco de Sonidos Animales (BSA) at the Instituto Alexander von Humboldt, Colombia. For some species, additional samples were obtained from commercial compilations (Moore et al. 2006), personal contributions, and online resources ([www.xeno-canto.org](http://www.xeno-canto.org)). I listened to all available recordings to infer their behavioral context, and identified songs as repeated vocalizations given in a stereotyped pattern, indicative of typical *Synallaxis* singing behavior; that is, I excluded alarm notes, scolding or begging calls, or unusual vocalizations given in response to tape playback or the presence of conspecifics. Recordings were also excluded if they were of low quality (i.e., obvious signal distortion or low signal-to-noise ratio). I identified songs for all species included in the molecular phylogeny (see Appendix A for song descriptions and spectrographs). For analysis, between three and ten

recordings per species were selected to maximize both geographic coverage and overall quality. I generated two spectrographs of each song in Raven Pro (version 1.3, [www.birds.cornell.edu/raven](http://www.birds.cornell.edu/raven)) using the following settings: For frequency measurements, Window type = Hann; window size = 800 samples; 3-dB filter bandwidth = 79.3 Hz; window overlap = 92%; hop size = 64 samples; DFT size = 1024 Hz; grid spacing = 43.1 Hz. For time measurements, I decreased window size and overlap to 150 samples and 57.3%, respectively.

Vocal data were gathered for all species and most subspecies of *Synallaxis*. Of the 45 taxa in the phylogeny, I did not gather vocal data for the outgroups (*Cranioleuca erythrops*, *Hellmayrea gularis*, *Certhiaxis cinnamomea*, and *C. mustelina*) due to poor resolution of deep nodes. The gene-based phylogeny revealed that *Synallaxis* is paraphyletic with respect to *S. propinqua*, and that *Schoeniophylax phryganophilus* is not closely related to *Synallaxis*; therefore, I excluded vocal data from these taxa, leaving 39 species for vocal character mapping. A total of 142 recordings was used in the analysis. To maximize sampling congruence between the vocal and molecular datasets, I excluded vocal data for *Synallaxis fuscorufa*, *infuscata*, and *whitneyi*, and included vocal data for the monotypic genera *Gyalophylax* and *Siptornopsis*, both of which appear to be closely related to *Synallaxis* (Whitney and Pacheco 1994; Remsen 2003). For species with multiple subspecies, I attempted to use vocal data from the subspecies used in the molecular phylogeny, preferably taken from recordings made close to the sampling locality. Several species were represented by multiple samples in the molecular dataset, each of which was treated as a separate taxon in the vocal analyses. Species with subspecific sampling were: *S. albescens* (*S. a. albescens*, *nesiotis*, and *australis*); *S. azarae* (*S. a. elegantior*, *fruticicola*, *infumata*, and *azarae*); *S. gujanensis* (*S. g. gujanensis* and *huallagae*); *S. stictothorax* (*S. s. maculata* and *chinchipensis*); and *S. unirufa* (*S. u. meridana* and *ochrogaster*). At least three recordings were available for each subspecies except *S. g. huallagae*, for which I used recordings

from the parapatric form *S. g. certhiola*. Three vocally distinct subspecies of *Synallaxis* (*S. brachyura cauceae*, *S. rutilans omissa*, and *S. s. scutata*) were excluded from this study because they were not represented in the molecular phylogeny.

For each taxon, I printed spectrographs and used them to identify vocal characters. Assignment of note shape and syntax character states was based on visual inspection of spectrographs. Although not free of subjectivity, visual sorting has been shown to produce categorizations similar to those provided by quantitative methods and is a widely accepted technique (Nowicki and Nelson 1990; Cortopassi and Bradbury 2000; Farnsworth and Lovette 2008). Temporal and frequency measurements were taken directly from on-screen spectrographs in Raven. Although absolute peak frequency values (i.e., frequency with maximum amplitude in the song) have been used in previous studies of vocalizations in the *Thamnophilidae* (e.g., Isler et al. 1998; Seddon 2005), I chose not to use them here, for two reasons. First, both sexes sing in *Synallaxis*, and there are clearly differences in song frequency between males and females (BJO pers. obs.), but the sexes are otherwise indistinguishable in the field. Because the majority of birds in this study were not collected, it was not possible to sort recordings by sex, as was done by Isler et al. (1998) and Seddon (2005). Secondly, substantial intraspecific variation in peak frequency values may have been attributable in part to variation in recording quality, conditions, or equipment. Overall, temporal features and patterns of frequency change within notes and songs showed much less individual variation than absolute frequency values (see Chapter 2). I thus adopted a conservative approach and did not include peak frequency data in the character matrix.

The initial dataset contained both discrete and continuous variables. Although values for continuous characters were retained, I followed the method of Price and Lanyon (2002) for establishing discrete states corresponding to ranges of mean values for each continuous

character. I calculated 95% confidence intervals around means for each species and established character states for which the intervals did not overlap for any pair of species. All characters could be parsed into at least two states using this method. The final character matrix contained 15 binary and 6 unordered multistate characters (Table 4.1). Characters were divided into three general categories based on whether they reflected syntax (1-4, 8-9), temporal measurements (5-7, 10-11), or shape of notes within songs (12-21).

I mapped vocal characters onto the phylogeny using MacClade 4.06 (Maddison and Maddison 2003). To assess the amount of homoplasy on the tree, I calculated the consistency index (CI; Kluge and Farris 1969) as well as the retention and rescaled consistency indices (RI and RC, respectively;  $RC = CI \times RI$ ; Farris 1989) for each character. Low values of these indices indicate a high number of convergences and reversals on the tree, and thus a high level of homoplasy, whereas values approaching one indicate high congruence with the phylogeny. A matrix of genetic distances was calculated for all samples in the phylogeny. I identified all taxon pairs with <2.5% DNA sequence divergence and plotted genetic distances versus the number of character state differences between taxa in the vocal matrix. I then drew an equal-sized random sample of more divergent pairs to examine the relationship between genetic and vocal distance in more distantly related taxa. All statistical analyses were performed using JMP 7 (SAS Institute, Cary, NC).

### **4.3. Results and Discussion**

Overall CI, RI, and RC values for the 21 vocal characters mapped onto the *Synallaxis* tree were 0.17, 0.37, and 0.06, respectively, indicating a high level of homoplasy. Temporal, shape, and syntax characters showed similar levels of homoplasy when mapped separately (Table 4.2), although syntax characters were most prone to changes on the tree (Table 4.3). Ancestral state reconstruction indicated rapid evolution of multiple vocal differences among terminal taxa, with



a high degree of conservatism at deeper nodes (Fig. 4.1), although resolution of some interior nodes was poor and character states for many interior branches were equivocal (see Appendix D for separate maps of each character on the tree). Genetic divergence between taxa averaged approximately 4.7% (N = 741 pairwise comparisons; s.d. = 0.014, range 0.001-0.067), although few pairs were within the 3.0 – 4.5% range (Fig. 4.2). The number of vocal character differences was positively correlated with genetic distance for all pairs of taxa that were 2.5% divergent or less (N = 77;  $r^2 = 0.34$ ,  $P < 0.0001$ ), but this relationship did not hold among a randomly selected set of more divergent pairs (N = 77;  $r^2 = 0.001$ ,  $P = 0.77$ ; Fig. 4.2). The analyses revealed a high level of homoplasy in *Synallaxis* vocal characters -- far more than expected given the number of taxa used in the study. Sanderson and Donoghue (1989) compared levels of homoplasy in 60 taxonomic studies to investigate the relationship between the value of the consistency index and the number of taxa under investigation. Using the equation derived from their regression ( $CI = 0.90 - 0.022(\text{number of taxa}) + 0.000213(\text{number of taxa})^2$ ), the expected CI for this study was 0.356, more than twice the observed overall CI and greater than the CI for any of the three categories of vocal characters (Table 4.3). Five characters did have CI's greater than 0.356: Longest Pause (0.50), Shortest Note (0.50), Fundamental Emphasis (1.00), Hiccup (1.00), and Peak Note (1.00). The latter character was an autapomorphy for *S. maranonica*. Of the remaining characters, all but Shortest Note were represented by uniquely derived character states among two or more taxa in a well-supported basal clade containing *S. albilora*, *S. cinerascens*, *S. gujanensis*, *S. maranonica*, and *S. scutata*, and this clade thus presented the strongest evidence for phylogenetic signal in vocalizations of *Synallaxis*. All values of the rescaled consistency index (RC) greater than 0.11 were associated with unique derived character states in this clade. Members of this clade have a two-parted song consisting of two notes with a long pause between the notes; in the sister taxa *S. g. huallagae* (here meant to refer to any taxon having the “southern

TABLE 4.1. Vocal characters and character states used in this study.

	Character	Description
1	2-part structure	First or last note is distinct from other notes in shape, length, and frequency. 0 = non-2-parted; 1 = two-parted.
2	Frequency rise	Song contains a positive frequency offset (>150 Hz) between any note and the preceding note. 0 = absent; 1 = present.
3	Frequency drop	Song contains a negative frequency offset (>150 Hz) between any note and the preceding note. 0 = absent; 1 = present.
4	Temporal pattern	Consistent pattern of note length changes over the duration of the song. 0 = no change; 1 = notes generally increase in length; 2 = notes generally decrease in length; 3 = notes both increase and decrease in length.
5	Longest pause	The length of the longest pause between notes in a song. 0 = no pause; 1 = 0.010-0.075 sec; 2 = 0.076-0.500 sec; 3 = greater than 0.500 sec.
6	Shortest note	The length of the shortest note in the song. 0 = less than 0.200 sec; 1 = longer than 0.200 sec.
7	Longest note	The length of the longest note in the song. 0 = less than 0.062 sec; 1 = 0.063-0.220 sec; 2 = longer than 0.220 sec.
8	Short position	The position of the shortest note in the song. 0 = middle; 1 = first note; 2 = terminal note.
9	Long position	The position of the longest note in the song. 0 = middle; 1 = first note; 2 = terminal note.
10	Total length	The length of the song, from the beginning of the initial note to the end of the terminal note. 0 = less than 0.850 sec; 1 = longer than 0.850 sec.
11	Trill	A set of three or more notes given at a rate greater than 10 notes/sec. 0 = less than 10 notes/sec; 1 = 10-12 notes/sec; 2 = 13-22 notes/sec; 3 = greater than 22 notes/sec.
12	U-note	Note shape resembles an inverted “U”. 0 = absent; 1 = present.
13	Hiccup	A short (<0.02 sec) broadband pulse that immediately precedes a longer note. 0 = absent; 1 = present.
14	Buzz	Broadband pulse with repeated frequency modulation. 0 = absent; 1 = present.
15	S-note	Note shape resembles an “S”, indicating a single abrupt frequency shift. 0 = absent; 1 = present.
16	Ascending note	Peak frequency of final quartile of note is >150 Hz higher than peak frequency of first quartile of note. 0 = absent; 1 = present.
17	Descending note	Peak frequency of final quartile of note is >150 Hz lower than peak frequency of first quartile of note. 0 = absent; 1 = present.
18	Peak note	Long note, ascending then descending with an abrupt peak in the middle. 0 = absent; 1 = present.
19	Terminal spike	An abrupt rise in frequency at the end of a note. 0 = absent; 1 = present.
20	Initial spike	An abrupt rise in frequency at the beginning of a note. 0 = absent; 1 = present.
21	Fundamental emphasis	Sound energy is concentrated in the fundamental frequency range. 0 = absent; 1 = present.

TABLE 4.2. Summary of state changes and homoplasy indices for each vocal character.

Character	Category	States	Steps on tree	CI	RI	RC
2-part structure	Syntax	2	8	0.13	0.46	0.06
Frequency rise	Syntax	2	10	0.10	0.47	0.05
Frequency drop	syntax	2	11	0.09	0.00	0.00
Temporal pattern	syntax	4	17	0.18	0.22	0.04
Short position	syntax	3	17	0.12	0.29	0.03
Long position	syntax	3	17	0.12	0.12	0.01
Longest pause	temporal	4	7	0.43	0.60	0.26
Shortest note	temporal	2	2	0.50	0.00	0.00
Longest note	temporal	3	10	0.20	0.47	0.09
Total length	temporal	2	8	0.13	0.56	0.07
Trill	temporal	4	13	0.23	0.17	0.04
U-note	shape	2	11	0.09	0.47	0.04
Hiccup	shape	2	1	1.00	1.00	1.00
Buzz	shape	2	3	0.33	0.33	0.11
S-note	shape	2	5	0.20	0.20	0.04
Ascending note	shape	2	10	0.10	0.44	0.04
Descending note	shape	2	8	0.13	0.50	0.06
Peak note	shape	2	1	1.00	0.00	0.00
Terminal spike	shape	2	6	0.17	0.44	0.07
Initial spike	shape	2	6	0.17	0.17	0.03
Fund. Emphasis	shape	2	2	1.00	1.00	1.00

TABLE 4.3. CI, RI, and RC values for three character categories. Syntax characters had the lowest mean values for all three indices.

Category	N	CI	RI	RC
Syntax	6	.13	.28	.03
Temporal	5	.25	.44	.11
Shape	10	.19	.43	.08

vocal type” of *S. gujanensis*; see Appendix A) and *S. albilora*, the second note is preceded by the “Hiccup”, which is a uniquely derived character in this pair of taxa. The sister taxa *S. cinerascens* and *S. scutata* differed from all other *Synallaxis* in that energy was concentrated on the fundamental frequency rather than higher harmonic bands. This could be due in part to the fact that these species have a much higher-pitched song than most other members of the genus, with peak frequencies typically in the 5-6 kHz range. Although this character was consistent across individuals of *S. cinerascens* and *S. scutata*, emphasis on higher harmonics was variable within other species, so “harmonic emphasis” could not be coded as a character. Shortest Note had a RI (and thus RC) of 0.00; due to variability in this character, 39 of 41 taxa in the tree were assigned the same character state, and Shortest Note was thus not particularly informative when coded as a discrete character. Frequency Drop also had a RI of zero; positive scores for this character were scattered among 11 terminal taxa.

Many taxon pairs currently recognized as forms of the same species showed dramatic vocal differences. For example, *S. stictothorax maculata* and *S. s. chinchipensis* differed in 14 vocal characters, the maximum recorded for any pair of taxa. Other vocally divergent subspecies pairs were *S. g. gujanensis* and *S. g. certhiola* (9 differences) and *S. unirufa ochrogaster* and *S. u. meridana* (7 differences). *S. albescens australis* differed from both *S. a. nesiotis* and *S. a. albescens* in six and four characters, respectively, whereas the latter two forms, which sound much more similar to each other than either does to *australis*, differed by only two. The four samples of *S. azarae* showed no differences from each other. *S. courseni* did not differ in any vocal character from *S. azarae* (and was less than 1% divergent in DNA sequence data from any population of that species). Overall, pairs of taxa showing fewer than three vocal differences represented either subspecies pairs within *S. albescens* and *azarae*, or involved taxa whose species status is provisional (Remsen et al. 2009) – specifically, *S. courseni* (no vocal differences

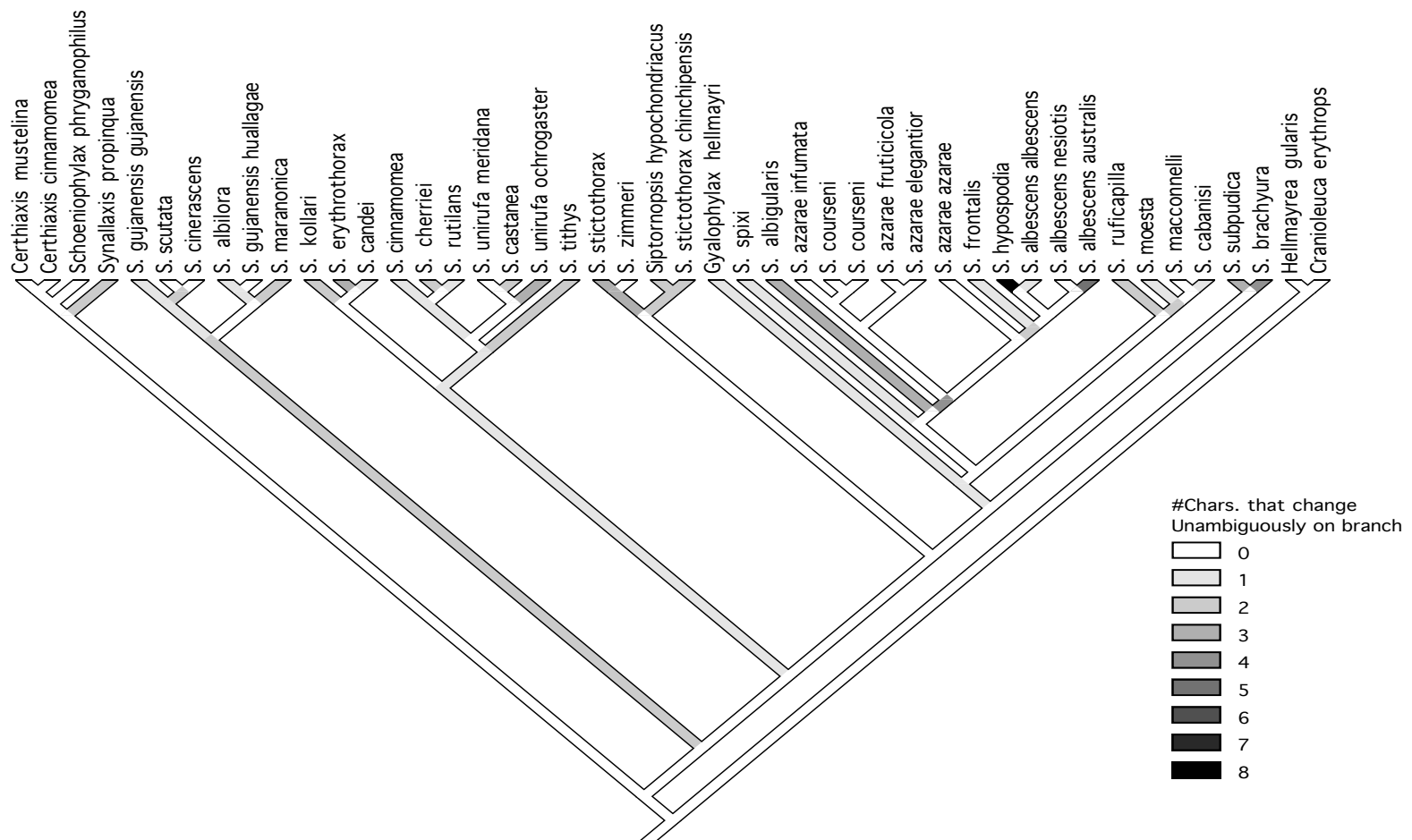


FIG. 4.1. Molecular phylogeny of *Synallaxis* showing unambiguous character state changes for all vocal characters.

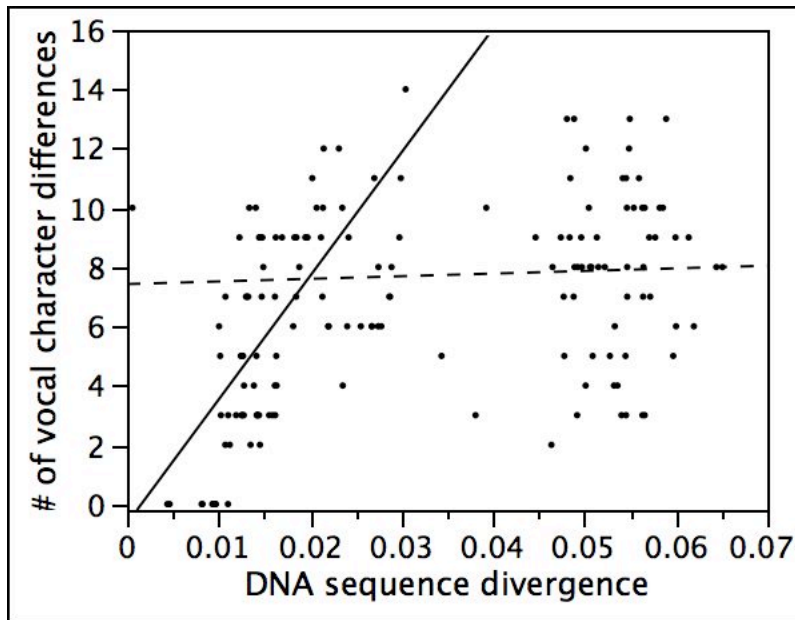


FIG. 4.2. The correlation between DNA sequence divergence and the number of vocal character differences for 77 taxon pairs showing <2.5% divergence (solid line) and an equal-sized random sample of more divergent pairs (dashed line).

from *S. azarae*) and *S. albilora* (two differences from *S. gujanensis certhiola*). With the exception of the subspecies pairs mentioned above, all taxa differing in three or more vocal characters represented pairs whose taxonomic status as full species is in little doubt, regardless of the species concept applied (Remsen 2003). It thus appears that the “yardstick” of three vocal characters, first developed by Isler et al. (1998) as a means to diagnose candidate taxa for species-level distinction in the *Thamnophilidae*, may also be a useful guideline for assessing species limits in *Synallaxis*. The applicability of this guideline to other genera in the *Furnariidae* should be investigated.

The pace of vocal character changes was rapid relative to genetic divergence. For example, *S. a. albescens* differed from *S. hypospodia* in ten vocal characters, but this taxon pair had a low level of sequence divergence in this study – both were part of a polytomy containing a

group of “rufous-capped” species (Fig. 4.1; see Chapter 1). Although genetic and vocal divergence were generally positively correlated, the pattern was driven by pairs of taxa with low pairwise genetic distances, and the correlation disappeared when these taxon pairs were excluded from analysis (Fig. 4.2). The rapid pace of vocal changes is evident in Figure 4.1, with many character state changes occurring toward the tips of the phylogeny. The overall pattern suggests that vocalizations diverge rapidly early in the speciation process but may converge later, perhaps due to a combination of constraints on syrinx morphology and the development of other isolating mechanisms. The general discord between vocal and genetic data in *Synallaxis* suggests that any reconstructions of song characters at interior nodes should be interpreted with caution.

The classic view of song holds that song characters are reliable indicators of male fitness (Reid et al. 2005; Kipper et al. 2006; Pfaff et al. 2007; Gil et al. 2007) and are thus important in mate attraction as well as territory defense. Studies of multiple species of oscine passerines in the temperate zone have revealed variability in the strength of correlations between the magnitude of traits supposedly under sexual selection (e.g., repertoire size) and the strength of female choice for those traits (Buchanan and Catchpole 1997; Gil and Slater 2000; Reid et al. 2004; Byers 2007). The few published field studies of territoriality in tropical suboscines suggest that females choose mates based on multiple cues (Morton and Stutchbury 2000; Fedy and Stutchbury 2004); therefore, song may or may not serve as a reliable mechanism to convey mate quality (Alatalo et al. 1986; Dolby et al. 2005; Searcy and Nowicki 2008). Tropical suboscines differ in many ways from the temperate-zone oscines that have been the classic models for vocal studies. Suboscine songs tend to be simple in structure relative to the complex songs of many oscines, and song elements are thought to be influenced more by genetics than learning (Kroodsma 1984; Kroodsma and Konishi 1991; Isler et al. 1998; Remsen 2003; Zimmer and Isler 2003). Although the general biology of many suboscines remains poorly known, they

tend to be more sedentary, have more protracted breeding seasons, form longer pair bonds, and produce fewer offspring annually than migratory temperate species (Stutchbury and Morton 2001; Wikelski et al. 2003). The singing behavior of suboscines is also quite different. In many temperate-zone oscines, males sing intensively during a short breeding season and are largely silent at other times of the year. By contrast, males and females duet in many suboscines, and singing occurs year-round (Morton 1996), probably serving to reinforce pair bonds as well as to defend territories (Seddon and Tobias 2006). The fact that many suboscine songs are simple, highly stereotyped, and relatively invariant within species (Lanyon 1978; Johnson 1980) suggests that sexual selection is not the dominant force driving song evolution, but supports the hypothesis that species recognition constrains diversification within a range of possible phenotypes determined by phylogeny (McCracken and Sheldon 1997) and morphology (Ryan and Brenowitz 1985; Palacios and Tubaro 2000; Podos et al. 2004). Under these conditions, song divergence may occur as a consequence of adaptation to different habitats (Wiley 1991) or through geographic isolation of populations (Seddon and Tobias 2007), with convergence arising as a result of phylogenetic constraints on the morphology of the vocal apparatus (Ames 1971; Podos et al. 2004). The latter explanation seems plausible for *Synallaxis*; in general, they are quite sedentary, many species have discontinuous or very small ranges, and evidence suggests that in one species, peripheral populations are vocally distinct (see Chapter 3). Moreover, in this study, syntactical characters showed the highest levels of homoplasy on the tree, indicating that many vocal differences were attributable to rearrangements of notes rather than evolution of novel note phenotypes, which would be correlated with changes in syringeal morphology (Ames 1971). On the other hand, if sexual selection is influencing song evolution, it may be acting on aspects of singing behavior (e.g. song volume, repetition rate) that could not be assessed confidently using my methods.



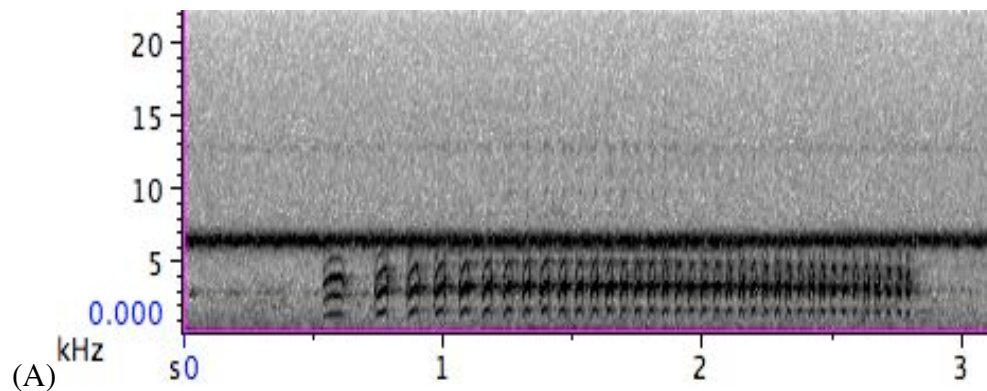
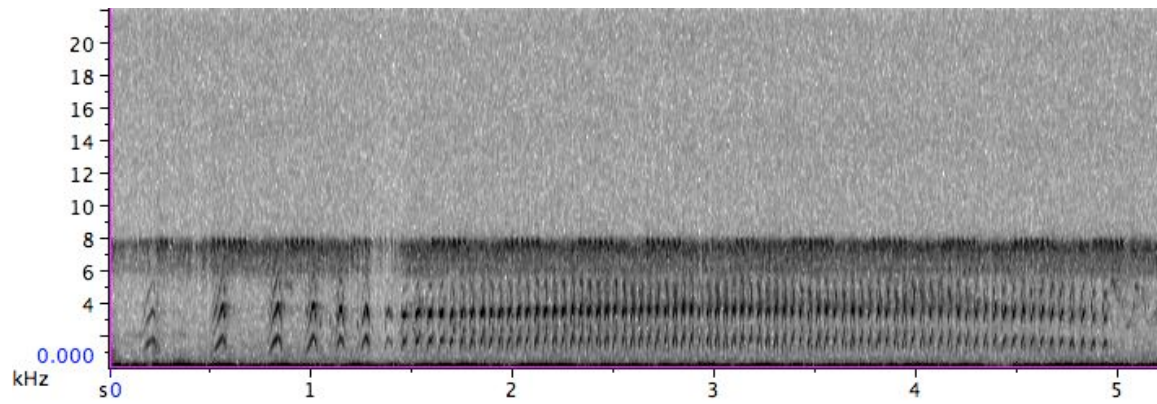
The ecological diversity of the Furnariidae presents a particular challenge for the interpretation of patterns of vocal diversity. A significant part of the challenge is identifying behaviors that can be interpreted as homologous (de Queiroz and Wimberger 1993). Most model species in avian vocal studies are familiar oscine passerines whose behavior has been studied intensively for decades; by contrast, most tropical suboscines are poorly known, and it may not be possible to confidently identify homologous singing behavior across such a complex and species-rich family as the Furnariidae. In this study, I attempted to minimize assumptions of homology by concentrating on a genus of ecologically and morphologically similar species. Even so, there is behavioral diversity within *Synallaxis* that I did not incorporate into my analysis and that may contain phylogenetic information (Slikas 1998). For example, singing behavior is more readily recognizable in some species than others. Some species sing for substantial portions of each day, often climbing higher within vegetation as they do so. Other species sing infrequently, usually in pairs at relatively close range. Others (notably *S. cabanisi*, *S. infuscata*, and *S. whitneyi*) seem not to have a stereotyped song at all – their vocal repertoires are reduced to irregular series of single notes (see Appendix A). Although I am confident in my assessment of homologous vocal behaviors within *Synallaxis*, it would be difficult to compare their songs with those of close relatives simply because they are so different behaviorally. For example, *Synallaxis propinqua* gives a series of harsh buzzes that appear as broadband pulses on a spectrograph (see Appendix A). The “song” is given in pairs and consists of these notes building to a crescendo; a cascading duet of barking notes follows. Acoustic dissimilarity aside (the song is much more reminiscent of other furnariid genera than any species of *Synallaxis*), this singing behavior is unique in the genus, with the possible exception of *S. stictothorax*. The problems would increase considerably if one were to compare *Synallaxis* songs to even more distantly related and ecologically dissimilar furnariids, such as those found in open habitats above tree line

in the Andes.

Furnariids present more practical challenges as well. As many Neotropical recordists are aware, furnariid responses to playback often include sounds seldom if ever heard in “natural” contexts. Although these signals are unlikely to be mistaken for the song (which is often known through consensus of multiple field ornithologists), they do indicate that many furnariid species are capable of making a larger variety of sounds than is generally appreciated; recordings of these alternate vocalizations are relatively rare. The significance of these sounds in intraspecific interactions, particularly courtship and mating, is completely unknown, and they may be considerably more relevant to the speciation process than what we perceive to be a song. Vaurie and Schwartz (1972) were the first to suggest that vocal behavior in *Synallaxis* may be so complex. They indicated that Venezuelan *S. unirufa* had an alternate song type used only during part of the year and associated with the peak of breeding in those populations. No mention of repertoires exists in the literature for any other synallaxine, but many species sing a “dawn song” much like members of the Tyrannidae (see Appendix A). Vaurie and Schwartz’s observations suggest that much is to be learned about the function of song in the Furnariidae.

Despite having no clearly homologous function, “unnatural” vocalizations may still contain phylogenetic information. What is widely accepted to be the song of *Synallaxis albescens* is a short, two-noted vocalization consisting of a rising note followed by a descending buzz (Lindell 1998; Remsen 2003; see Appendix A). In this study, *S. albescens* was found to be closely related to *S. hypospodia* despite ten vocal differences. Figure 4.3A is a spectrograph of a vocalization of *S. albescens* that I recorded in Guyana in February 2001. It is very similar to the song of *S. hypospodia* (Fig. 4.3B). It is also very similar to the song of *Gyalophylax hellmayri*, which this study found to be basal to the clade containing both *S. albescens* and *S. hypospodia*. To interpret this vocalization as the song of *albescens* would be to ignore that it is rarely heard (I

am aware of very few recordings), whereas the two-noted song is given frequently and is accompanied by singing behavior typical of other species of *Synallaxis*. Although the function of this odd vocalization is unknown, it provides supporting evidence for the close relationship between *S. albescens* and *S. hypospodia*, as well as the existence of phylogenetically conserved, latent vocal traits that may have biological significance but are only rarely heard by human observers. Observations such as this hint at the vocal complexity of a group not historically known for its singing ability and suggest that our knowledge of the structure and function of song in this lineage may not yet be adequate for proper reconstruction of evolutionary relationships using vocal characters.



(B)

FIG. 4.3. Spectrographs of an alternate song of *Synallaxis albescens* (A), recorded by the author in Guyana, February 2001 (MLNS 134799); and the typical song of *S. hypospodia* (B) from Bolivia (MLNS 52436).

## Chapter 5. Summary and Conclusions

The analysis of simple vocal signals, such as those produced by most species in the Furnariidae, is highly sensitive to individual and geographic variation, both of which were until recently thought to be insignificant in suboscines. My data demonstrate substantial variation in *Synallaxis* vocalizations at multiple levels of analysis. In Chapter 2, I demonstrated that significant changes in signal phenotype can be induced through a playback stimulus, illustrating that an individual's motivational state is likely a substantial component of vocal variation. In Chapters 2 and 3, I found a high level of correlation between vocal variables, suggesting that measurements of multiple note features are redundant and could introduce substantial error in analyses. In Chapter 3, I found that multivariate techniques outperformed analyses of single vocal characters, and were the only way to address correlations among variables. Geographic and individual variation precluded precise definition of vocal characters at the genus level (Chapter 4), resulting in coarse categorizations when the characters were coded discretely. As a result, I recovered little phylogenetic information when I mapped these characters onto a molecular phylogeny.

The fact that many closely related species sound similar indicates that there is some phylogenetic signal in vocalizations, but my data suggest that quantitative analysis of vocal characters has many drawbacks. The results of character mapping (Chapter 4) indicate that vocal divergence appears to proceed rapidly in the early stages of speciation. This is consistent with the general observation that cryptic species with a presumed recent evolutionary history often sound very different. However, the lack of a strong relationship between vocal and genetic distance in *Synallaxis* illustrates that vocal signal phenotypes can converge later in the diversification of a lineage. In this study, allopatric forms of *Synallaxis azarae* were not diagnosable in multivariate analyses, and the southernmost form of *S. azarae* showed evidence

of signal convergence with *S. frontalis* in their area of sympatry. Whereas interspecific territoriality could be invoked to explain the latter observation, it does not explain convergence in two populations separated by thousands of kilometers of Andean topography. Although allopatry seems the most likely mechanism for vocal diversification (Chapter 3), my study suggests that many factors influence vocal phenotype and that physical or neurological constraints can inhibit diversification, promoting vocal convergence in distantly related forms.

The rapid diversification of vocal characters among closely related taxa suggests that vocal divergence is an integral part of the speciation process. However, the use of vocal characters in suboscine systematics depends on the confident assessment of homologous vocalizations, as well as a thorough understanding of their role in the behavioral processes fundamental to reproductive isolation and speciation. The data from my dissertation suggest that although vocal characters can be phylogenetically informative, their evolution is correlated with a multiplicity of ecological and behavioral factors, the influences of which are likely to vary substantially as the taxonomic scale of analysis broadens. Although perhaps appropriate for small groups of closely related species, vocal character analyses are unsuitable for studies of larger taxonomic groups.

Variation in singing behavior among the 33 species of *Synallaxis* suggests that determining homology may not be possible given the current state of knowledge. The species differ in what I term “vocal propensity” – the tendency to produce stereotyped vocalizations in a manner sufficiently reminiscent of temperate-zone oscines to be labeled as “songs” by ornithologists. Indeed, vocal propensity is variable across the Furnariidae, and it is notable that basal lineages (e.g., Sclerurinae, Dendrocolaptinae) have considerably more complex songs than other subfamilies. This suggests strongly that comparison of vocal signals in disparate lineages is not justifiable, and that the role of vocal signals in reproductive isolation cannot be generalized

across the Furnariidae – hardly surprising given the family’s ecological and behavioral diversity.

Given the variability in vocal behavior within one genus, I suggest that “songs” in the classical sense may not exist in all species of the Furnariidae, and that a dichotomous view of the function of vocalizations (including the overwhelming tendency to attempt to identify “songs”) may obscure the biological significance of simple vocal signals. Fundamental differences in selection pressures acting on life-history traits in tropical vs. temperate birds suggest that what we perceive as songs are not necessarily mating signals in the tropics, and should not be viewed through the same lens of sexual selection that has generated such a large body of literature from the temperate zone. Even if extra-pair copulations are more common in tropical species than is generally believed, as has been suggested recently (Macedo et al. 2008), the basic fact remains that tropical birds have low reproductive rates (Cardillo 2002); therefore, the connection between EPCs and song diversification in tropical suboscines is unclear. The results of Bard et al.’s (2002) study, in which birds were equally responsive to playbacks of neighbors and strangers, suggest that song perception is not particularly fine-tuned, and is consistent with the hypothesis that songs serve a more significant role in territory defense than mate attraction. The possibility that vocalizations also function across species boundaries has hardly been explored, but seems plausible given the prevalence of interspecific territoriality in tropical bird communities. Finally, suboscine repertoires include vocalizations rarely heard or recorded by human observers (see Appendix A). From the standpoint of mate choice, these may be more significant than what we call “songs”.

The recent development of sound analysis techniques, transferrable digital media, and the popularization of recording have fomented great enthusiasm for the study of bird vocalizations. However, vocal data must be gathered and interpreted with caution, particularly when they form the basis for taxonomic recommendations in the absence of other lines of evidence. Some

researchers have gone so far as to downplay the well-known (and not completely understood) visual acuity of birds, suggesting that vocalizations are important isolating mechanisms in birds that inhabit forest interiors where the light is dim. In light of such statements, Raposo and Höfling's (2004) criticism of the "super-valorization" of song characters has some merit. The vocalizations relevant to mating and reproduction – that is, those likely to influence reproductive isolation and speciation – are by default associated with close-range encounters and visual displays that are rarely observed. Future research should focus on the role of vocalizations in these displays through detailed behavioral studies, perhaps involving captive birds. Neurological studies of suboscine vocalizations need to expand in both geographic and taxonomic scope. Most fundamentally, more recordists need to be afield, collecting high-quality recordings of all types of vocal signals, supplementing the recordings with detailed field data, and archiving them in permanent storage facilities.



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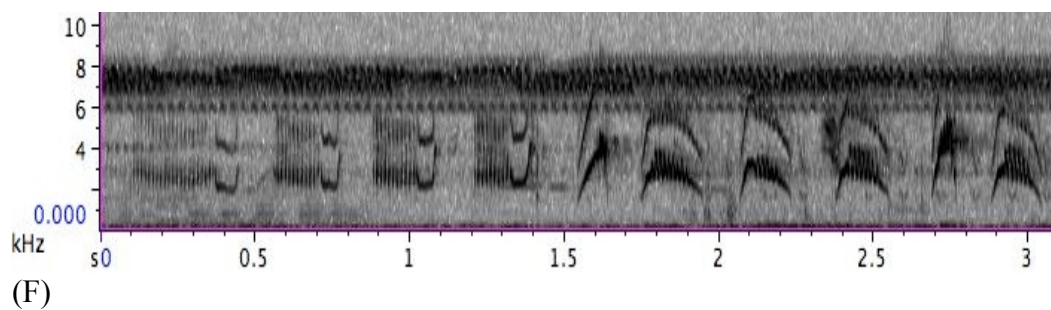
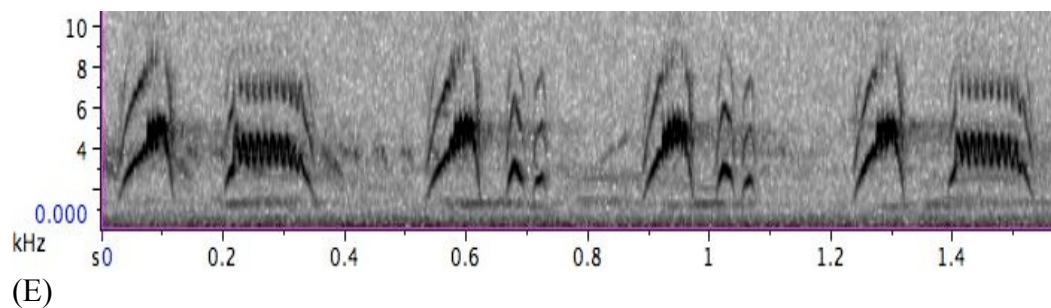
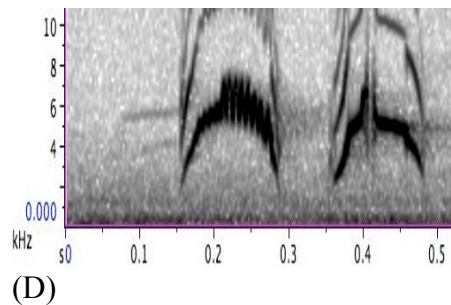
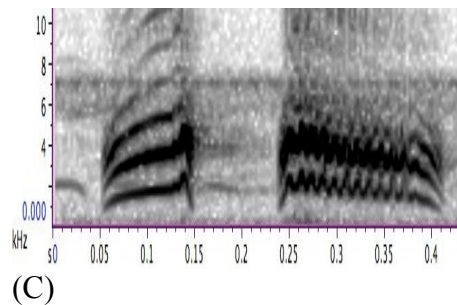
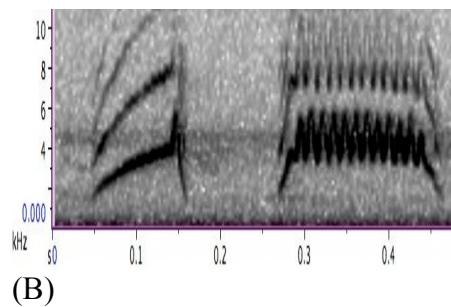
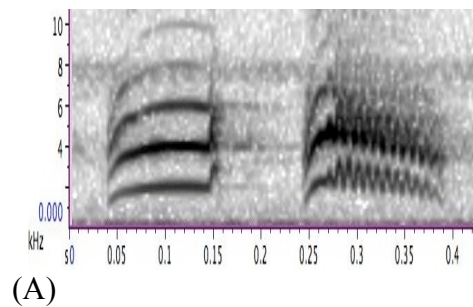
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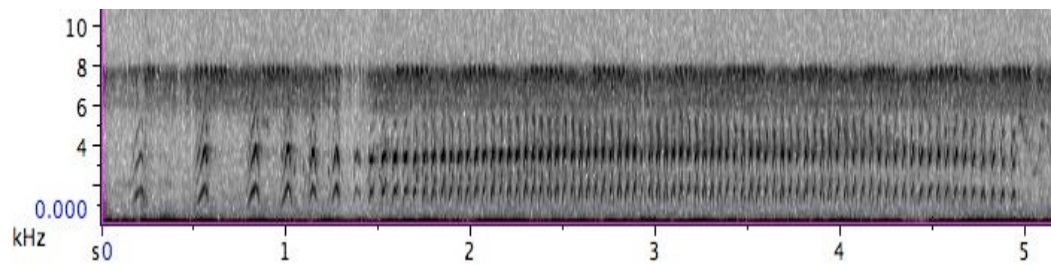
## **Appendix A. Species Accounts**

In the following species accounts, I refer to “songs” and “calls” to avoid confusing terminology and to maintain consistency with existing literature. Likewise, I refer to unusual complex vocalizations as “alternate songs” or “dawn songs” (the latter only when I know that a recording was made at dawn). Although the function of multi-note vocalizations is debatable, alarm and scold calls are much less variable in general (Marler 1955), and my assessment of a vocalization’s function reflects high confidence in assigning a behavioral context to it (in some cases the context was clear from the recordists’ announcements made at the time of the recording). Nevertheless, the primary purpose of these accounts is to document the extent of geographic and repertoire variation in each species and to facilitate comparison among species, regardless of behavioral context.

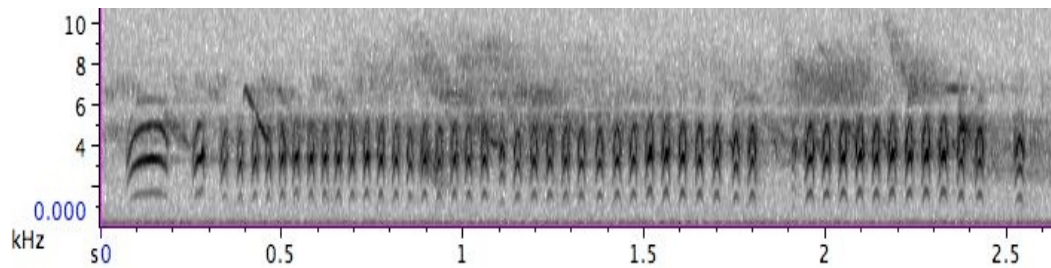
## *Synallaxis albescens*

The song of *S. albescens* is a two-noted vocalization consisting of a short rising note followed by a descending buzz (A-C). The song shows some geographic variation. The song of *S. a. australis* (D) is very different from that of any other subspecies; it is much higher-pitched, and consists of a buzzy note followed by two notes in rapid succession. After playback, birds typically sing normal songs at a rapid rate, but excited birds may also give a variety of notes interspersed among normal songs (E, F). An alternate vocalization is an accelerating trill, similar to the song of *S. hypospodia* (G). A long rattle is sometimes given by agitated birds (H). Call notes are short and strongly inflected (I, J); a dry “pit”, usually doubled, has also been recorded (K).

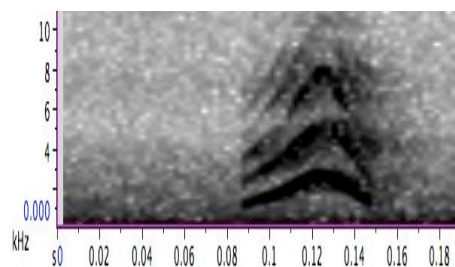




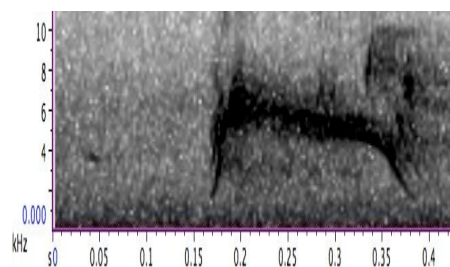
(G)



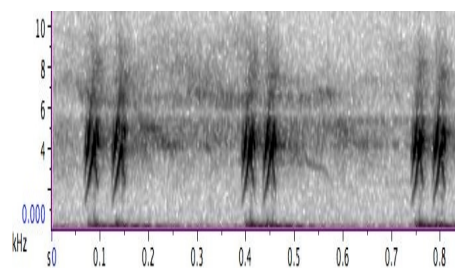
(H)



(I)



(J)



(K)

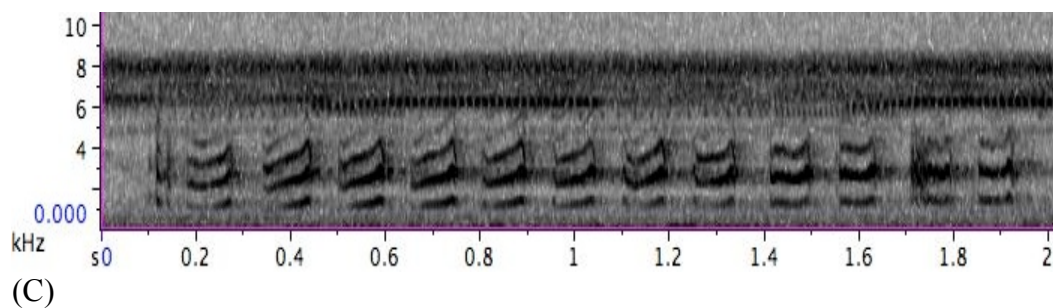
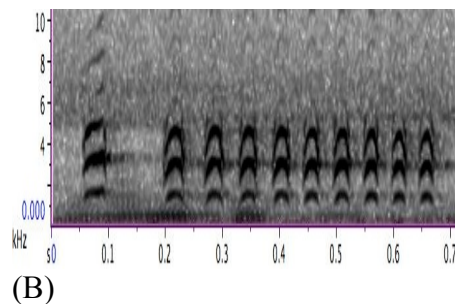
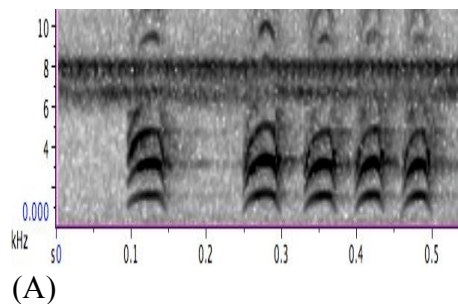
- A. Song of *S. a. latitabunda*, Panama. Energy is concentrated in the first harmonic band. (E. S. Morton; MLNS 7029)
- B. Song of *S. a. albescens*, Edo. São Paulo, Brazil. Energy is concentrated in the fundamental frequency band. (P. A. Schwartz; MLNS 66123)
- C. Song of *S. a. inaequalis*, Edo. Amazonas, Brazil. (C. A. Marantz; MLNS 127736)
- D. Song of *S. a. australis*, Depto. Cochabamba, Bolivia. (P. A. Hosner; MLNS 132544)



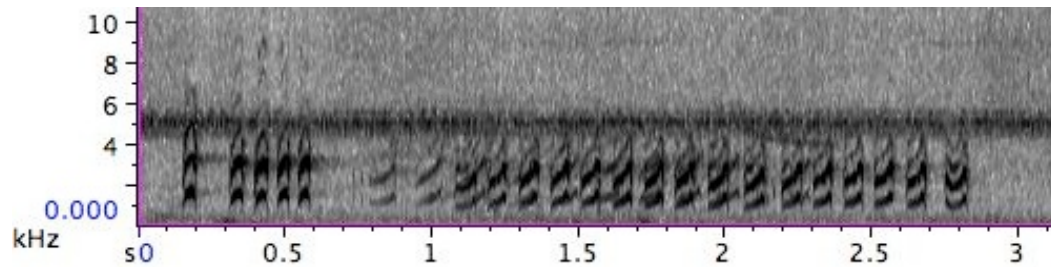
- E. Excited song sequence, *S. a. albescens*, Dist. Federal, Brazil. (T. A. Parker III; MLNS 34090)
- F. Excited song sequence after playback, *S. a. albescens*, Depto. Beni, Bolivia. (T. A. Parker III; MLNS 51864)
- G. Accelerating trill, *S. a. josephinae*, Guyana. (B. J. O'Shea; MLNS 134799)
- H. Agitated rattle, *S. a. nesiotis*, Edo. Guárico, Venezuela. (P. A. Schwartz; MLNS 66117)
- I. Call note, *S. a. insignis*, Depto. Antioquia, Colombia. (A. M. Cuervo; BSA 19220)
- J. Call note, *S. a. australis*, Prov. La Pampa, Argentina. A similar call note has been recorded from other populations. (B. M. Whitney; MLNS 46104)
- K. Doubled alarm note, *S. a. nesiotis*, Edo. Guárico, Venezuela. (P. A. Schwartz; MLNS 66117)

### *Synallaxis albigularis*

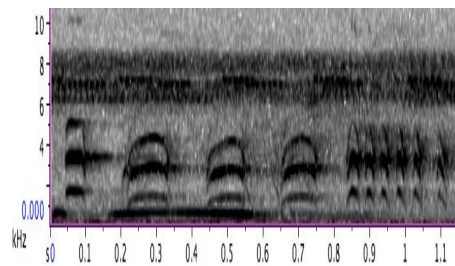
The song of *S. albigularis* consists of an introductory note followed by a trill of three to ten notes on a lower pitch (A, B). Variation in trill length does not have any geographic basis. All notes are similar in shape, resembling an inverted “U”. A series of rising notes (C) is given frequently as an immediate response to the song of another individual (D). Two song variants are known – a slow song (E), in which the trill is replaced by fewer, longer notes and followed by chatter; and an extended song (G), which is typically alternated with the normal song. Alarm/scolding calls include a stuttering series of low-pitched dry notes (F) and a long rattle (H).



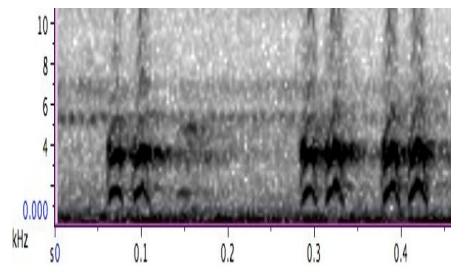




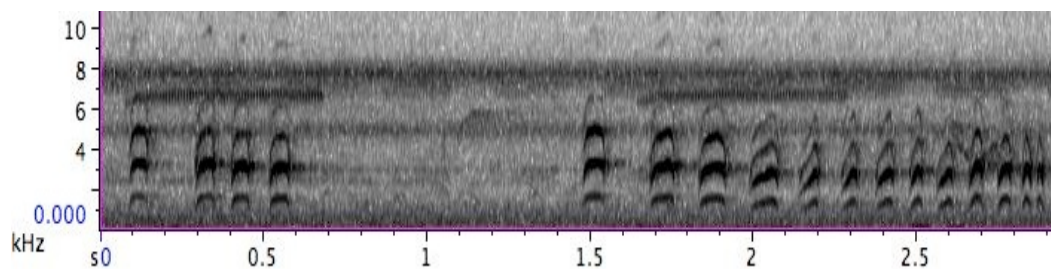
(D)



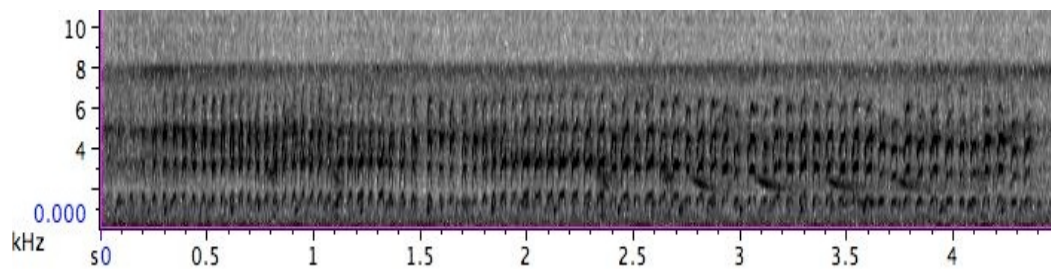
(E)



(F)



(G)



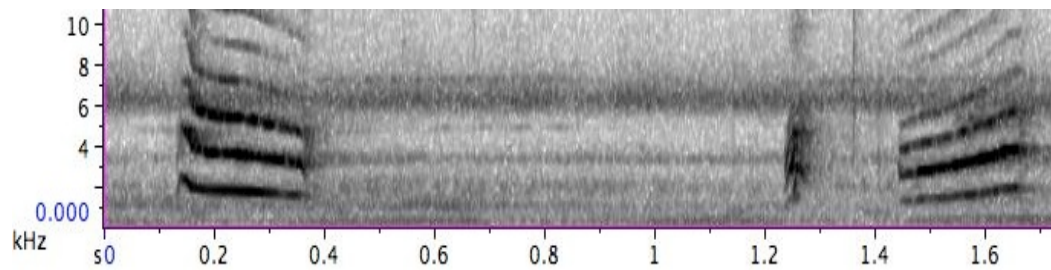
(H)

- A. Song of *S. a. albigularis*, Depto. Loreto, Peru. (M. L. Isler; MLNS 48417)
- B. Song of *S. a. albigularis*, Depto. Madre de Dios, Peru. (T. A. Parker III; MLNS 13639)
- C. Rising series of *S. a. albigularis*, Depto. Loreto, Peru. Given during response to playback. (T. A. Parker III; MLNS 29237)
- D. Rising series given in response to another bird's song, *S. a. subsp. nov.*, Depto. Huánuco, Peru. A preliminary note overlaps with the third note of the song. (V. L. Emanuel; MLNS 17857)

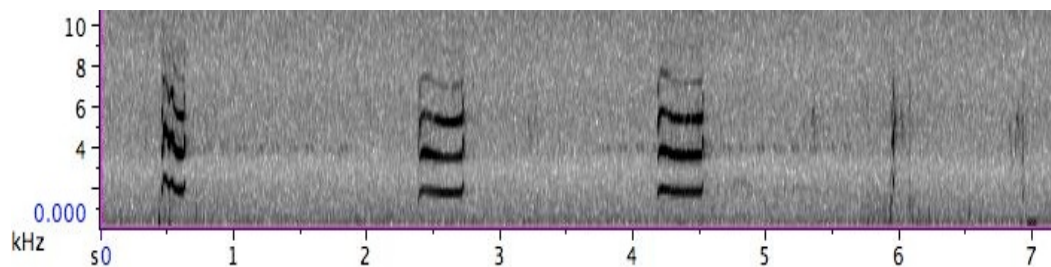
- E. Slow song of *S. a. albigularis*, Depto. Loreto, Peru. (T. A. Parker III; MLNS 29237)
- F. Alarm notes of *S. a. subsp. nov.*, Depto. Huánuco, Peru. These notes are given in an irregular, stuttering series with other vocalizations sometimes interspersed. (V. L. Emanuel; MLNS 17882)
- G. Extended song of *S. a. albigularis*, Depto. Cusco, Peru. The song is preceded by a normal song, with which it is alternated. The alternating pattern is typical of dawn singing in *Synallaxis*, but it is unknown whether this recording was made at dawn. (T. A. Parker III; MLNS 30061)
- H. Extended rattle of *S. a. albigularis*, Depto. Cusco, Peru. (T.A. Parker III; MLNS 30060)

### *Synallaxis albilora*

The song of *S. albilora* is a two-noted vocalization (A) very similar to the “southern” song of *S. gujanensis*. As in the song of that species, the second note of *albilora*’s song is preceded by a short, dry note (the “hiccup”). A long, querulous call note (B) is also given, often in an irregular series for minutes on end.



(A)

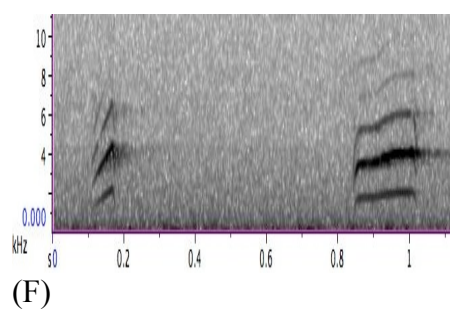
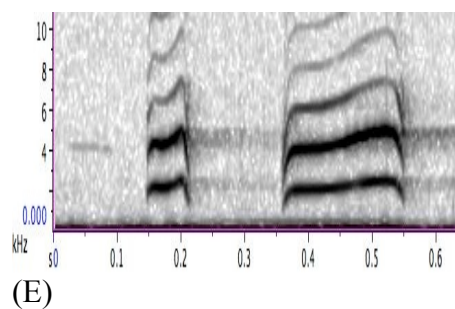
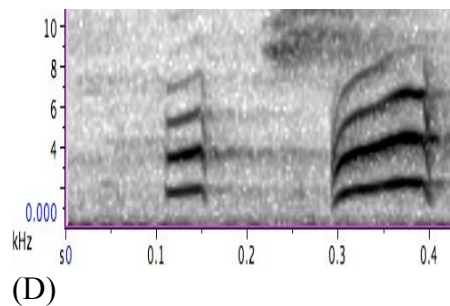
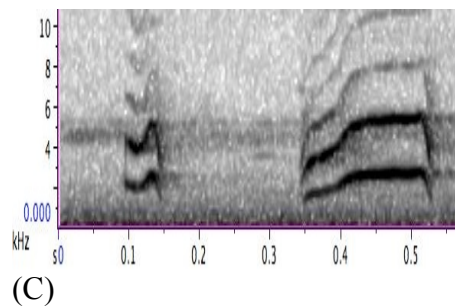
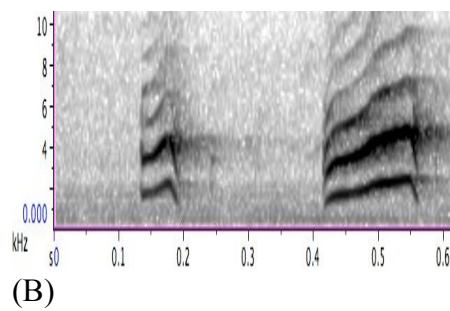
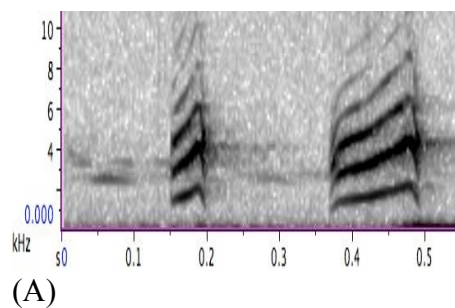


(B)

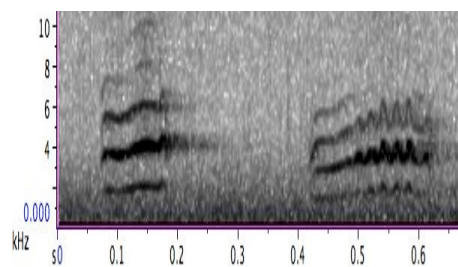
- A. Song of *S. albilora*, Edo. Mato Grosso, Brazil. (C. A. Marantz; MLNS 89169)
- B. Call notes of *S. albilora*, Depto. Santa Cruz, Bolivia. The sharp notes at ca. 6 and 7 sec. are given as the bird flies. This note is answered by other individuals, when present, suggesting that it functions primarily as a contact call. (D. F. Lane; from personal archives)

## *Synallaxis azarae*

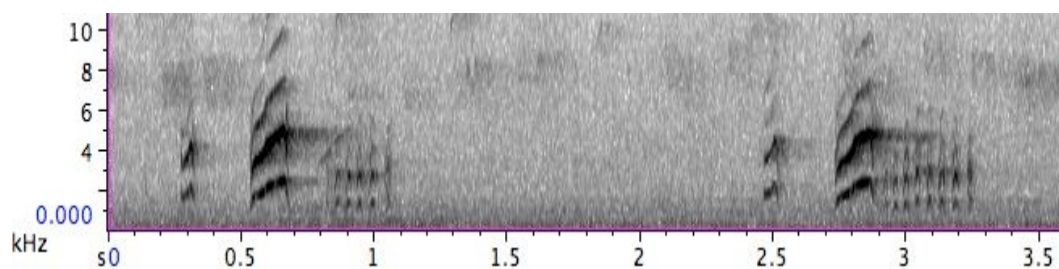
The song of *S. azarae* consists of two rising notes (A-E), the second longer and higher-pitched than the first, although frequency differences between notes are occasionally small. No alternate songs are known. Two variants are known from central Peru: the first (F), from near the type locality of *S. a. infumata* in the department of Huánuco, has a long interval between the first and second notes. In the second variant (G), from the Mantaro Valley in the department of Junín, the second note is lower-pitched than the first and is strongly modulated, with a purring quality. One member of a pair often responds to the other's song with a chatter of variable length, consisting either of short notes (H,J) or longer ones (I). When excited, birds sometimes give a long series of rising notes (K). The scold note (L) has a dry quality and is given in an irregular series; it is sometimes doubled or trebled (M). A soft doubled note (N) is sometimes given; the behavioral context of this call is unclear. Two recordings of a juvenile bird include what may be a parental contact call (O) and a rudimentary song (P).



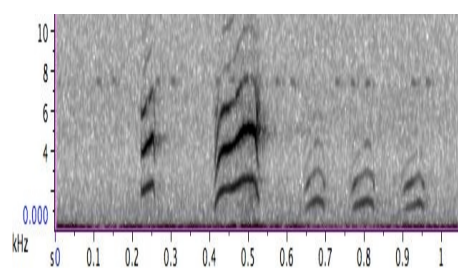




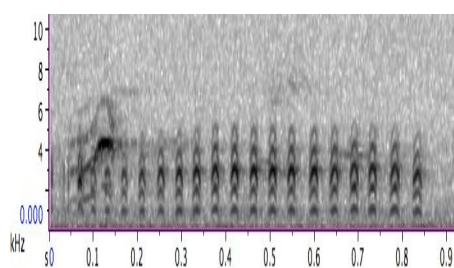
(G)



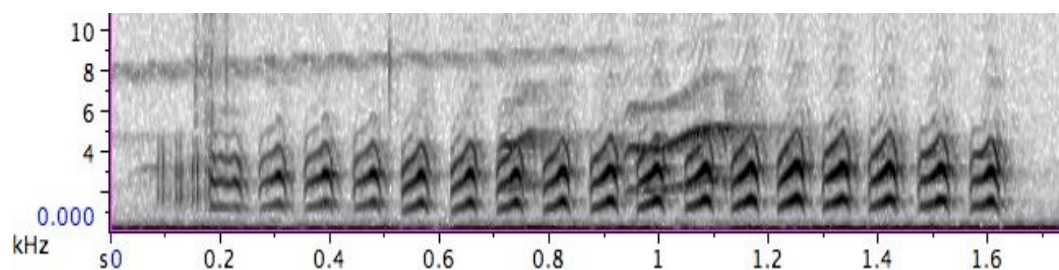
(H)



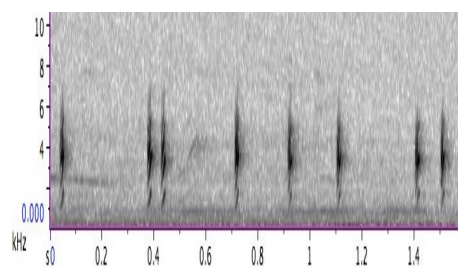
(I)



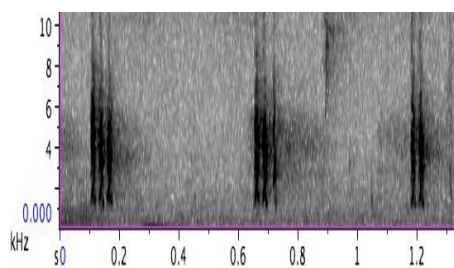
(J)



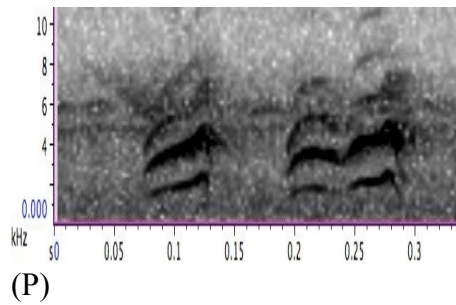
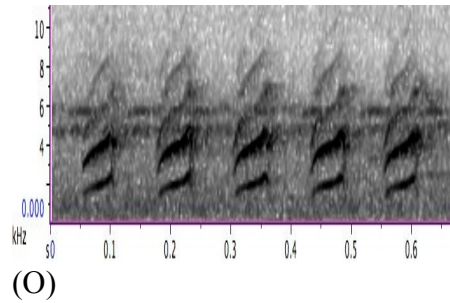
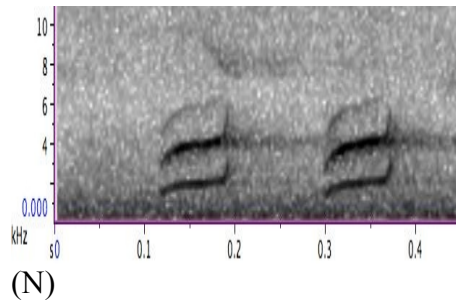
(K)



(L)



(M)

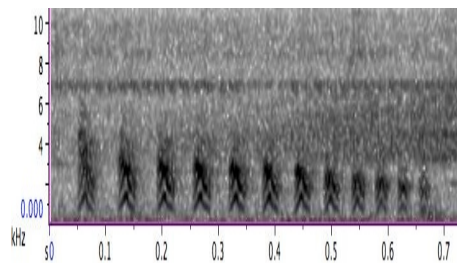


- A. Song of *S. a. elegantior*, Edo. Mérida, Venezuela. (P. A. Schwartz; MLNS 66112)
- B. Song of *S. a. media*, Prov. Pichincha, Ecuador. (D. L. Ross, Jr.; MLNS 84072)
- C. Song of *S. a. ochracea*, Prov. El Oro, Ecuador. (P. A. Hosner; MLNS 129483)
- D. Song of *S. a. azarae*, Depto. La Paz, Bolivia. (P. A. Hosner; MLNS 132713)
- E. Song of *S. a. superciliosa*, Prov. Jujuy, Argentina. (M. J. Andersen; MLNS 129336)
- F. Song variant featuring long interval between notes, from near type locality of *S. a. infumata*, Depto. Huánuco, Peru. (A. B. Van den Berg; MLNS 28872)
- G. Song variant from Mantaro Valley, Depto. Junín, Peru. (D. F. Lane; from personal archives)
- H. Fast chatter given in response to song of mate, *S. a. media*, Prov. Pichincha, Ecuador. (G. F. Budney; MLNS 83891)
- I. Slower series in response to song of mate, *S. a. azarae*, Depto. La Paz, Bolivia. (A. B. Hennessey; MLNS 121724)
- J. Long chatter in response to song of mate, *S. a. elegantior*, Edo. Mérida, Venezuela. Only a portion of the mate's song is visible in the spectrograph. (P. A. Schwartz; MLNS 66111)
- K. Excited series given after tape playback, *S. a. superciliosa*, Prov. Jujuy, Argentina. This vocalization was accompanied by extended and vigorous singing by the pair; one song is visible in the background. (M. J. Andersen; MLNS 129300)

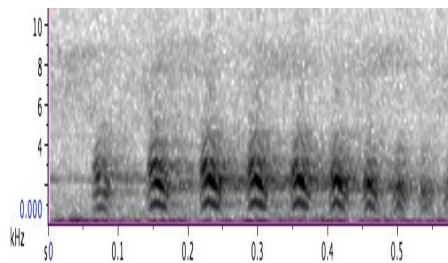
- L. Single scold notes, *S. a. elegantior*, Edo. Mérida, Venezuela. (P. A. Schwartz; MLNS 66111)
- M. Doubled and trebled scold notes, *S. azarae* (subspecies unknown), Prov. Loja, Ecuador. (L. R. Macaulay; MLNS 130408)
- N. Double note given after tape playback, *S. a. azarae*, Depto. Cochabamba, Bolivia. (D. F. Lane; from personal archives)
- O. Call given by juvenal-plumaged *S. a. ochracea*, Prov. El Oro, Ecuador. This call was given repeatedly. (P. K. Donahue; MLNS 55770)
- P. Rudimentary song given by same juvenile *S. a. ochracea*. This song was given several seconds after the call in (O) and is only given once in the recording. (MLNS 55770)

### *Synallaxis brachyura*

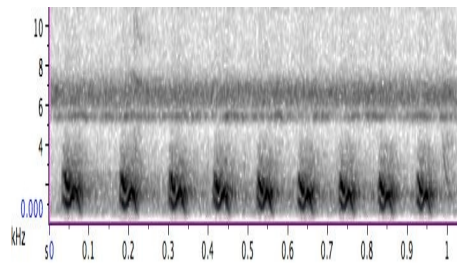
The song of *S. brachyura* is a low-pitched, hollow-sounding series of accelerating notes with a “bouncing-ball” pattern, very different from any other species in the genus (A, B). In most taxa, the notes resemble an inverted “V”, but in *S. b. caucaae*, the notes are S-shaped (C), rendering this population quite distinct vocally. Members of a pair counter-sing frequently. In response to playback, songs are usually shorter (B) and are given more rapidly. A different vocalization, which may be an alternate song, has been recorded in response to playback as well (D). The scold note is incisive and often doubled (E).



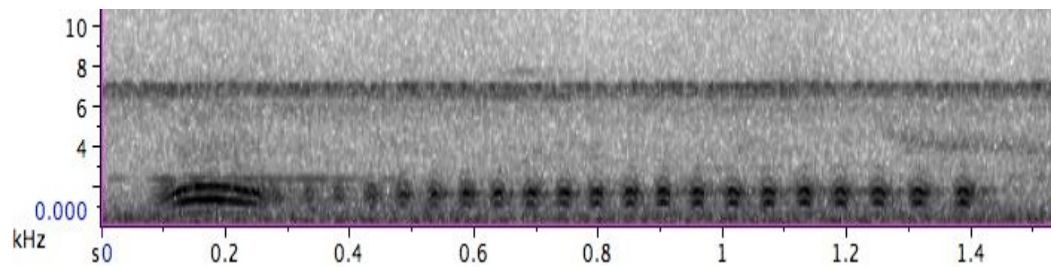
(A)



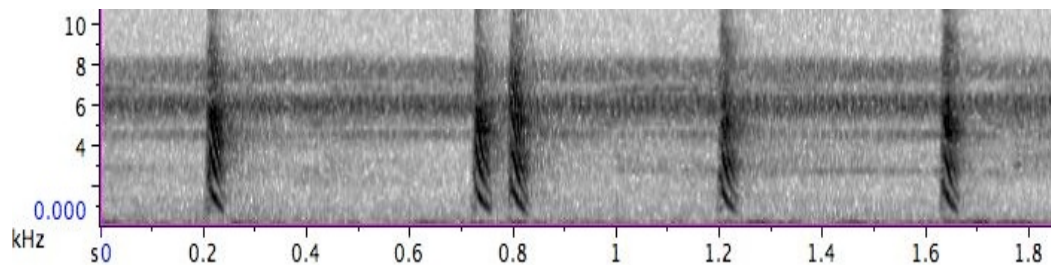
(B)



(C)



(D)



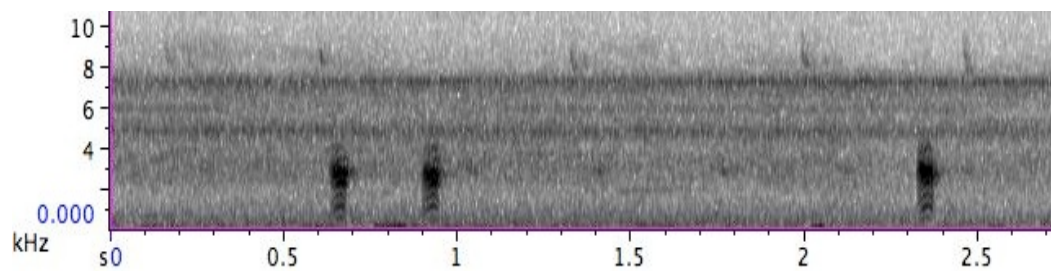
(E)

- A. Song of *S. b. nigrofumosa*, Prov. Heredia, Costa Rica. (A. B. Van den Berg; MLNS 28103)
- B. Short song after playback, *S. b. brachyura*, Depto. Cundinamarca, Colombia. (G. A. Bravo; from personal archives)
- C. Song of *S. b. caucae*, Depto. Valle del Cauca, Colombia. (M. Álvarez; BSA 12867)
- D. Possible alternate song, after playback, *S. b. brachyura*, Prov. Pichincha, Ecuador. (B. Spencer; MLNS 31345)
- E. Scold notes, *S. b. nigrofumosa*, Prov. Darién, Panama. (T. A. Parker III; MLNS 25696)

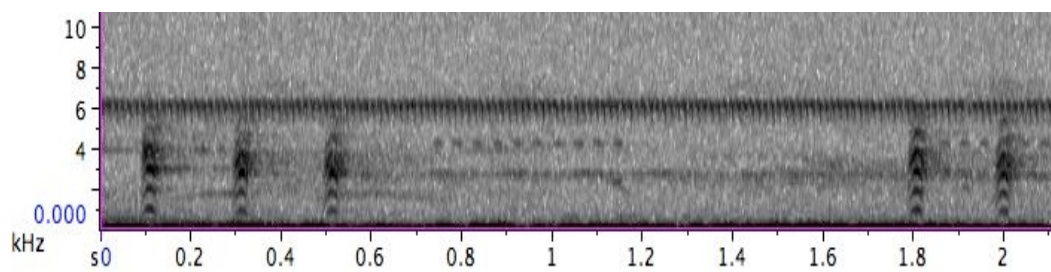
### *Synallaxis cabanisi*

There is little consensus regarding the true song of *S. cabanisi*. The most frequently recorded vocalization is a series of low-pitched notes, shaped like an inverted “U” and with strong harmonic structure, often doubled or trebled but given as an irregular series overall (A, B). In general, these notes are given more slowly by the nominate subspecies (A) than by *S. c. fulviventris* (B). Birds typically respond to playback with a more rapid series of these notes (C). A more complex vocalization is known from the population of nominate *cabanisi* in Mato Grosso, Brazil (D); this song consists of 2-4 short notes followed by a higher, emphatic note, and is superficially similar to the songs of *S. ruficapilla* and *S. macconnelli*. An alternate song (E) appears to be a jumbled rearrangement of the notes given by the Brazilian population. A short, rattling trill, falling then rising in pitch, has been recorded from a subadult bird (F).

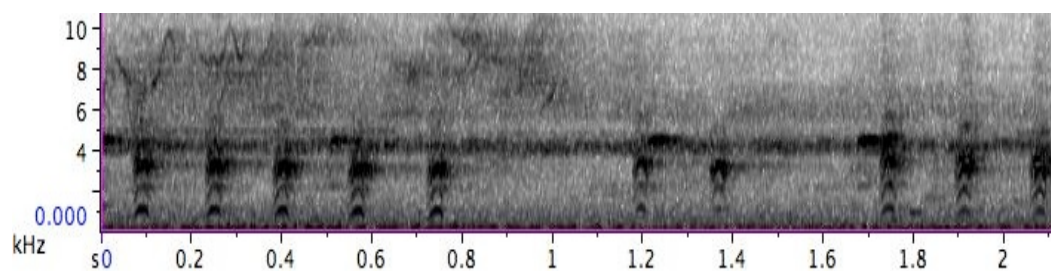




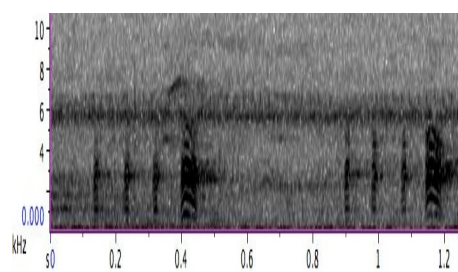
(A)



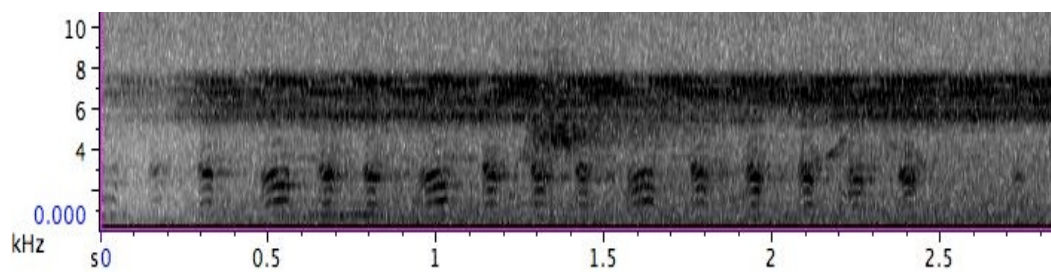
(B)



(C)

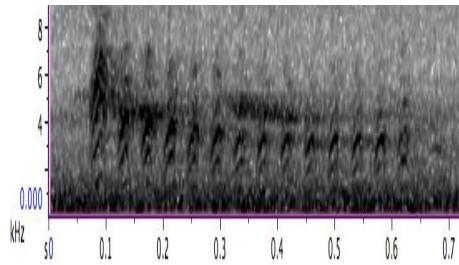


(D)



(E)



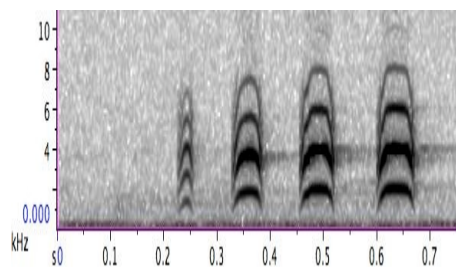


(F)

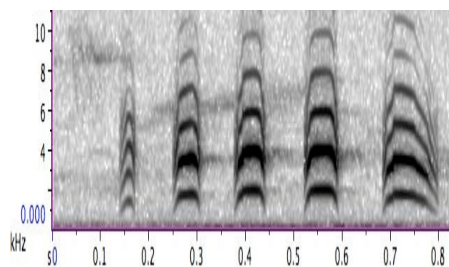
- A. Song of *S. c. cabanisi*, Depto. Cusco, Peru. (T. A. Parker III; MLNS 30053)
- B. Song of *S. c. fulviventris*, Depto. La Paz, Bolivia. (T. A. Parker III; MLNS 17136)
- C. Extended singing in response to playback, *S. c. fulviventris*, Depto. Cochabamba, Bolivia. (T. A. Parker III; MLNS 33692)
- D. 2 consecutive songs of *S. c. cabanisi*, Edo. Mato Grosso, Brazil. (T. A. Parker III; MLNS 52115)
- E. Alternate song, *S. c. cabanisi*, Depto. Cusco, Peru. (D. F. Lane; from personal archives)
- F. Rattle by subadult, *S. c. cabanisi*, Depto. Cusco, Peru. (D. F. Lane; from personal archives)

### *Synallaxis candei*

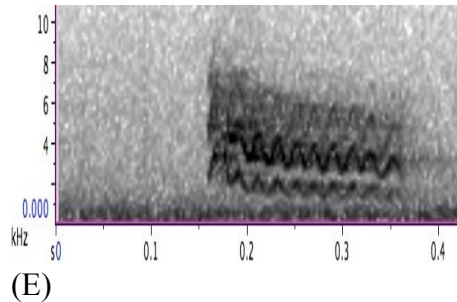
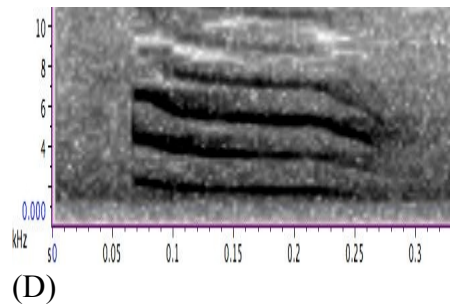
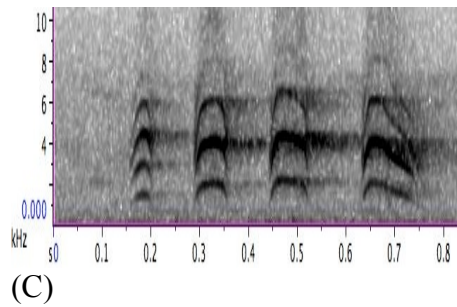
The song of *S. candei* is a piercing series of 3-5 notes (usually 4), the first shorter and lower-pitched than the rest (A-C). In most songs, each note is slightly longer than the preceding note. The song shows little geographic variation and no alternate songs are known. Occasionally birds add a lower-pitched final note to the series (B, C). Calls include a plaintive, descending note (D) and a burry descending note with strong modulation (E).



(A)



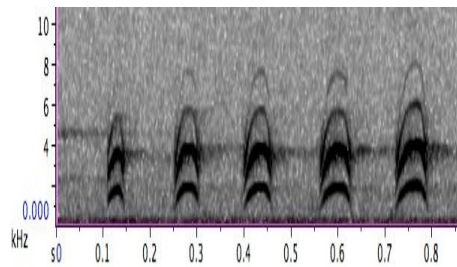
(B)



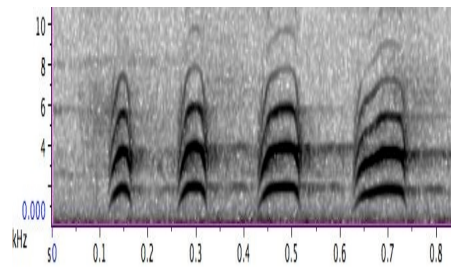
- A. Typical 4-note song, *S. c. venezuelensis*, Edo. Zulia, Venezuela. (P. A. Schwartz; MLNS 66168)
- B. Song with terminal note, *S. c. venezuelensis*, Edo. Zulia, Venezuela. P. A. Schwartz; MLNS 66168)
- C. Song with terminal note, *S. c. candei*, Depto. Bolívar, Colombia. (M. Álvarez; BSA 4602)
- D. Plaintive call note, *S. c. venezuelensis*, Edo. Falcón, Venezuela. (N. Athanas; XC 6867)
- E. Burry call note, *S. c. venezuelensis*, Edo. Falcón, Venezuela. (P. Coopmans; MLNS 40397)

### *Synallaxis castanea*

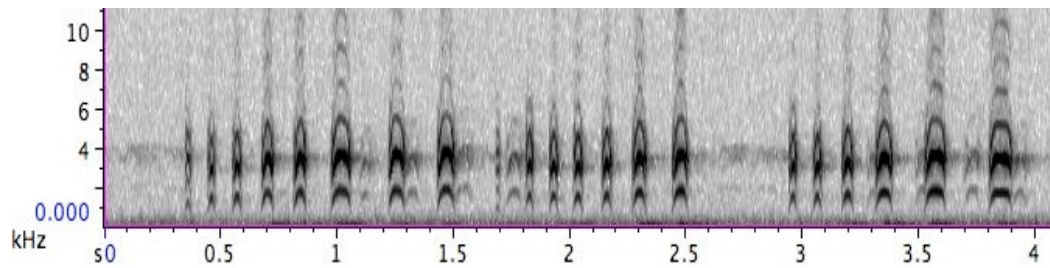
This species has several different song types. The most common songs consist of slightly rising series of 3-5 U-shaped notes that may sound clipped (A) or more drawn out (B). The pattern is similar to that of *S. candei*. In response to playback, singing becomes erratic and rapid (C). Song variants include a rising-then-falling series (D) and a more musical series of rising, modulated notes that apparently functions as a dawn song (E). Various sputtering notes and low trills (not pictured) have been recorded in the vicinity of the nest (P.A. Schwartz; MLNS 66151).



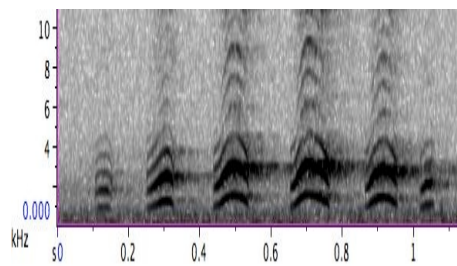
(A)



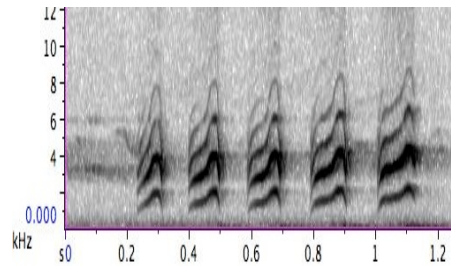
(B)



(C)



(D)



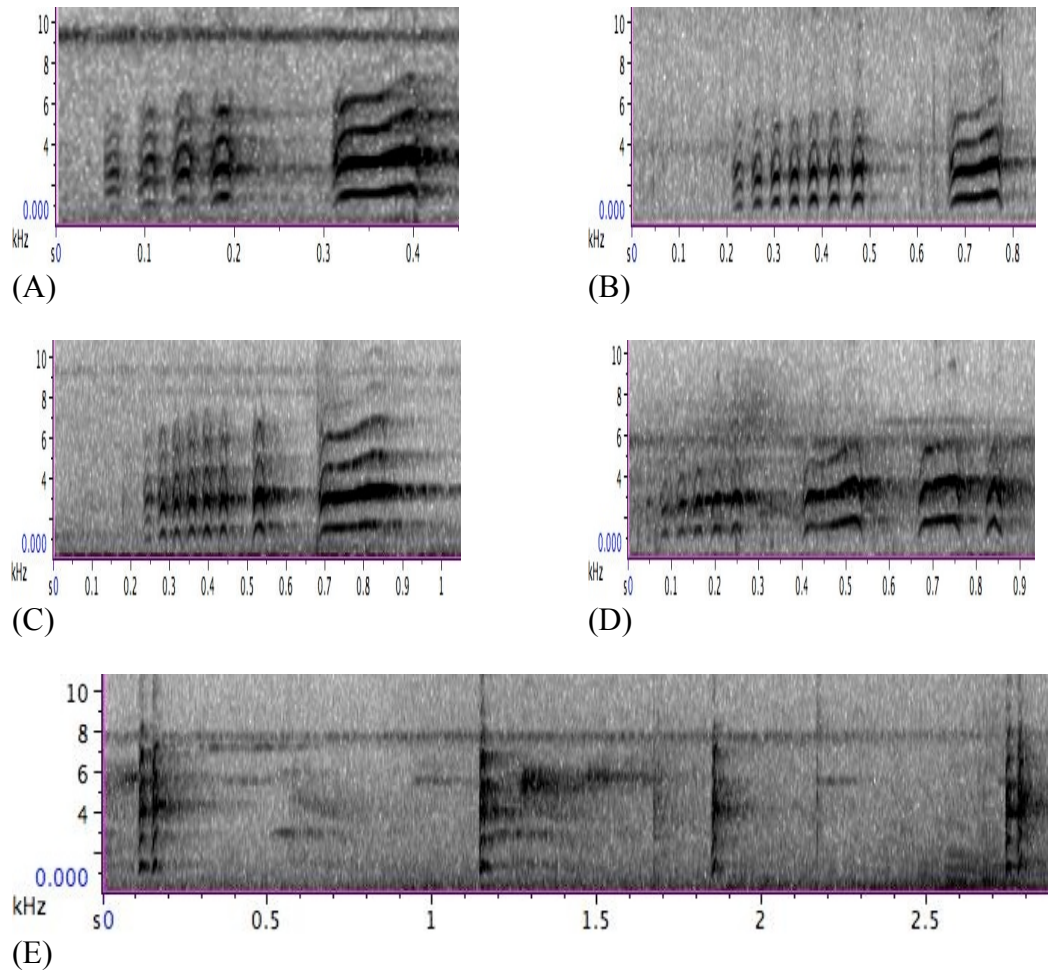
(E)

- A. Song of *S. castanea*, Dist. Federal, Venezuela. (P. A. Schwartz; MLNS 66143)
- B. Song of *S. castanea*, Edo. Aragua, Venezuela. (P. A. Schwartz; MLNS 66153)
- C. Extended singing by one bird in response to playback. The faint spectrograph traces between notes are from another individual in the background. (P. A. Schwartz; MLNS 66144)
- D. Alternate song. (M. L. Isler; MLNS 47836)
- E. Another alternate song, described as "dawn song" by the recordist. (P.A. Schwartz; MLNS 66145)

### *Synallaxis cherriei*

The song of *S. cherriei* is an ascending series of short notes followed by an emphatic, rising, long terminal note (A, B). The length of the song is variable, but there is no clear pattern of geographic variation. In response to playback, birds typically repeat the song at a rapid rate,

often for many minutes on end; songs after playback are similar to those given under natural conditions but tend to be shorter. A song variant (C) contains an extra note between the trill and terminal note, producing a hiccup-like effect. The dawn song (D) is interspersed with normal songs and given in rapid sequences. A call note is a sharp, dry “pit”, often doubled (E).



A. Short song, *S. c. cherriei*, Edo. Mato Grosso, Brazil. (C. A. Marantz; MLNS 88447)

B. Longer song, *S. c. saturata*, Depto. San Martín, Peru. (D. F. Lane; from personal archives)

C. Song featuring extra note between trill and terminal note, *S. c. cherriei*, Edo. Mato Grosso, Brazil. This song was interspersed with normal songs at irregular intervals during the singing bout. (B. M. Whitney; MLNS 108208)

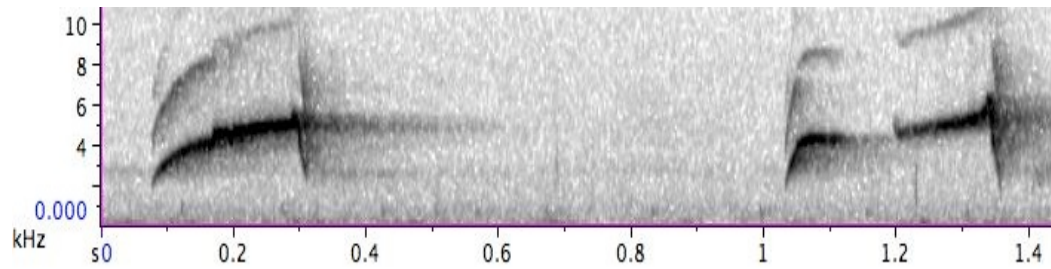
D. Dawn song, *S. c. cherriei*, Edo. Mato Grosso, Brazil. (T. A. Parker III; MLNS 52210)

E. “Pit” notes, *S. c. cherriei*, Edo. Mato Grosso, Brazil. (D. Michael; MLNS 106147)

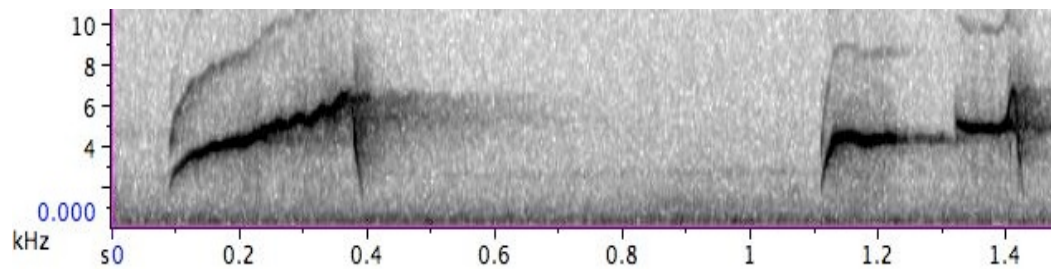


## *Synallaxis cinerascens*

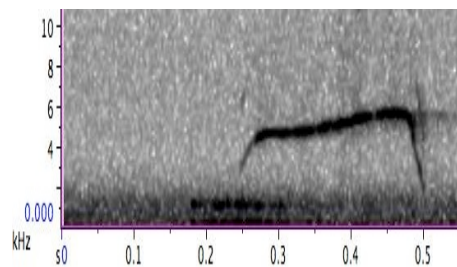
The song of *S. cinerascens* is a high-pitched, three-noted vocalization (A, B), similar in temporal pattern to the song of *S. albilora* and the southern populations of *S. gujanensis*, and in both pattern and quality to the song of *S. scutata*. Unlike any other species of *Synallaxis* except *S. scutata*, the song's energy is invariably concentrated in the fundamental frequency rather than on higher harmonic bands. The first note of the song is sometimes given as a call note (C), often interspersed among normal songs, but sometimes as a series of regularly spaced notes (E). A modulated note is given while foraging (D) and may serve as a contact call.



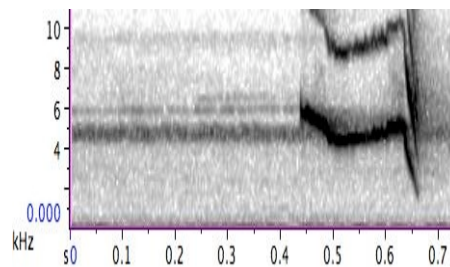
(A)



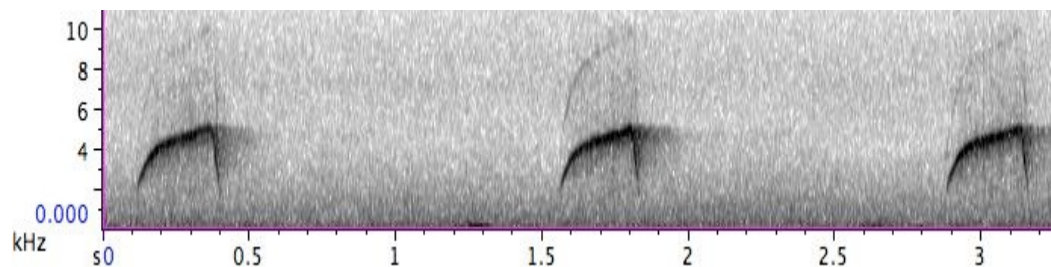
(B)



(C)



(D)



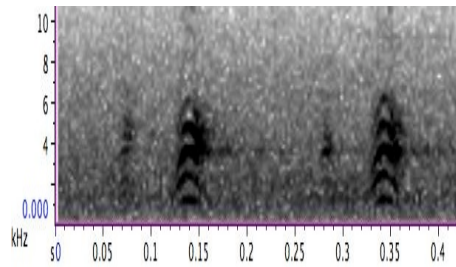
(E)

A. Song of *S. cinerascens*, Edo. Rio de Janeiro, Brazil. (T. A. Parker III; MLNS 39101)

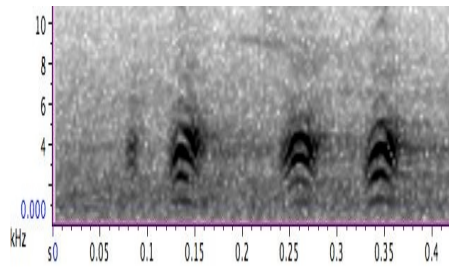
- B. Song of *S. cinerascens*, Prov. Misiones, Argentina. (D. W. Finch; MLNS 57863)
- C. First note of song, given as call note, Edo. Rio Grande do Sul, Brazil. (W. Belton; MLNS 19093)
- D. Call given while foraging, Prov. Misiones, Argentina. (M. J. Andersen; MLNS 132497)
- E. Call series, Edo. Minas Gerais, Brazil. This note is very similar to (C) in quality. (F. Lambert; XC 29489)

### *Synallaxis cinerea*

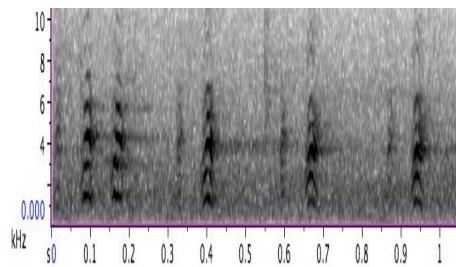
This is another species that does not appear to have a stereotyped song. Vocalizations are various arrangements of a U-shaped note with strong harmonic structure, rather similar to that of *S. cabanisi*. This note is usually preceded by a very short introductory note and is almost always doubled or trebled (A). The U-shaped note is sometimes given in a short series after one introductory note (B). The pattern of note delivery in (C) is common and has a distinctive cadence; it may be the song, although it is not given at regular intervals and is always interspersed among shorter phrases. A rattling call note has been recorded (D).



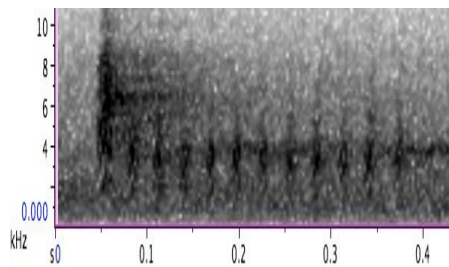
(A)



(B)



(C)



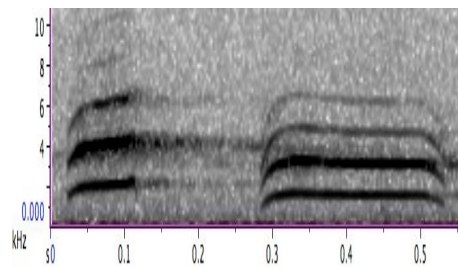
(D)

A-C. *S. cinerea*, samples from one singing bout, Edo. Bahía, Brazil. (B. M. Whitney; MLNS 103006)

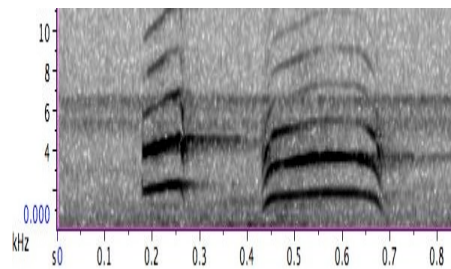
D. Dry rattle, showing emphasis on first note. (B. M. Whitney; MLNS 103007)

## *Synallaxis cinnamomea*

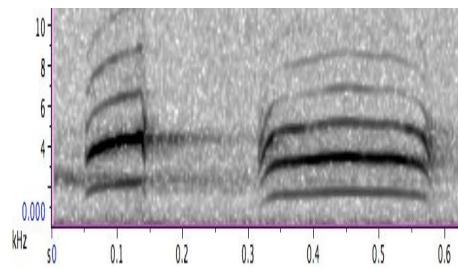
The song of *S. cinnamomea* is a plaintive, two-noted vocalization (A-E). The second note is always longer and lower-pitched than the first. In the eastern subspecies (*striatipectus*, *pariae*, *carri*, *terrestris*), the notes are longer and the second note is noticeably inflected (D, E). The call note, apparently given by all subspecies, is a querulous, descending note that sometimes features slight modulation (F). A short, buzzy rattle is also given when birds are agitated, typically as they fly from one perch to the next (F). A rapid series of ascending notes has been recorded from Tobago (G). The dawn song, when given, is interspersed among series of normal songs. Dawn songs may be short (H) or long (I).



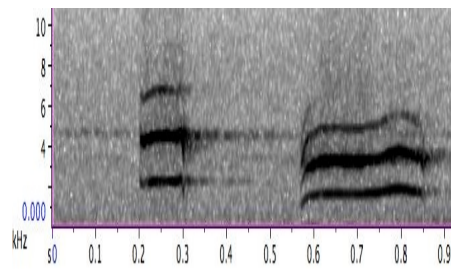
(A)



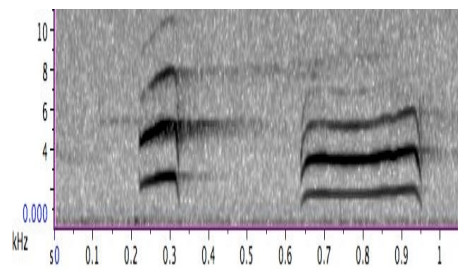
(B)



(C)

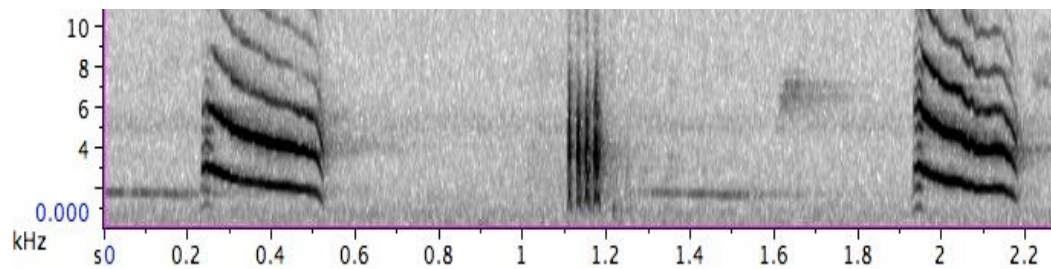


(D)

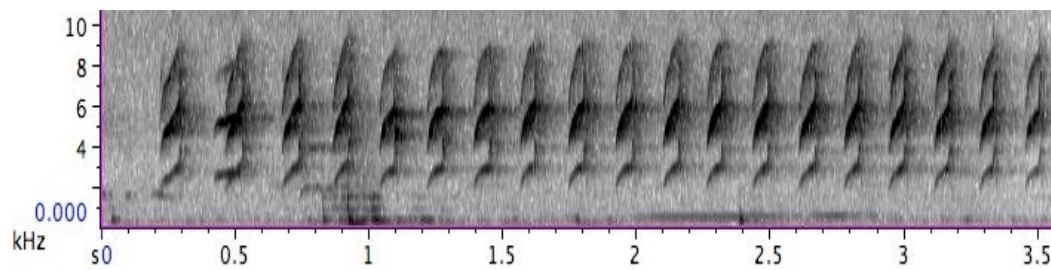


(E)

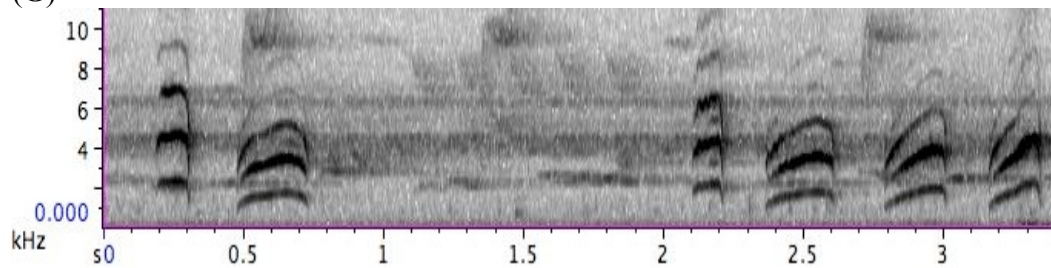




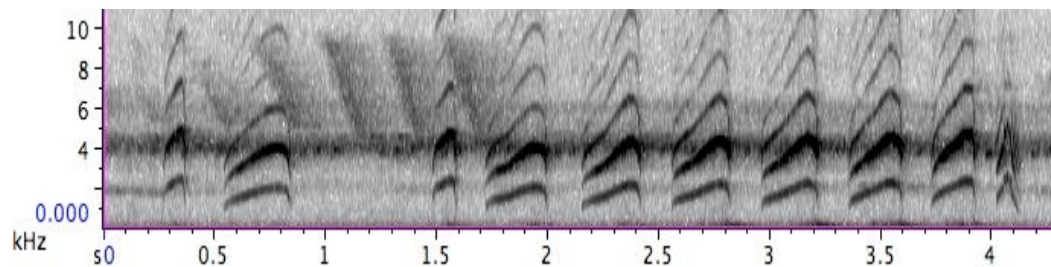
(F)



(G)



(H)



(I)

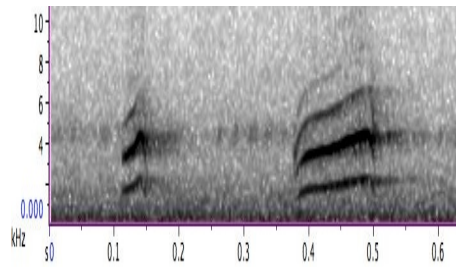
- A. Song of *S. c. cinnamomea*, Depto. Cundinamarca, Colombia. (G. A. Bravo; from personal archives)
- B. Song of *S. c. aveledoi*, Edo. Lara, Venezuela. (P. A. Schwartz; MLNS 66164)
- C. Song of *S. c. bolivari*, Dist. Federal, Venezuela. (P. A. Schwartz; MLNS 7037)
- D. Song of *S. c. pariae*, Edo. Sucre, Venezuela. (D. Edwards; XC 27926)
- E. Song of *S. c. terrestris*, Tobago. (R. Ward; MLNS 7040)



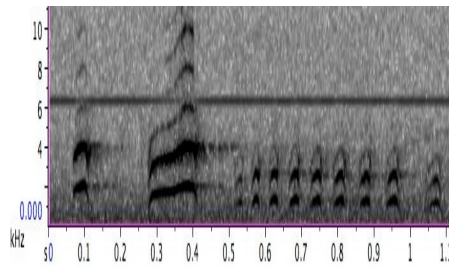
- F. Descending call note and short rattle in response to playback, *S. c. aveledoi*, Edo. Lara, Venezuela. (P. A. Schwartz; MLNS 66164)
- G. Excited call series, *S. c. terrestris*, Tobago. (R. Ward; MLNS 7040)
- H. Dawn song, short version, *S. c. bolivari*, Edo. Aragua, Venezuela. (P. A. Schwartz; MLNS 66160)
- I. Dawn song, longer version, *S. c. bolivari*, Edo. Aragua, Venezuela. (P. A. Schwartz; MLNS 66159)

### *Synallaxis courseni*

The song of *S. courseni* is indistinguishable from that of *S. azarae*, although it tends to be slightly shorter and higher-pitched than songs of parapatric *azarae* populations in southern Peru. Members of a pair often counter-sing, and one occasionally responds to the other with a rapid series of call notes (B), identical to that of *azarae* in structure and timing (See (H) under *S. azarae*). There are few recordings of *S. courseni*, but it is assumed that other call notes are similar if not identical to those of *S. azarae*.



(A)



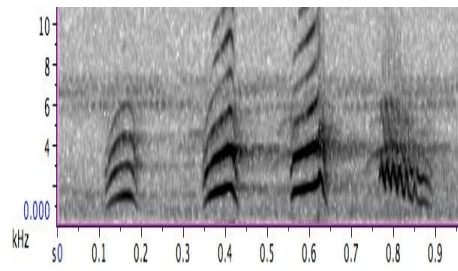
(B)

- A. Song of *S. courseni*, Depto. Apurímac, Peru. (A. M. Cuervo; from personal archives)
- B. Call series (after 0.5 s) in response to song of mate. (W. ten Have; XC 3769)

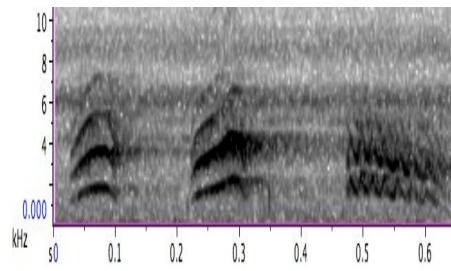
### *Synallaxis erythrothorax*

The song of this species consists of a rising series of 2-4 notes followed by a distinctive descending terminal note with extensive frequency modulation (A-D). The terminal note is occasionally omitted. The number of notes in a song varies individually, and birds typically sing songs with the same number of notes within a singing bout. When singing in pairs, one member usually sings a shorter song than the other. The Pacific slope taxon (*S. e. pacifica*) has more U-shaped introductory notes than does the nominate subspecies, and its song sounds more clipped as a result. An alternate song shows little frequency change in the modulated note, but a descending terminal note is added (E). An excited series of notes by a pair responding to playback has been recorded (F). This species has a dawn song that is superficially similar to the

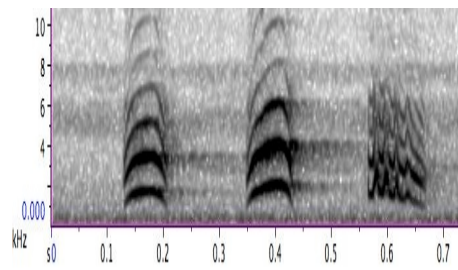
normal song, but the introductory series does not increase in frequency and two unmodulated descending notes replace the modulated terminal note (G).



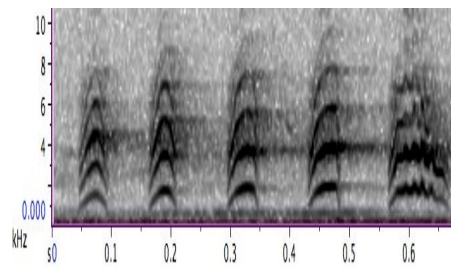
(A)



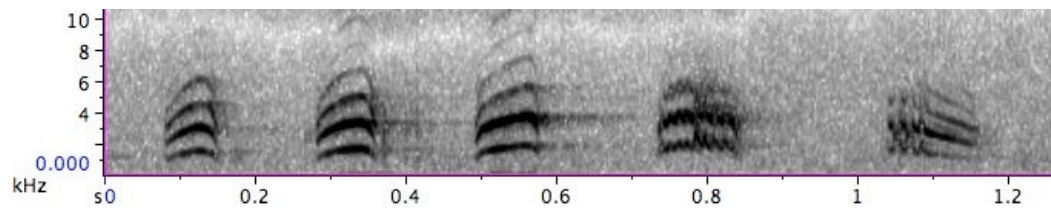
(B)



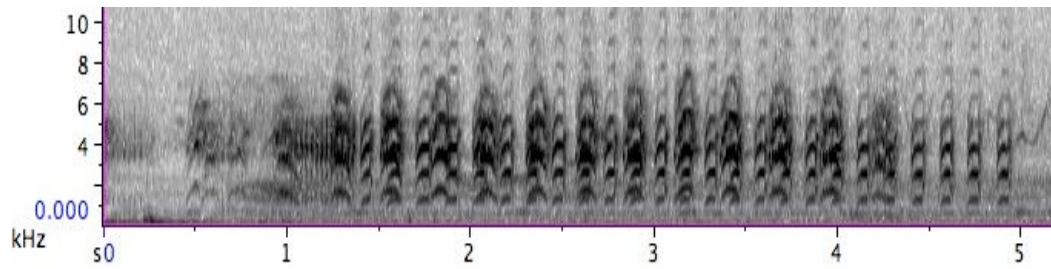
(C)



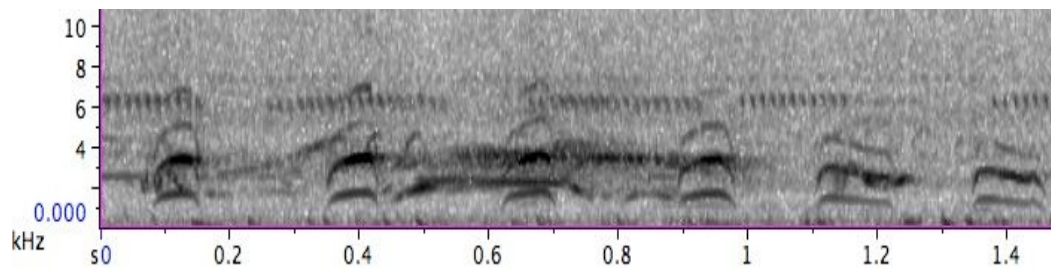
(D)



(E)



(F)



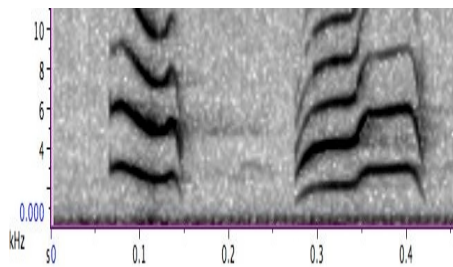
(G)

A. Song of *S. e. erythrothorax*, Edo. Veracruz, Mexico. (L. I. Davis; MLNS 7042)

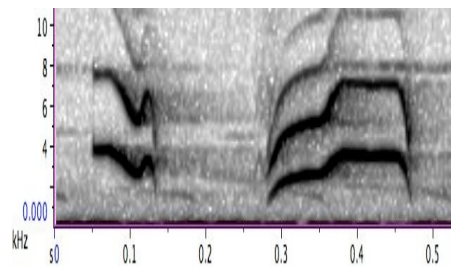
- B. Song of *S. e. erythrothorax*, Belize. (D. Delaney; MLNS 55416)
- C. Song of *S. e. pacifica*, Edo. Chiapas, Mexico. (C. A. Marantz; from archives of M. A. Patten)
- D. Song of *S. e. pacifica*, El Salvador. (W. A. Thurber; MLNS 20755)
- E. Alternate song, *S. e. erythrothorax*, Belize. (D. F. Lane; from personal archives)
- F. Excited calls from pair after playback, *S. e. pacifica*, El Salvador. One bird is producing the short, evenly spaced notes while the other gives a longer note at approximately half the rate. This series is preceded by low-pitched buzzing, visible as vertical bands in the spectrograph. (W. A. Thurber; MLNS 122)
- G. Dawn song, *S. e. erythrothorax*, Edo. Veracruz, Mexico. The song is partially obscured by background noise; it consists of four notes on one pitch followed by two descending notes. (L. I. Davis; MLNS 7044)

### *Synallaxis frontalis*

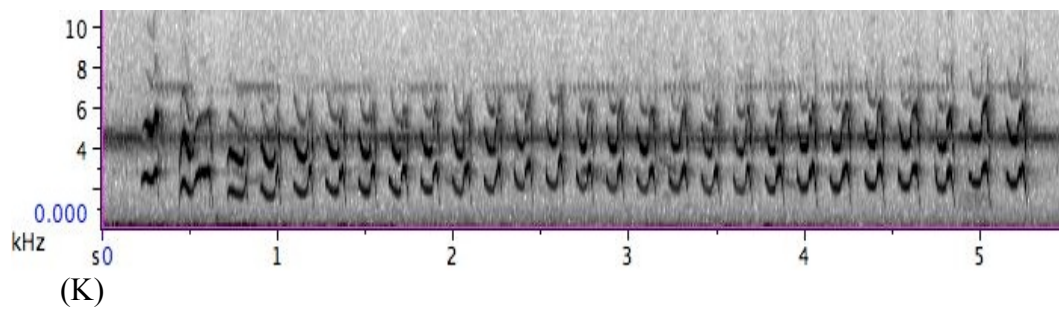
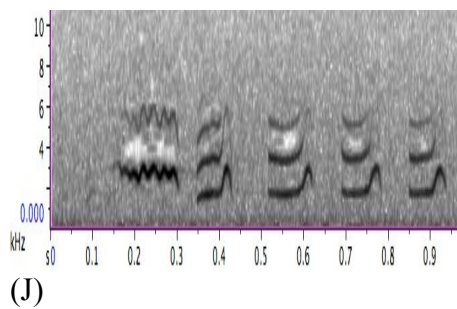
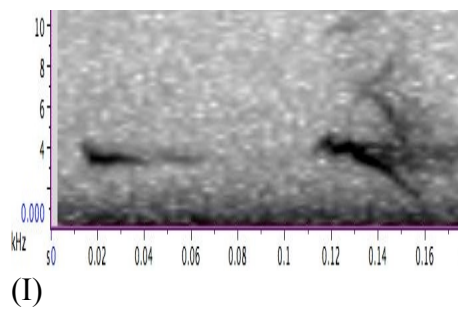
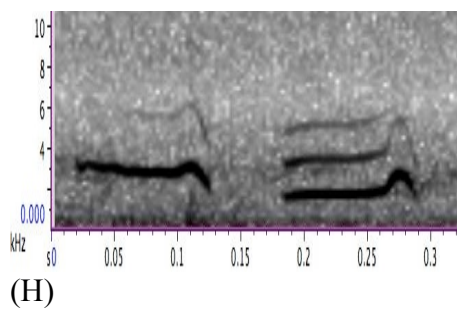
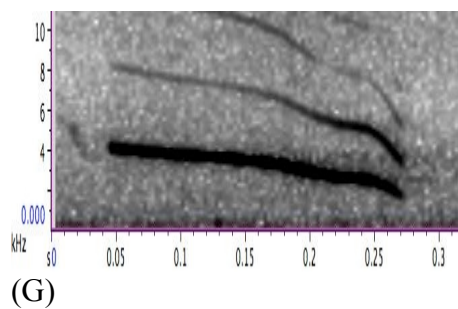
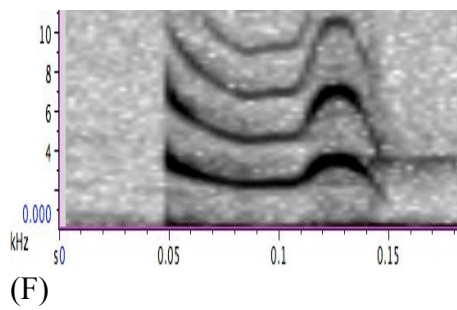
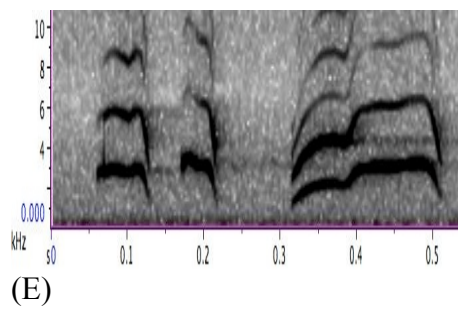
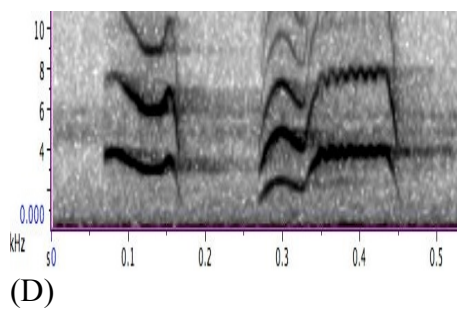
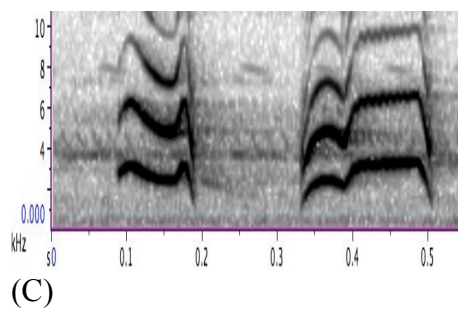
The song of *S. frontalis* is a two-noted vocalization consisting of a short descending note followed by a strongly upslurred, longer note (A-D). There is occasionally slight frequency modulation in the second note (C, D). A three-noted song variant (E) is uncommon; rarely, the second note is repeated once (not pictured). There is considerable individual variation, and therefore no discernable pattern of geographic variation in the song. *S. frontalis* has a rich repertoire of call notes and alternate vocalizations, all highly variable, and several of which may be used in rapid succession when birds are excited. The most common call is a slurred note (F), variants of which are often incorporated in more complex vocalizations (H, J, K). A piercing, descending note is also common (G). A soft “hiccupping” call may serve as a contact note at close range (I). Extended songs may incorporate repetition of either the slurred call note (K) or the second note of the normal song (J).



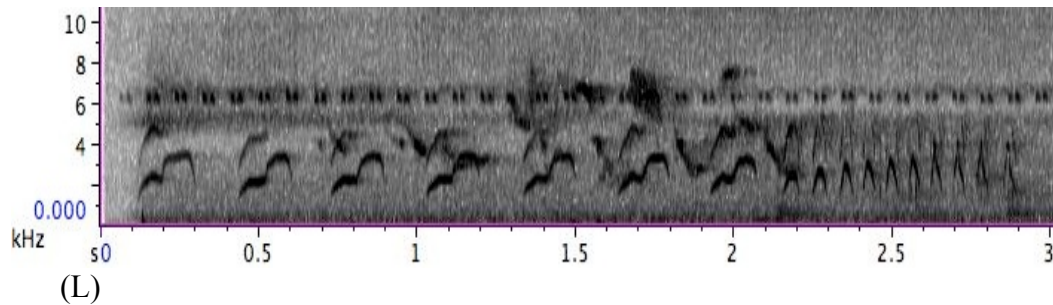
(A)



(B)





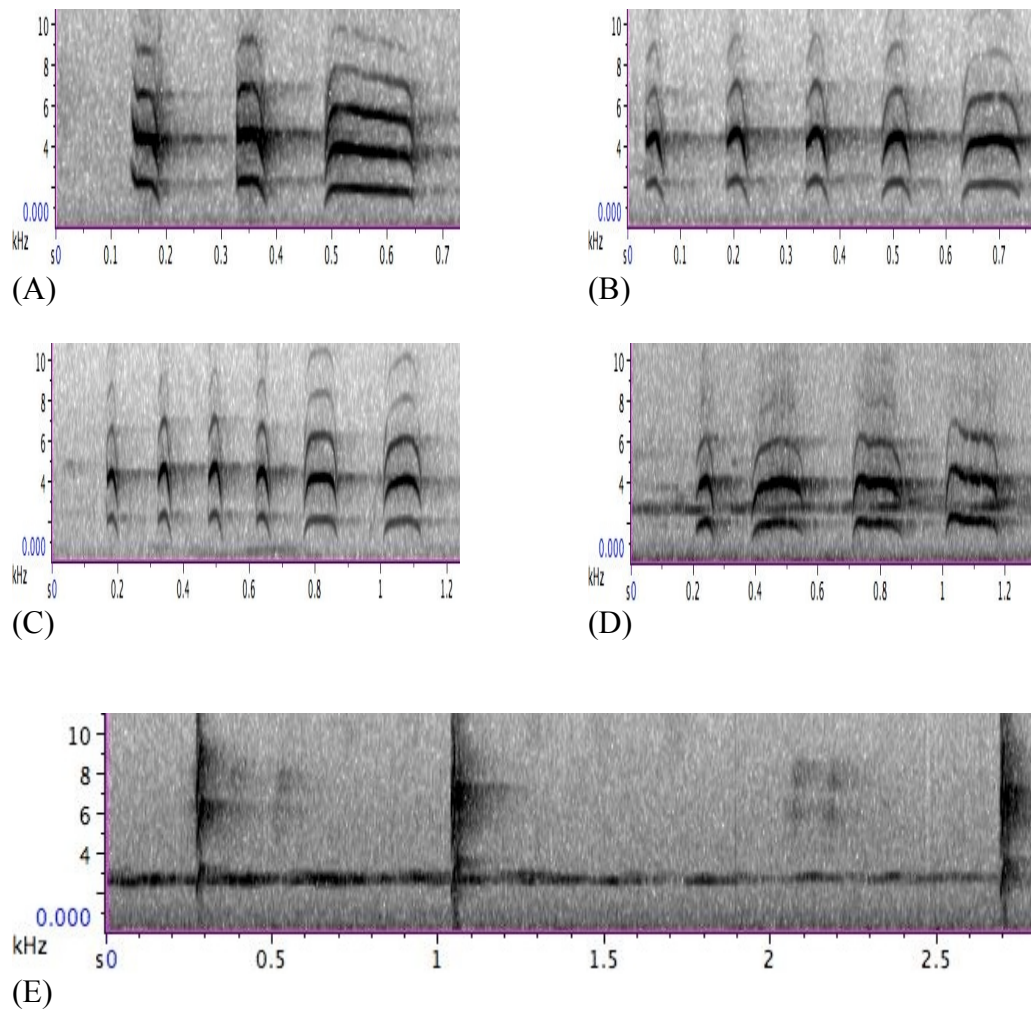


- A. Song of *S. frontalis*, Edo. Rio Grande do Sul, Brazil. (W. Belton; MLNS 19259)
- B. Song of *S. frontalis*, Prov. Jujuy, Argentina. (M. J. Andersen; MLNS 129754)
- C. Song of *S. frontalis*, Prov. Corrientes, Argentina. (P. A. Hosner; MLNS 132867)
- D. Song of *S. frontalis*, Depto. Alto Paraná, Paraguay. (K. Zyskowski; from personal archives)
- E. Song with doubled introductory note, Depto. Chuquisaca, Bolivia. (N. Krabbe; from personal archives)
- F. Slurred call note, Edo. Rio Grande do Sul, Brazil. (W. Belton; MLNS 19261)
- G. Descending call note, Depto. Chuquisaca, Bolivia. (N. Krabbe; from personal archives)
- H. Doubled call note, Depto. Chuquisaca, Bolivia. (N. Krabbe; from personal archives)
- I. Soft “hiccupping” call, Depto. Alto Paraguay, Paraguay. (K. Zyskowski; from personal archives)
- J. Soft modulated note followed by short slurred calls, Depto. Chuquisaca, Bolivia. (N. Krabbe; XC 16231)
- K. Long series of slurred calls following normal song, Edo. Bahía, Brazil. (T. A. Parker III; MLNS 35691)
- L. Unusual extended song, Prov. Jujuy, Argentina. The series of sharp U-shaped notes is part of the song. (N. Krabbe; from personal archives)

### *Synallaxis fusciorufa*

The song of *S. fusciorufa* consists of 2-4 incisive U-shaped notes followed by a longer note at a lower frequency (A, B). When members of a pair counter-sing, one bird usually has a shorter song than the other. Songs given after tape playback tend to be longer (up to 5 introductory notes) and may contain an extra terminal note (C). An alternate song consists of a short note

followed by a short series of longer notes, with a different quality than the normal song (D). Calls include a sharp “pit” repeated at irregular intervals (E).

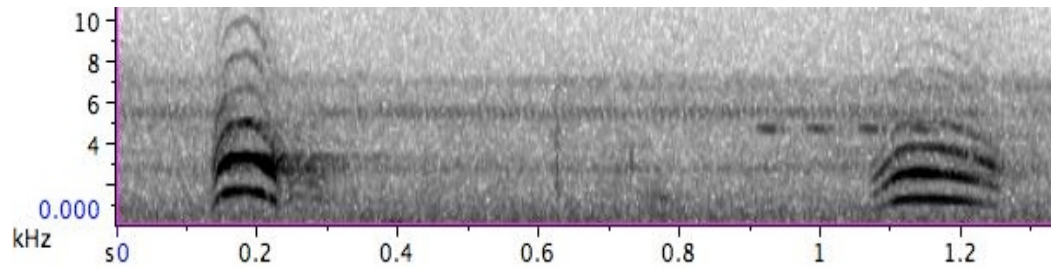


- A. Song of *S. fusciorufa*, Depto. Magdalena, Colombia. (P. Coopmans; MLNS 68024)
- B. Song of *S. fusciorufa*, Depto. Magdalena, Colombia. (P. Coopmans; MLNS 68032)
- C. Song after playback, with extra terminal note. (P. Coopmans; MLNS 68032)
- D. Alternate song. (R. Strewe; BSA 12352)
- E. “Pit” notes (with band of amphibian noise at ~2.5-3 kHz). (P. Coopmans; MLNS 68036)

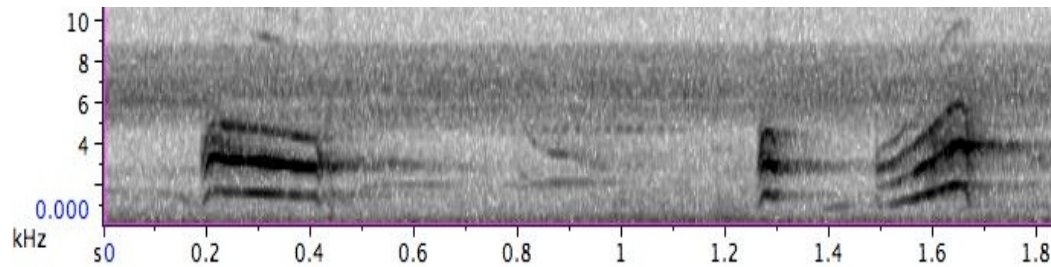
### *Synallaxis gujanensis*

The song of *S. gujanensis* has two distinct geographic types. North of the Amazon River, the song consists of two U-shaped notes separated by a long pause, the first note slightly higher-

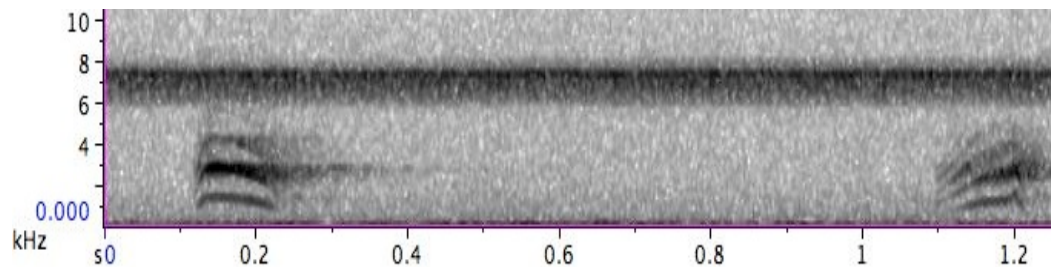
pitched than the second (A). The southern song type is very different and consists of a descending note, followed by a long pause, then a sharply ascending note that is preceded by a short “hiccup” note, producing a 3-note effect (B). The southern song type is very similar to the song of *S. albilora*. The location of the boundary between song types in Amazonian headwaters of Peru is unclear; recordings from Depto. Loreto are of the northern song type (including those from the S bank of the Amazon; see [E]), whereas those in Depto. San Martín sing the southern song type. Birds occasionally sing only the first note of a song. “Burry” variants of both song types have been recorded; these songs feature slight modulation of the first (southern type) or second (northern type) note (C, D). A variant of the northern song type, recorded on the S bank of the Amazon in Depto. Loreto, Peru, contains a short middle note and is thus similar to the southern song type in temporal pattern (E). The most common call note of southern populations is a querulous note of varying length and inflection (F, G); this call note is not known from northern populations. A rapid series of short, inflected notes is given when birds are excited (H). Alarm notes include a series of pulsed “chit” notes, given at irregular intervals (I). A short note, repeated at long intervals, has been recorded from northern birds, and may function as a foraging or contact call (J).



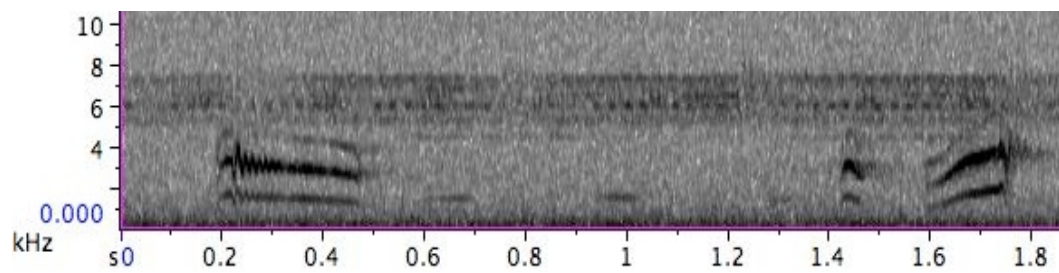
(A)



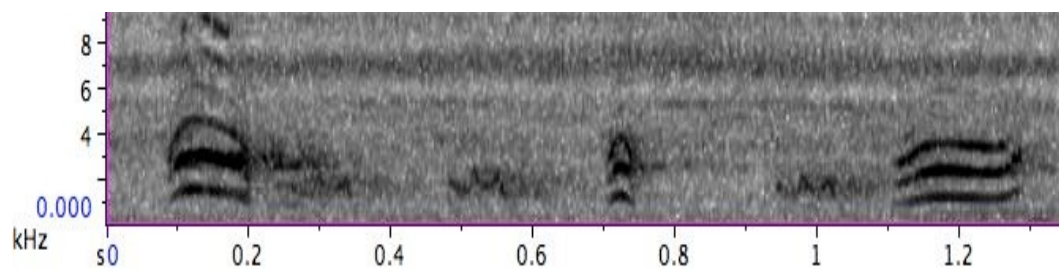
(B)



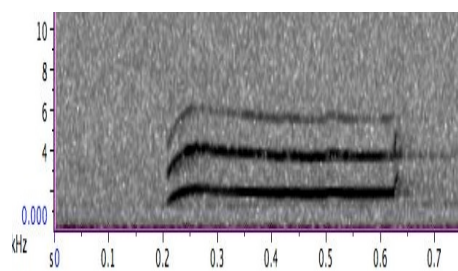
(C)



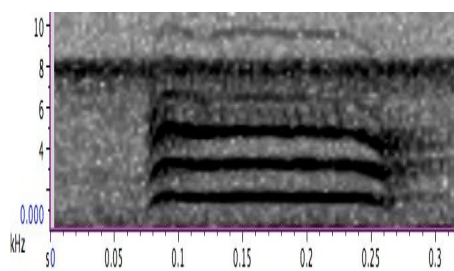
(D)



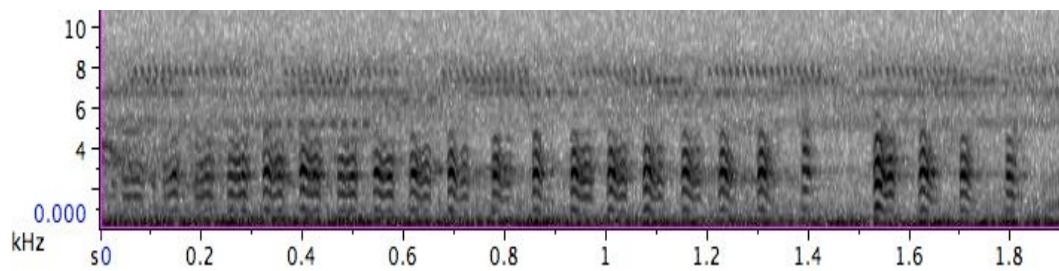
(E)



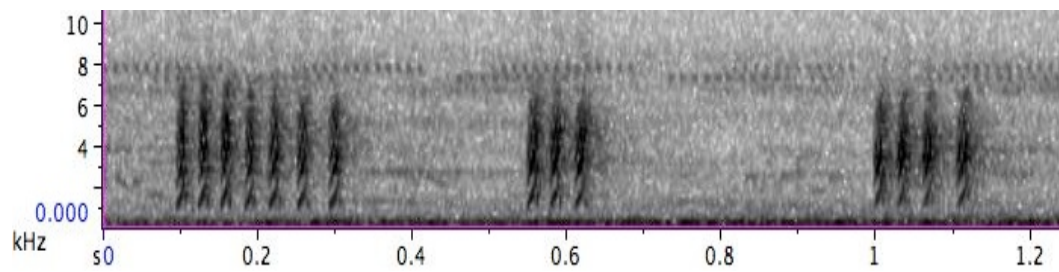
(F)



(G)

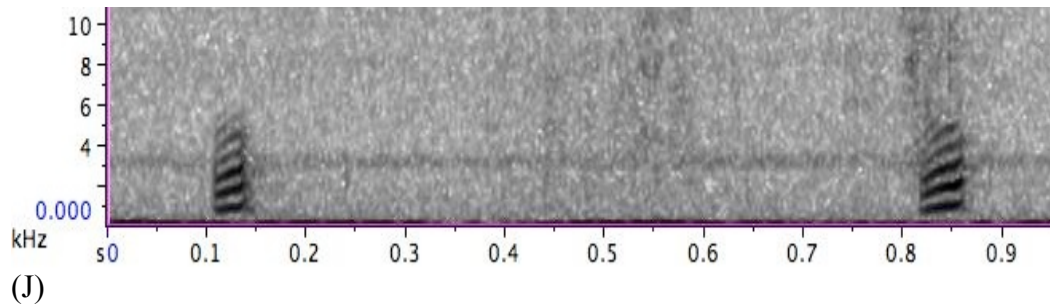


(H)



(I)

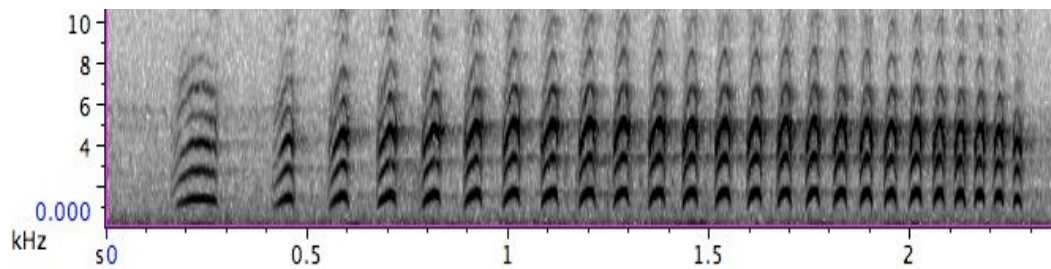




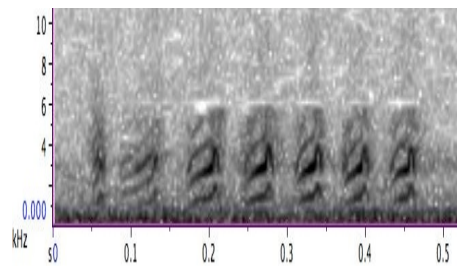
- A. Northern song type, *S. g. gujanensis*, Edo. Pará, Brazil. (T. A. Parker III; MLNS 35635)
- B. Southern song type, *S. g. inornata*, Depto. Beni, Bolivia. (T. A. Parker III; MLNS 51834)
- C. Northern song with modulated second note, *S. g. gujanensis*, Edo. Bolívar, Venezuela. (J. D. MacDonald; MLNS 44281)
- D. Southern song with modulated first note, *S. g. canipileus*, Depto. Madre de Dios, Peru. (T. A. Parker III; MLNS 17606)
- E. Northern song variant with middle note, *S. gujanensis* [subspecies unknown], Depto. Loreto, Peru. (F. Lambert; XC 12043)
- F. Long call note, *S. g. certhiola*, Depto. Santa Cruz, Bolivia. (T. A. Parker III; MLNS 52463)
- G. Short call note, *S. g. canipileus*, Depto. Pando, Bolivia. (T. A. Parker III; MLNS 38988)
- H. Excited call series, *S. g. inornata*, Depto. Beni, Bolivia. (T. A. Parker III; MLNS 51836)
- I. Alarm notes, *S. g. inornata*, Depto. Beni, Bolivia. (T. A. Parker III; MLNS 51836)
- J. Calls given while foraging, *S. g. gujanensis*, Suriname. (B. J. O'Shea; MLNS 134508)

### *Synallaxis hypospodia*

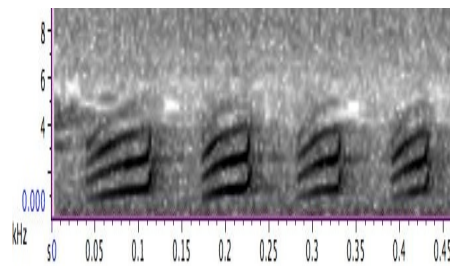
The song of *S. hypospodia* is a long, accelerating trill with a “bouncing ball” pattern (A). The first note is separated from the trill series by a distinct pause. There is some variation in length, but the song is similar throughout the species’ range. Calls include a series of short (B) or long (C) inflected notes, and a dry, descending rattle that is often given when birds are agitated (D).



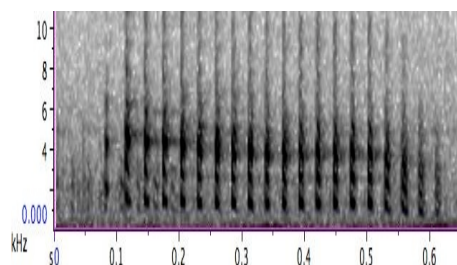
(A)



(B)



(C)

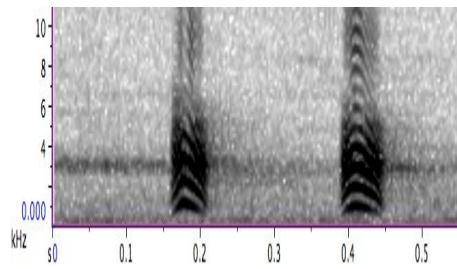


(D)

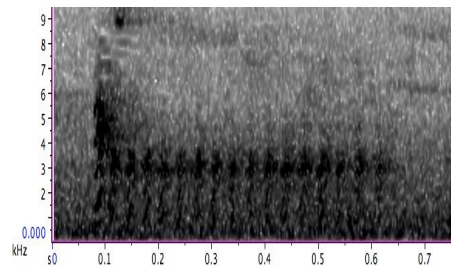
- A. Song of *S. hypospodia*, Edo. Mato Grosso, Brazil. (D. W. Finch; MLNS 52801)
- B. Series of short call notes, Depto. Santa Cruz, Bolivia. (S. Mayer; XC 2725)
- C. Series of longer call notes, Depto. Beni, Bolivia. (A. B. Hennessey; XC 3082)
- D. Dry rattle given after playback, Edo. Mato Grosso, Brazil. (D. W. Finch; MLNS 52801)

### *Synallaxis infuscata*

This species apparently does not have a true song. Most vocalizations consist of a U-shaped note with strong harmonic structure given at irregular intervals but often doubled (A). When the note is doubled, the second note is usually lower-pitched than the first. After playback, birds typically repeat this note incessantly, often for several minutes on end, at a rate of up to 6 notes/sec. A churring rattle has also been recorded (B).



(A)



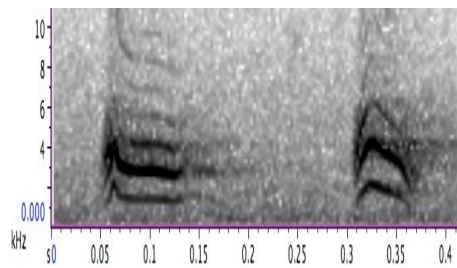
(B)

A. Typical doubled note of *S. infuscata*, Edo. Alagoas, Brazil. (C. A. Marantz; MLNS 127969)

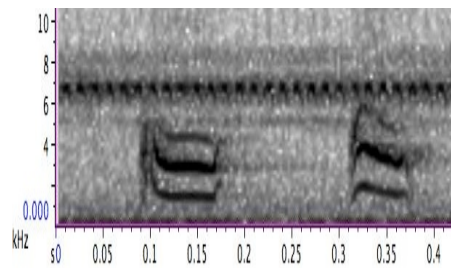
B. Rattle of *S. infuscata*, Edo. Pernambuco, Brazil. (G. A. Pereira; XC 5630)

### *Synallaxis kollari*

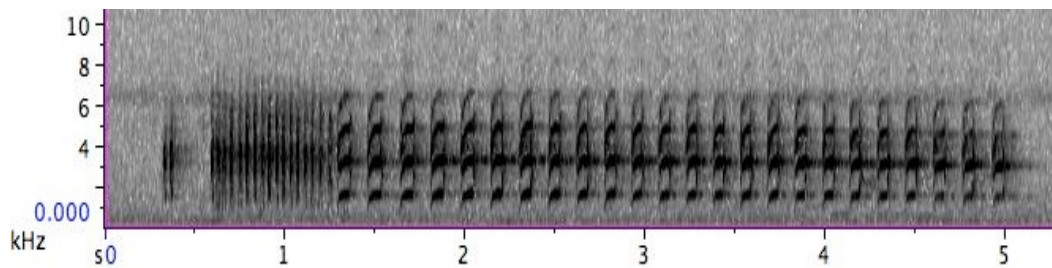
The song of *S. kollari* is a two-noted vocalization with an incisive quality; the second note is higher-pitched than the first (A, B). In response to playback, birds repeat this vocalization at a rapid rate. An extended series of notes is also given, sometimes preceded by a dry rattle (C). The function of this vocalization is unclear.



(A)



(B)



(C)

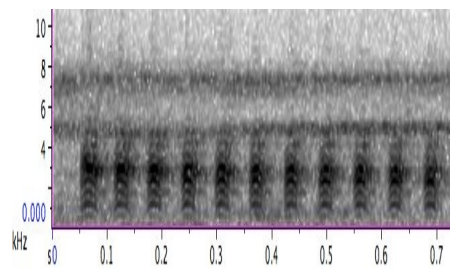
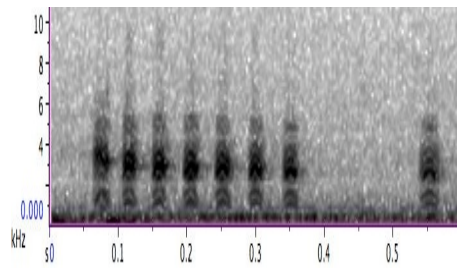
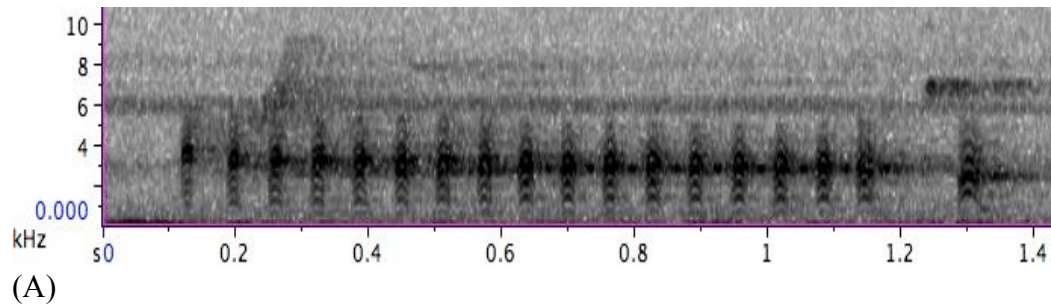
A. Song of *S. kollari*, Guyana. (D. W. Finch; MLNS 63927)

B. Song of *S. kollari*, Edo. Roraima, Brazil. (L. N. Naka; from personal archives)

C. Extended call series preceded by dry rattle. (D. W. Finch; MLNS 63925)

## *Synallaxis macconnelli*

This species is less vocal than many other species of *Synallaxis*. Its song is a rather nasal, rapid trill of evenly spaced notes that does not rise or fall in frequency but sometimes has a distinct terminal note. In the nominate subspecies, the terminal note is higher-pitched than the trill. In *S. m. obscurior*, the terminal note is lower-pitched than the trill and is frequently omitted altogether. The length of the trill is variable but tends to be longer after playback. No recordings of call notes are available.



A. Song of *S. m. macconnelli*, Edo. Bolívar, Venezuela. (T. A. Parker III; MLNS 30457)

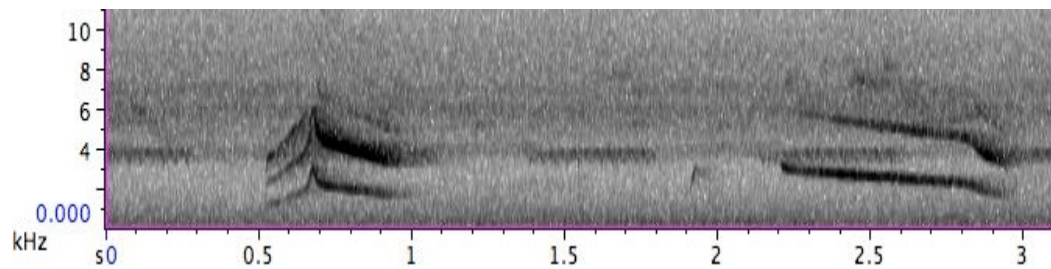
B. Song of *S. m. obscurior*, Suriname. (P. Trail; MLNS 21019)

C. Song of *S. m. obscurior* without terminal note, Suriname. (T. H. Davis; MLNS 25509)

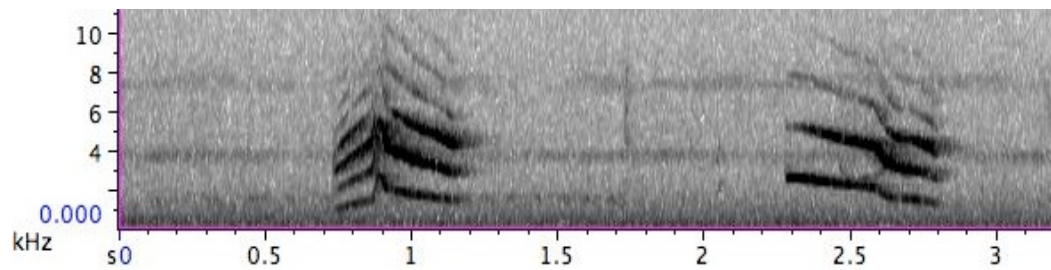
## *Synallaxis maranonica*

The song of *S. maranonica* is a two-noted vocalization with a long pause between the notes (A, B). The first note has an unusual peaked shape caused by an abrupt inflection in the middle of the note. The second note is high-pitched and descending, with a complaining quality. As in several other species of *Synallaxis*, a series of soft notes is sometimes given in response to a mate's song (C). A descending call note has been recorded; it is similar to the second note of the song (D).

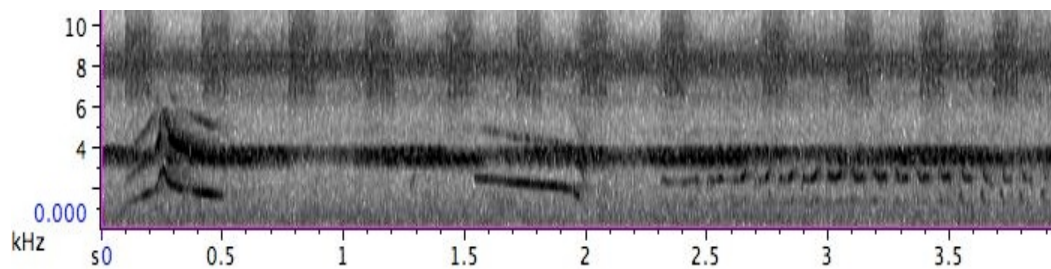




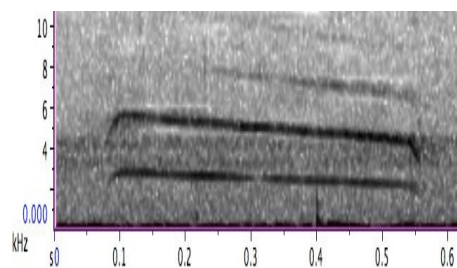
(A)



(B)



(C)

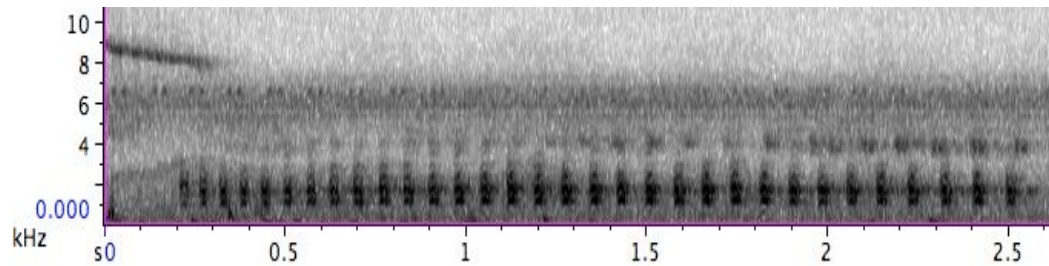


(D)

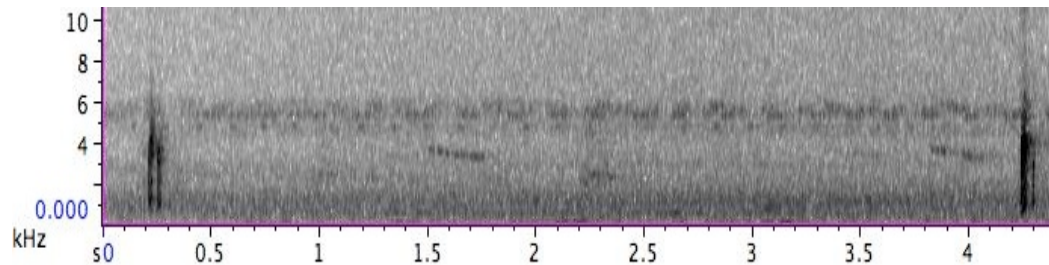
- A. Song of *S. maranonica*, Prov. Zamora-Chinchipe, Ecuador. (P. Coopmans; MLNS 68191)
- B. Song of *S. maranonica*, Prov. Zamora-Chinchipe, Ecuador. (P. Coopmans; MLNS 68281)
- C. Trill in response to mate's song. (P. Coopmans; MLNS 68275)
- D. Call note. (H. van Oosten; XC 8288)

## *Synallaxis moesta*

The song of *S. moesta* is a low-pitched series of short, evenly spaced notes without an introductory or terminal note (A). It is similar throughout the species' range. The length is variable, but songs tend to be longer (up to several sec) after playback. Members of a pair often overlap songs, especially when excited. Calls include a harsh, two-syllable note (B).



(A)



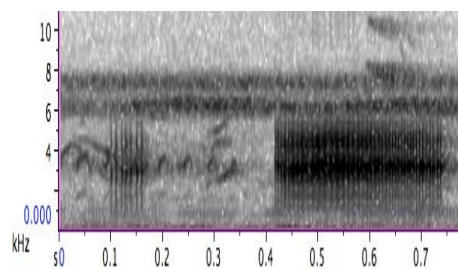
(B)

A. Song of *S. m. brunneicaudalis*, Prov. Napo, Ecuador. (M. Lysinger; from Moore et al. 2006)

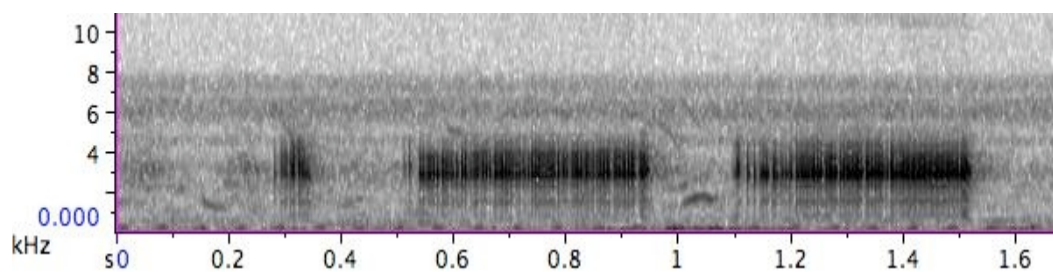
B. Call notes, *S. m. brunneicaudalis*, Depto. San Martín, Peru. (D. Edwards; XC 27708)

## *Synallaxis propinqua*

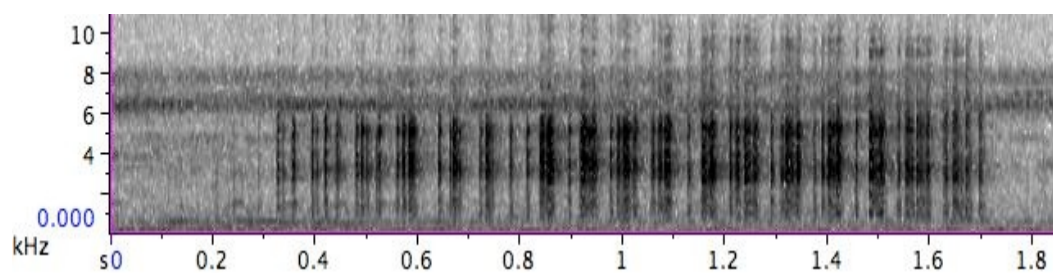
The singing behavior of *S. propinqua* differs from that of many other species of *Synallaxis*. Various vocalizations are given that sometimes culminate in a distinctive duet. Vocalizations are of two general types – a toneless, scraping sound (A-G, J), and a staccato chatter (E-J). Foraging birds give a toneless call with a scraping quality; it is often two-parted (A) but may be extended to three syllables (B). Alternatively, this call is given as a longer series in which the pulses of sound become gradually longer and more distinct (C, D). The scraping call forms the introduction to the duetting vocalization (E, F); in the duet, both birds give an accelerating and descending chatter, with one bird giving harsh notes while the other gives staccato notes (F). Excited birds may alternate harsh and staccato notes (G). Staccato notes are also given alone, sometimes in a slow series (H) but often accelerating into a rapid chatter (I). A harsh accelerating call with more tonality than the scraping call is also given (J). Call notes resemble notes in the staccato series (K).



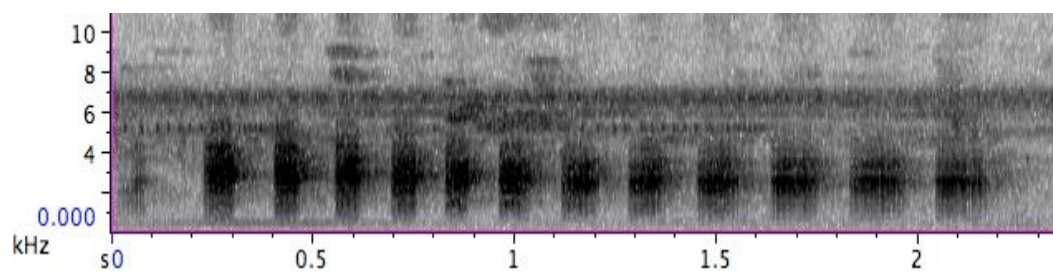
(A)



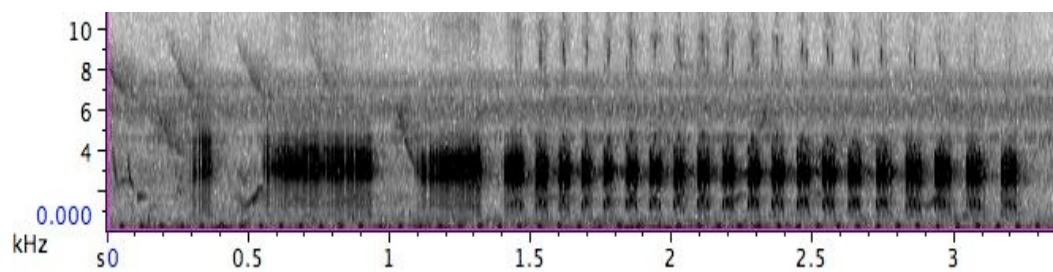
(B)



(C)

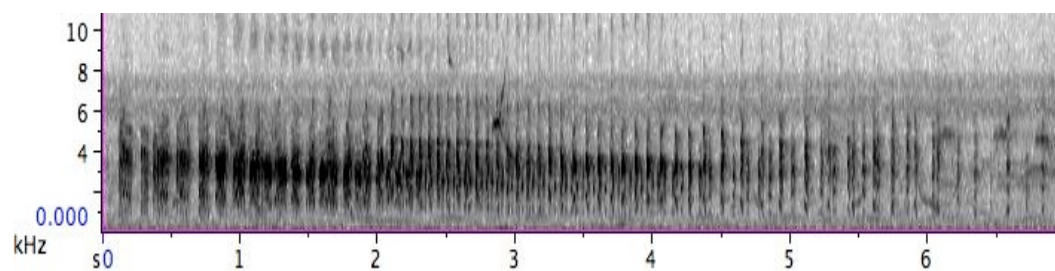


(D)

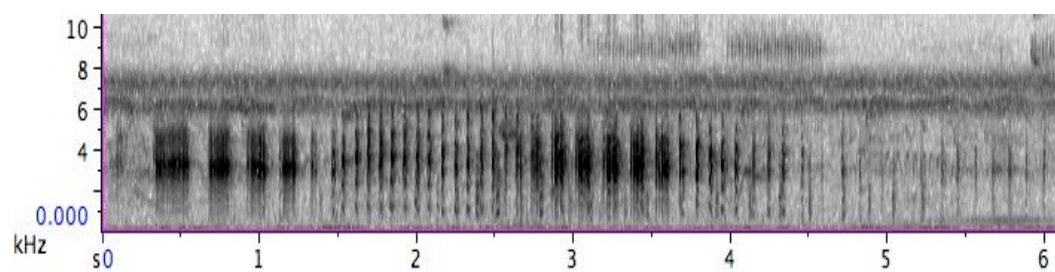


(E)

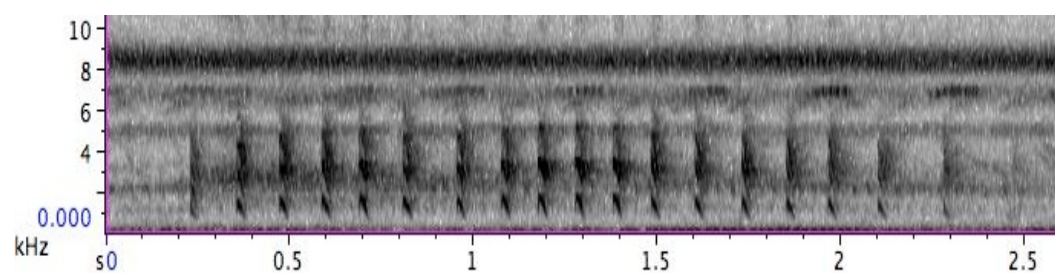




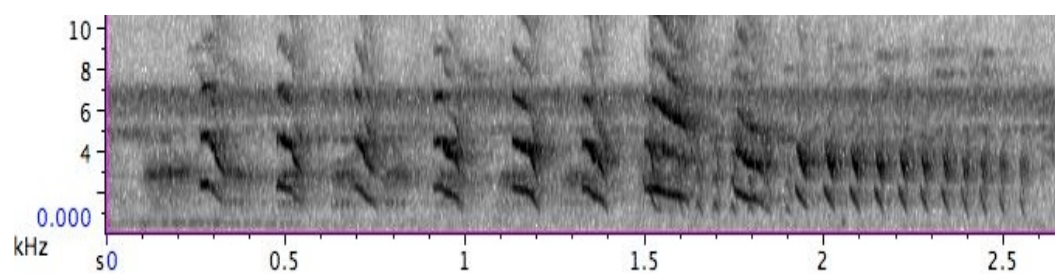
(F)



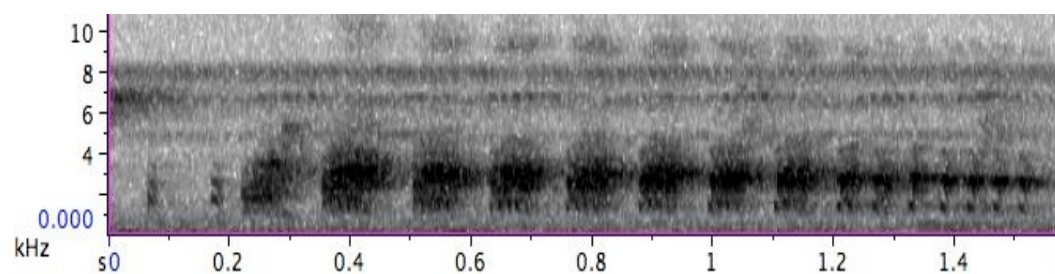
(G)



(H)

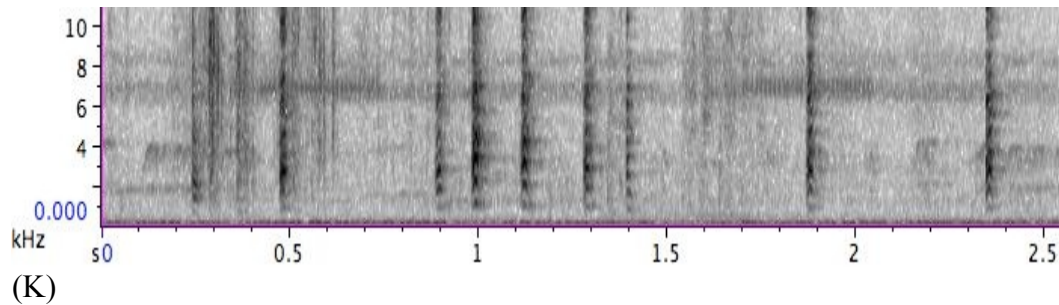


(I)



(J)



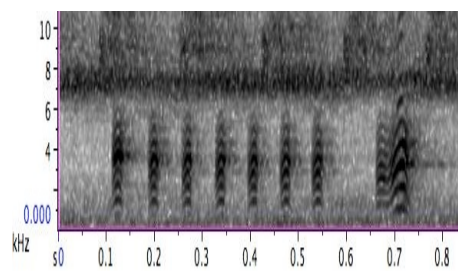


*Note: All recordings of S. propinqua presented here were recorded by T.A. Parker III, in Depto. Loreto, Peru.*

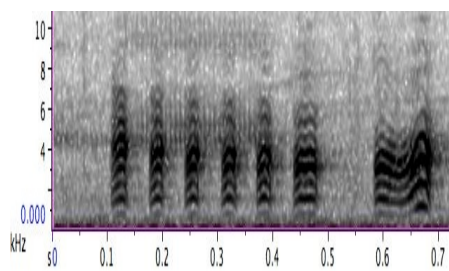
- A. Two-parted toneless call; MLNS 30749.
- B. Three-parted toneless call; MLNS 30745.
- C. Irregular toneless series showing gradual lengthening of sound pulses; MLNS 29233.
- D. Decelerating toneless series; MLNS 45940.
- E. Grating call transitioning to chatter. This is typically given by one pair member in a duet. MLNS 30745.
- F. Pair duet showing harsh and staccato note types; MLNS 30745.
- G. Grating calls with staccato notes interspersed; MLNS 30752.
- H. Slow series of staccato notes; MLNS 34288.
- I. Staccato notes merging into chatter; MLNS 45940.
- J. Harsh descending series; MLNS 29228.
- K. Call notes; MLNS 34279.

### *Synallaxis ruficapilla*

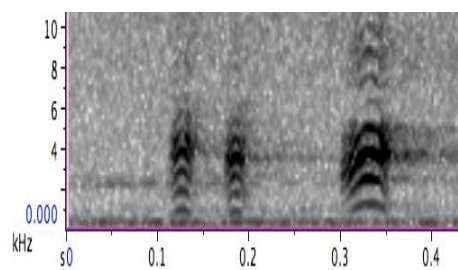
The song of *S. ruficapilla* is a rapid series of 4-7 (occasionally 2-3) U-shaped notes followed by an emphatic, higher-pitched terminal note, the shape of which is somewhat variable (A-C). Birds occasionally omit the terminal note and give a long series of short notes. In response to playback, birds sometimes repeat the song several times without pause (F) or sing an extended song (E). The most common call note is a dry rattle (D); other calls include a descending nasal note and an incisive doubled note (G).



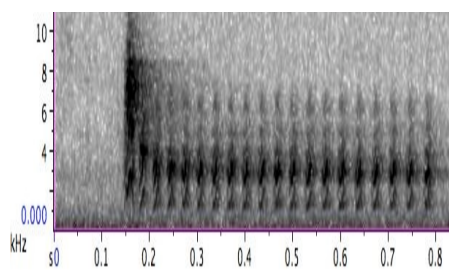
(A)



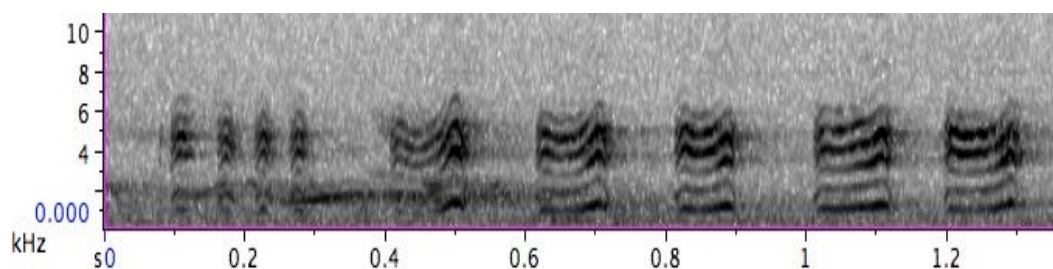
(B)



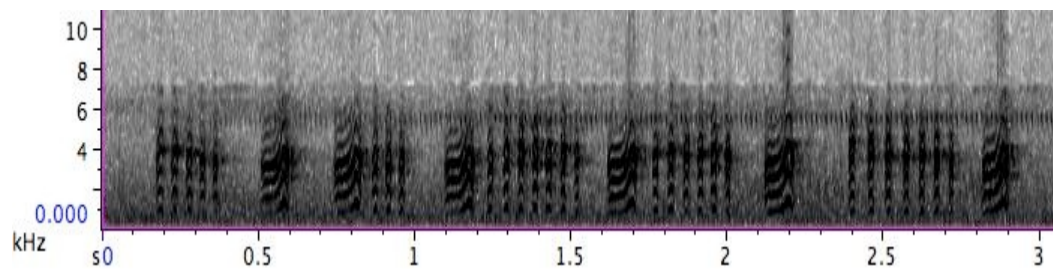
(C)



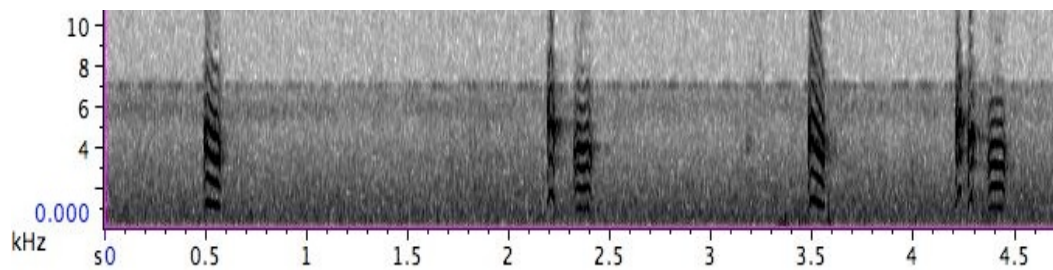
(D)



(E)



(F)



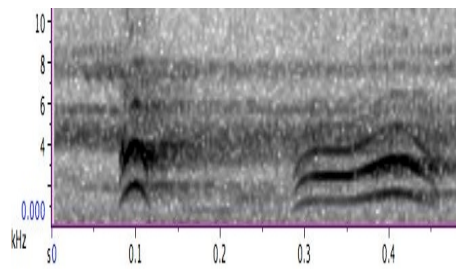
(G)

A. Song of *S. ruficapilla*, Edo. São Paulo, Brazil. (C. A. Marantz; MLNS 88727)

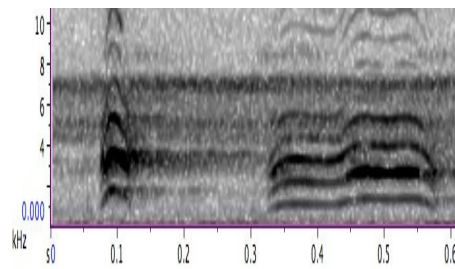
- B. Song of *S. ruficapilla*, Prov. Misiones, Argentina. (P. A. Hosner; MLNS 132952)
- C. Short song with U-shaped terminal note, Edo. Espírito Santo, Brazil. (R. Ward; MLNS 7049)
- D. Rattle, Edo. Rio de Janeiro, Brazil. (T. A. Parker III; MLNS 32077)
- E. Extended song, Edo. Rio Grande do Sul, Brazil. (F. Jacobs; XC 24085)
- F. Rapid singing, Edo. Santa Catarina, Brazil. (E. Patrial; XC 28287)
- G. Two call note types, Edo. Santa Catarina, Brazil. The nasal descending notes are at 0.5 and 3.5 sec. (E. Patrial; XC 28287)

### *Synallaxis rutilans*

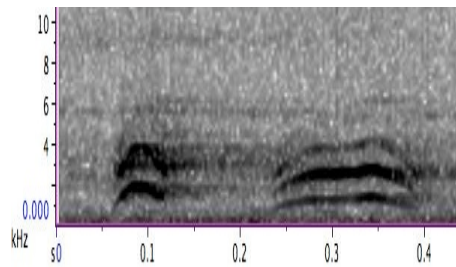
The song of *S. rutilans* is a two-noted vocalization featuring a short U- or S-shaped note followed by a longer, lower-pitched note with strong inflection (A-J). The degree of inflection varies geographically; it is least pronounced in *S. r. dissors* of the Guiana Shield and in samples from northwestern Amazonia. The one available recording of *S. r. omissa* suggests that this taxon is vocally distinct from other populations (D). The most frequently recorded call, apparently common to all subspecies, is a querulous note that may be preceded by a harsh “chit” (K, L). The “chit” notes may also be given alone, typically in an irregular series.



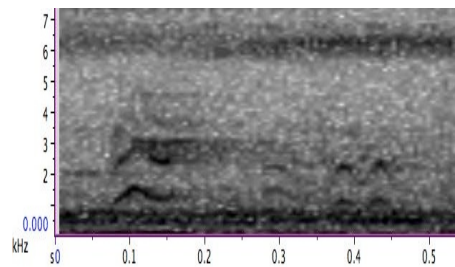
(A)



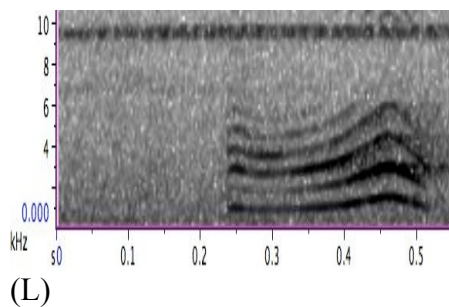
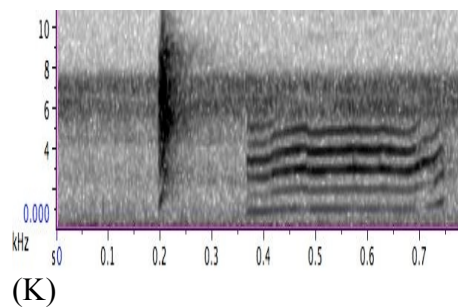
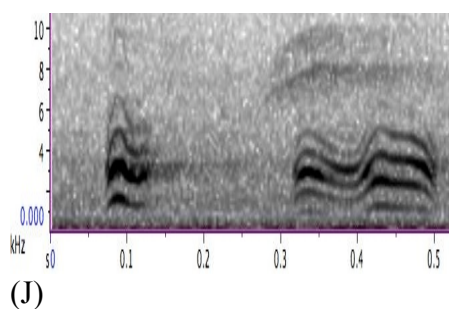
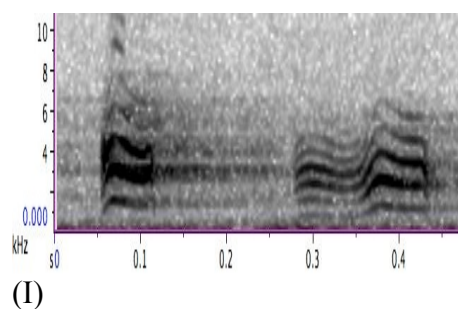
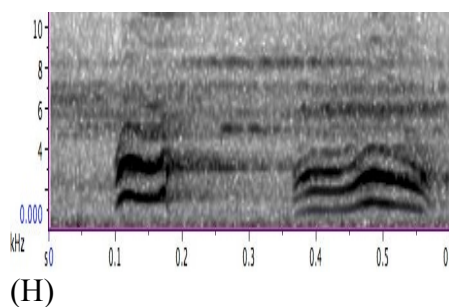
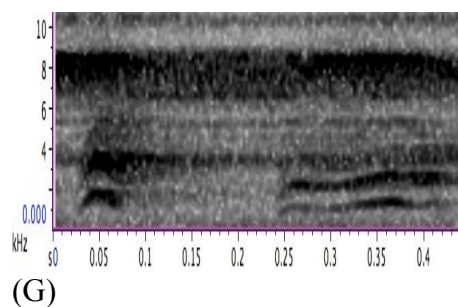
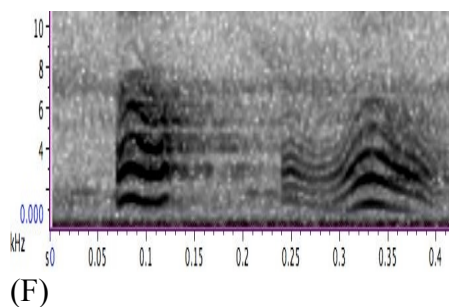
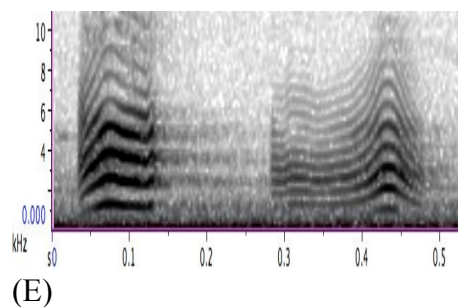
(B)



(C)



(D)



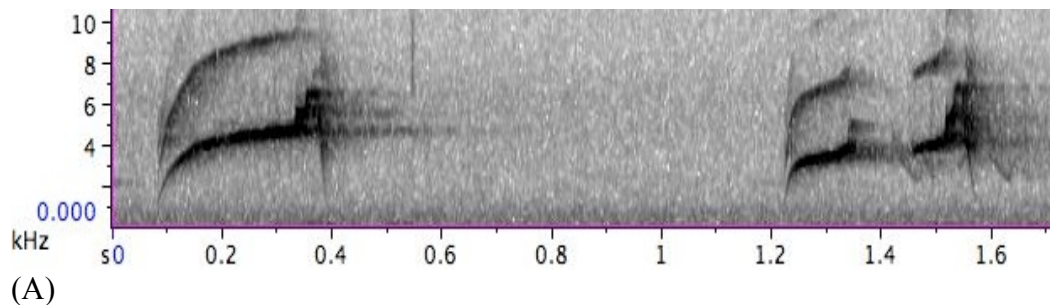
- A. Song of *S. r. caquetensis*, Depto. Caquetá, Colombia. (M. Álvarez; BSA 2000)
- B. Song of *S. r. caquetensis*, Depto. Loreto, Peru. (T. A. Parker III; MLNS 29260)
- C. Song of *S. r. dissors*; Edo. Bolívar, Venezuela. (P. A. Schwartz; MLNS 66249)
- D. Song of *S. r. omissa*, Edo. Pará, Brazil. Although the spectrograph trace is faint, it clearly shows the strong modulation in the second note, producing a stuttering sound. (S. Dantas; XC 20638)

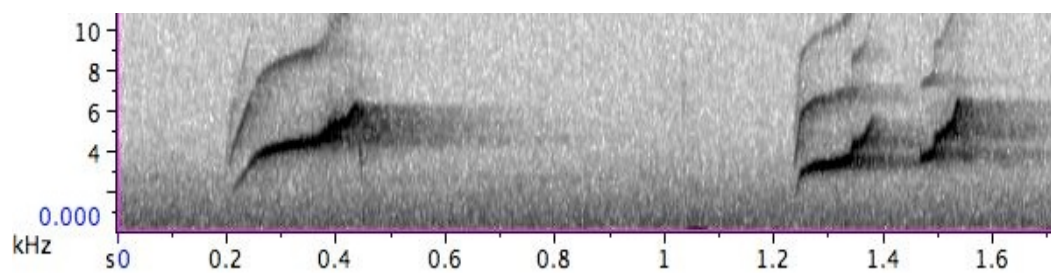


- E. Song of *S. r. rutilans*, Edo. Pará, Brazil. (C. A. Marantz; MLNS 126645)
- F. Song of *S. r. amazonica*, Edo. Pará, Brazil. (C. A. Marantz; MLNS 117146)
- G. Song of *S. r. amazonica*, Edo. Amazonas, Brazil. (C. A. Marantz; MLNS 117019)
- H. Song of *S. r. amazonica*, Edo. Mato Grosso, Brazil. (C. A. Marantz; MLNS 88521)
- I. Song of *S. r. amazonica*, Depto. Madre de Dios, Peru. (T. A. Parker III; MLNS 35545)
- J. Song of *S. r. tertia*, Depto. Beni, Bolivia. (P. A. Hosner; MLNS 132772)
- K. “Chit” call followed by querulous note, *S. r. caquetensis*, Depto. Loreto, Peru. (T. A. Parker III; MLNS 29149)
- L. Variant of querulous note, *S. rutilans* (subspecies unknown), Brazil. (B. M. Whitney; MLNS 108435)

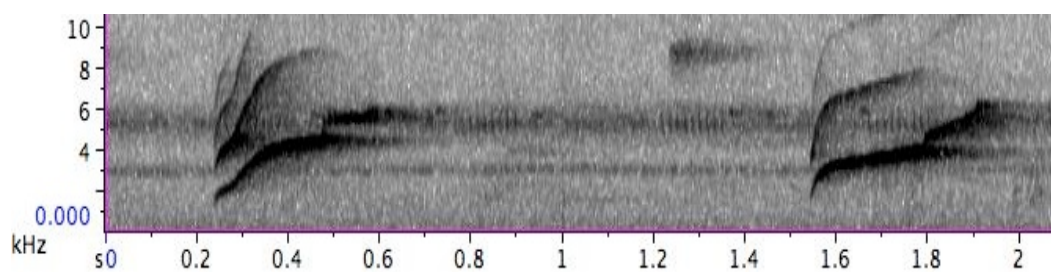
### *Synallaxis scutata*

The song of *S. scutata* is a high-pitched vocalization consisting of a long, upslurred introductory note followed by a long pause, then either one or two short notes (*S. s. whitii*; A, B) or a longer, upslurred note that may be followed by a short terminal note at a higher pitch (*S. s. scutata*; C, D). The overall length of the song is longer in *S. s. scutata* than in *S. s. whitii*. An undescribed population with diagnostic plumage characters in Depto. Puno, Peru, is not distinguishable vocally from *S. s. whitii* (E). The song of *S. s. whitii* is strongly similar to that of *S. cinerascens*. Calls include a sharp, high-pitched note (F) that descends sharply at the end and is sometimes doubled, and a softer rising note (G). Various contact notes have also been recorded (H).

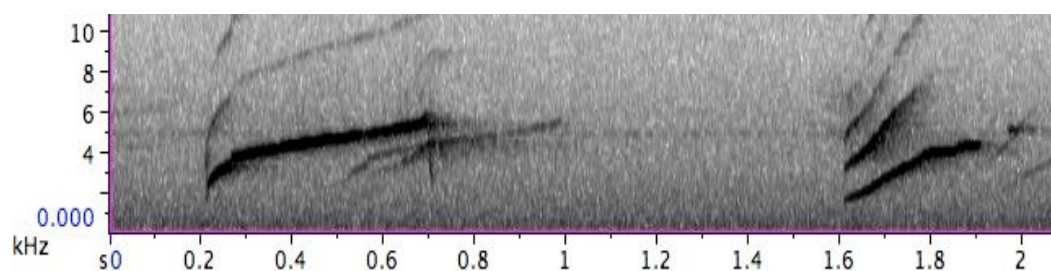




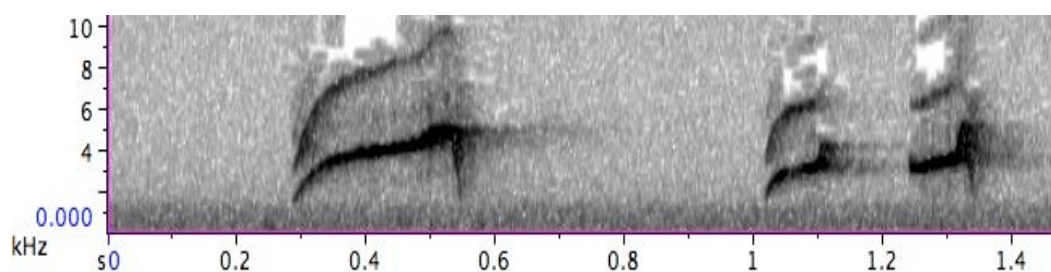
(B)



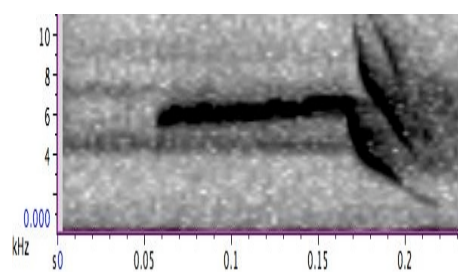
(C)



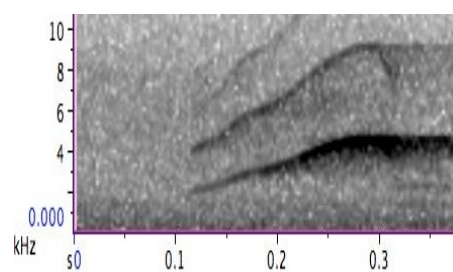
(D)



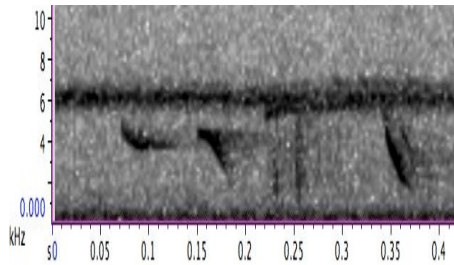
(E)



(F)



(G)

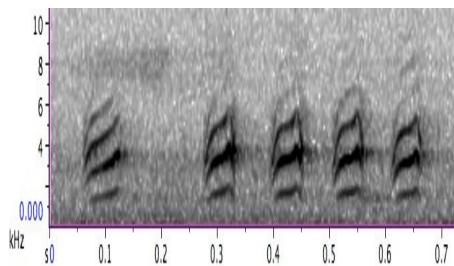


(H)

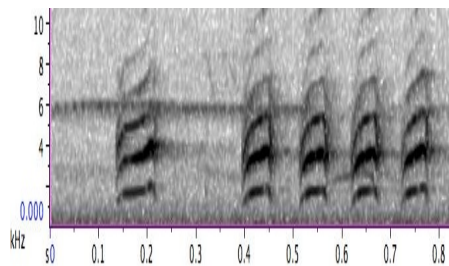
- A. Song of *S. s. whitii*, Argentina. (B. M. Whitney; MLNS 46129)
- B. Song of *S. s. whitii*, Depto. La Paz, Bolivia. (A. B. Hennessey; MLNS 110602)
- C. Song of *S. s. scutata*, Edo. Minas Gerais, Brazil. (H. G. Remold; MLNS 114858)
- D. Song of *S. s. scutata*, Edo. Mato Grosso, Brazil. (D. W. Finch; MLNS 52808)
- E. Song of *S. scutata subsp. nov.*, Depto. Puno, Peru. (D. F. Lane; from personal archives)
- F. Sharp call note, *S. s. whitii*, Argentina. (B. M. Whitney; MLNS 50828)
- G. Rising call note, *S. s. whitii*, Argentina. (B. M. Whitney; MLNS 46131)
- H. Contact notes, Prov. Jujuy, Argentina. (N. Krabbe; XC 29263)

### *Synallaxis spixi*

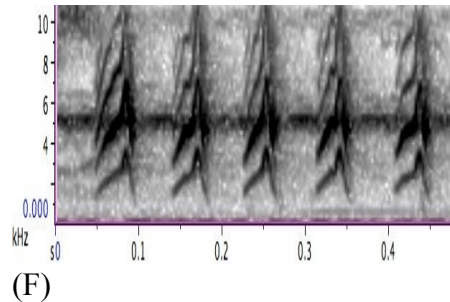
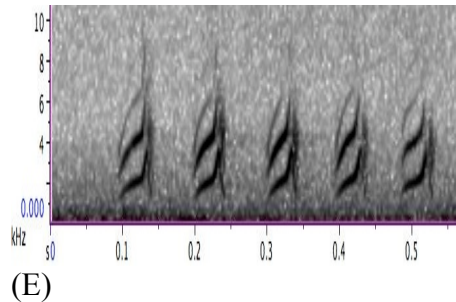
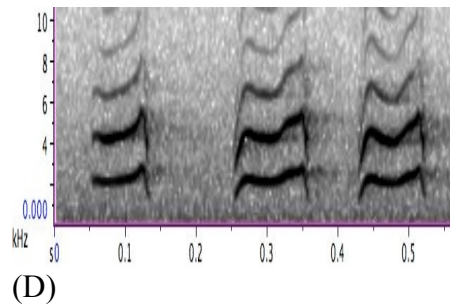
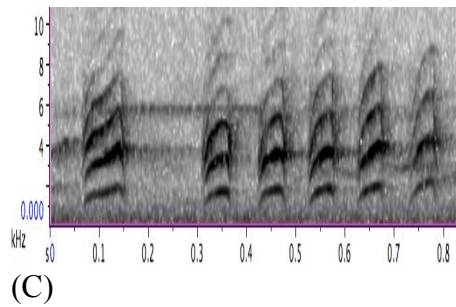
The song of *S. spixi* is similar in pattern to that of *S. albigularis*, consisting of an introductory note followed by a series of 3-5 (occasionally 2) notes at a slightly lower pitch (A, B). The notes are U-shaped but rise in frequency, unlike those of *S. albigularis*. Songs after playback have shorter notes and are delivered more rapidly than normal songs. After playback, birds may add a short terminal note at a lower pitch, or sing songs that rise noticeably in frequency (C). A short alternate song with relatively drawn-out notes has been recorded (D). The alarm call is a distinctive series of modulated notes that may be given slowly or rapidly (E, F).



(A)



(B)

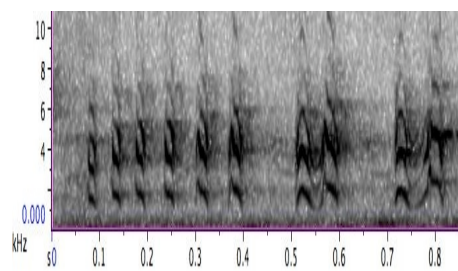


- A. Song of *S. spixi*, Edo. Espírito Santo, Brazil. (T. A. Parker III; MLNS 22032)
- B. Song of *S. spixi*, Edo. Rio de Janeiro, Brazil. (T. A. Parker III; MLNS 22113)
- C. Excited song (natural conditions, pair counter-singing), Edo. Rio de Janeiro, Brazil. (T. A. Parker III; MLNS 22113)
- D. Short series of drawn-out notes, Prov. Misiones, Argentina. This was answered by normal song from another individual. (D. W. Finch; MLNS 57870)
- E. Slower call series, Edo. Rio Grande do Sul, Brazil. (W. Belton; MLNS 19095)
- F. Rapid call series, Prov. Misiones, Argentina. (M. J. Andersen; MLNS 133932)

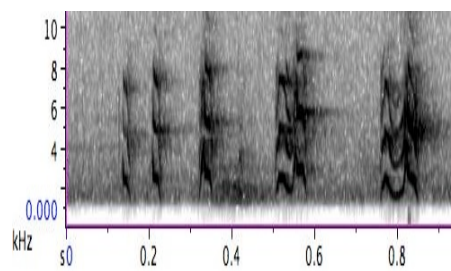
### *Synallaxis stictothorax*

The song of *S. stictothorax* (including *S. s. maculata*) consists of a series of staccato notes followed by two incisive modulated notes that rise in frequency (A, B). The number of notes in the introductory series is variable, as is the length of the song, which may be extended by insertion of extra notes (C). The song of *S. s. chinchipensis* differs greatly. It consists of two or three progressively higher-pitched trilled phrases separated by short upslurred notes (D). All subspecies also give an excited trill (E), typically as a duet, with one pair member starting almost immediately after the other. When excited, birds give a variety of sharp call notes (F) that sometimes coalesce into trills or are interspersed among normal songs. A single call note has been recorded as well (G). The scold note is a sharp ascending call that is usually doubled or tripled (H).

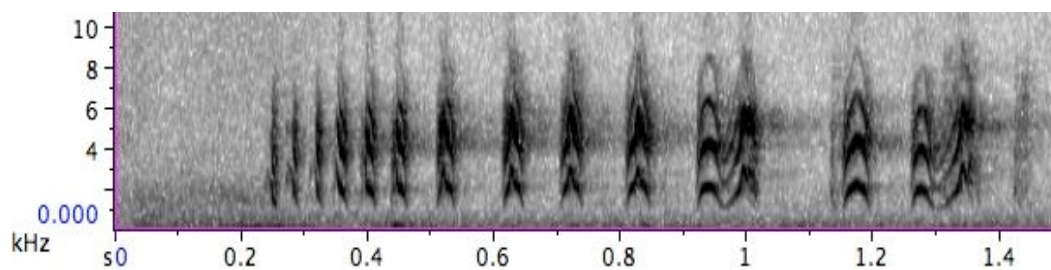




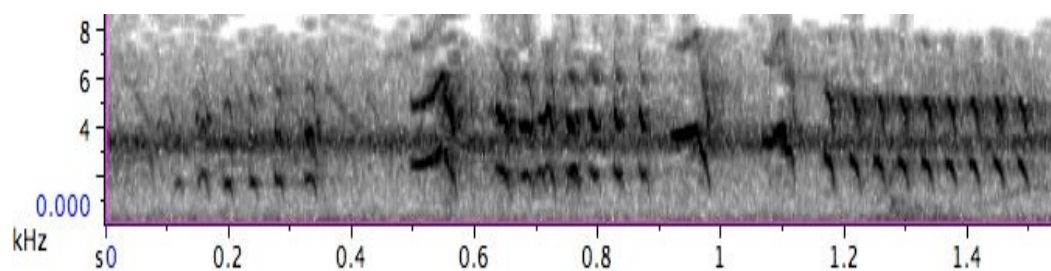
(A)



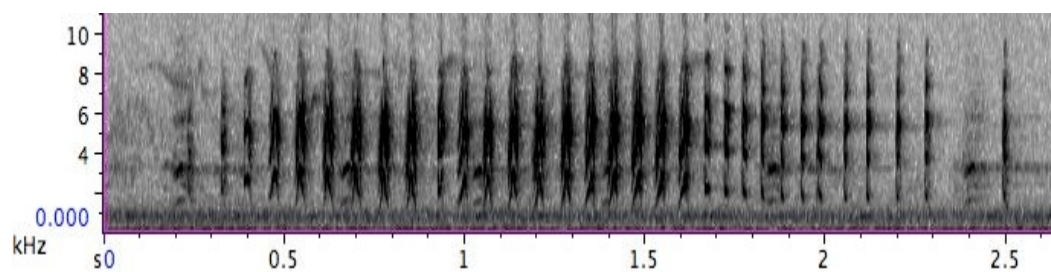
(B)



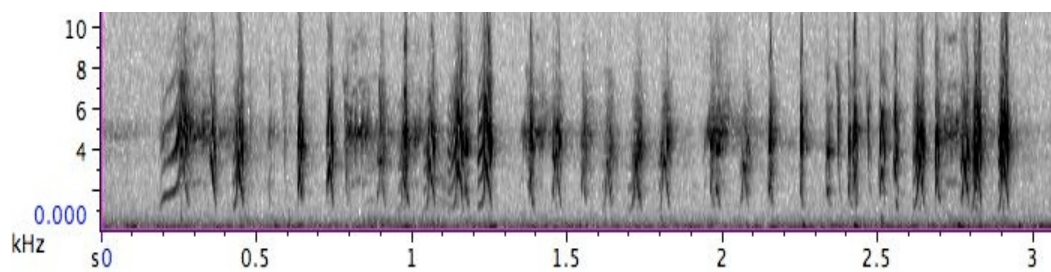
(C)



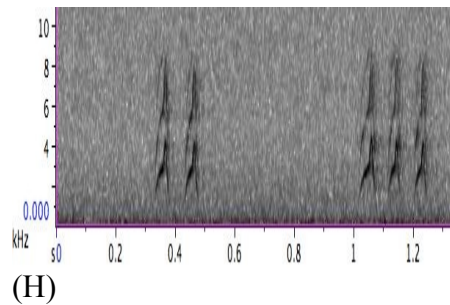
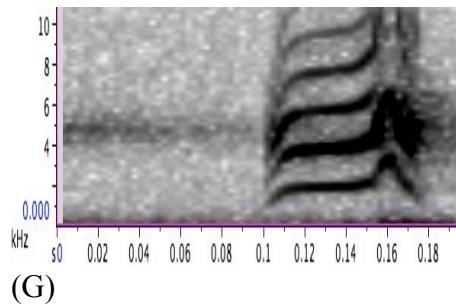
(D)



(E)



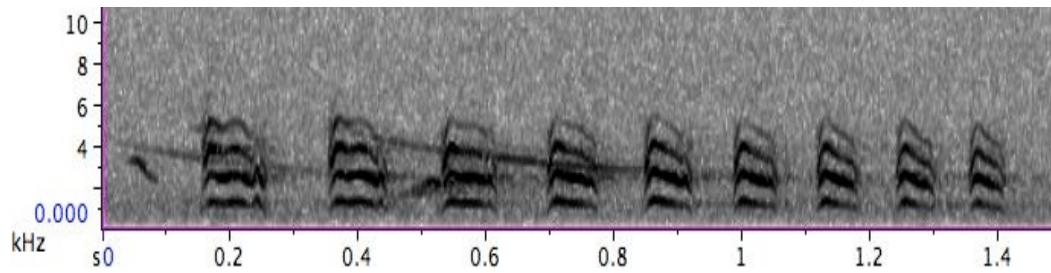
(F)



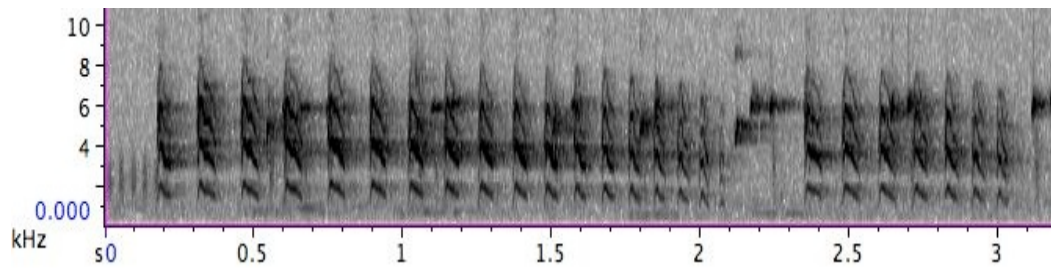
- A. Song of *S. s. maculata*, Depto. Lambayeque, Peru. (P. K. Donahue; MLNS 82238)
- B. Song of *S. s. stictothorax*, Prov. Manabí, Ecuador. (A. Spencer; XC 17651)
- C. Longer song of *S. s. maculata*, Depto. Lambayeque, Peru. (P. K. Donahue; MLNS 82238)
- D. Song of *S. s. chinchipensis*, Depto. Cajamarca, Peru. (F. Lambert; XC 12113)
- E. Excited trill from one bird, *S. s. maculata*, Depto. Lambayeque, Peru. (T. A. Parker III; MLNS 21981)
- F. Rapid series of jumbled notes, *S. s. maculata*, Depto. Lambayeque, Peru. (T. A. Parker III; MLNS 13241)
- G. Single call note, *S. s. maculata*, Depto. Lambayeque, Peru. (T. A. Parker III; MLNS 13241)
- H. Scold call, *S. s. maculata*, Depto. Tumbes, Peru. (T. A. Parker III; MLNS 17588)

### *Synallaxis subpudica*

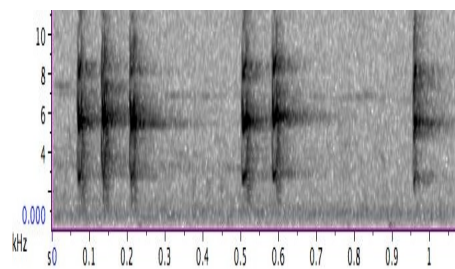
The song of *S. subpudica* is a long series of notes that accelerates and descends in frequency toward the end (A, B). Between one and three short descending series are almost always given at the end of the long series. The song is often given as a duet, with one pair member joining its mate approximately halfway through a song. Members of a pair sound quite different; one gives a flatter series of notes at a lower frequency (A) while the other gives more sharply descending notes at a higher frequency (B). The sharp call note is frequently doubled or tripled (C). There are relatively few recordings of this species, and its repertoire may be more extensive than indicated here.



(A)



(B)

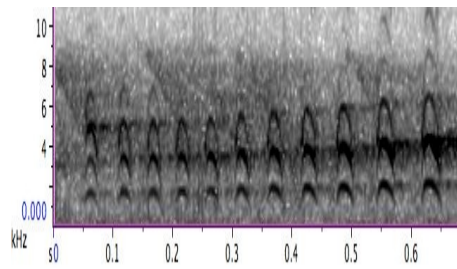


(C)

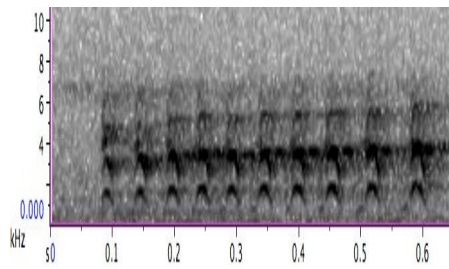
- A. Short series of *S. subpudica* showing flatter note type, Depto. Boyacá, Colombia. (C. D. Cadena; BSA 6362)
- B. Full song of *S. subpudica* with short series at end of song, Depto. Cundinamarca, Colombia. This song features the sharply descending note type. (F. G. Stiles; BSA 10987)
- C. Call notes. (F. G. Stiles; BSA 10987)

### *Synallaxis tithys*

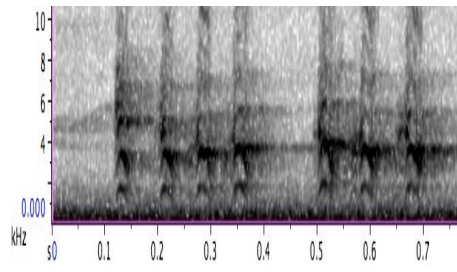
The song of *S. tithys* is a rising series of staccato U-shaped notes with a hard quality (A, B). Call notes include a harsh modulated note (D). There are relatively few recordings of this species, but its repertoire does not appear to be extensive and song variation is minimal.



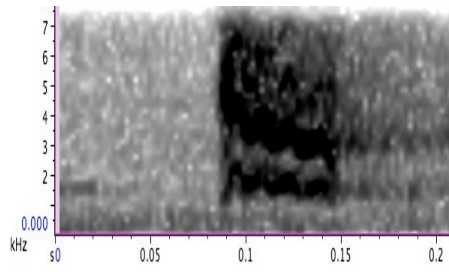
(A)



(B)



(C)



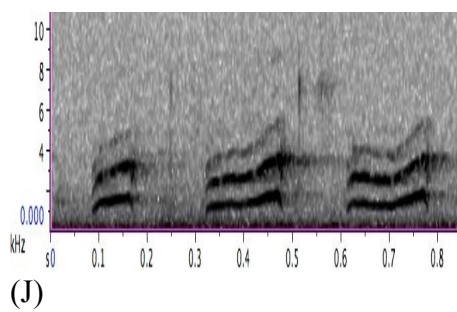
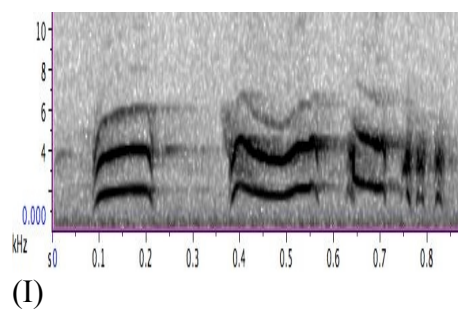
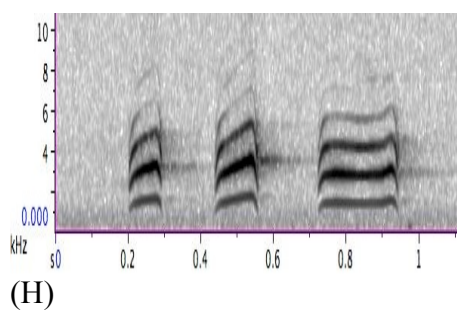
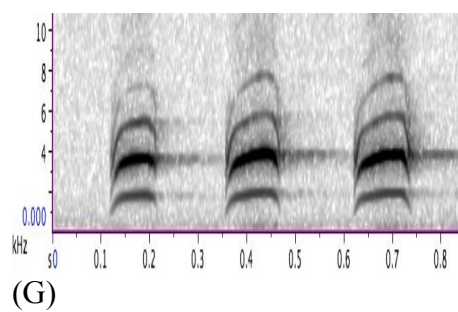
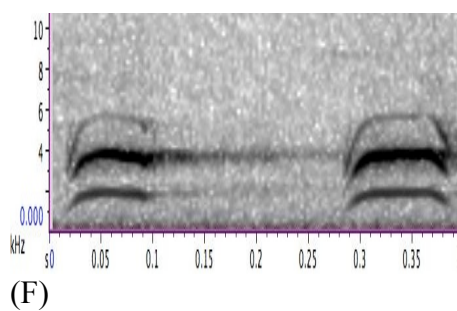
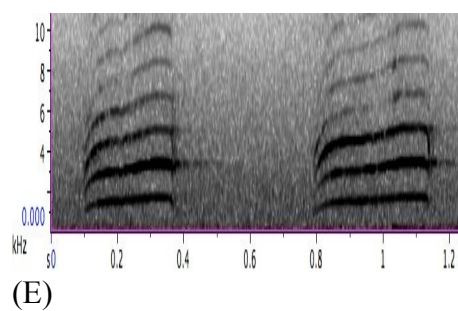
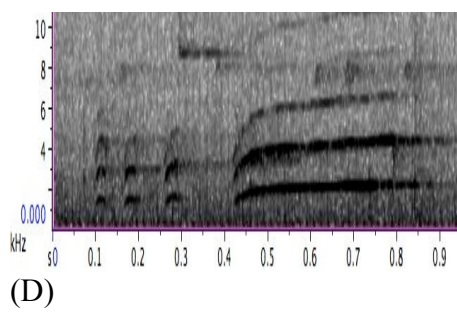
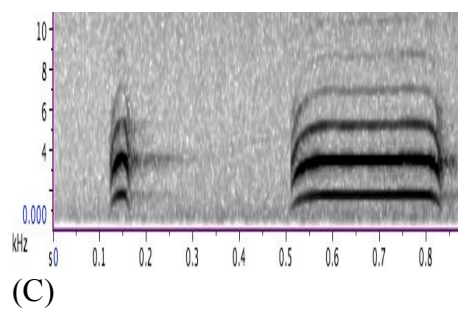
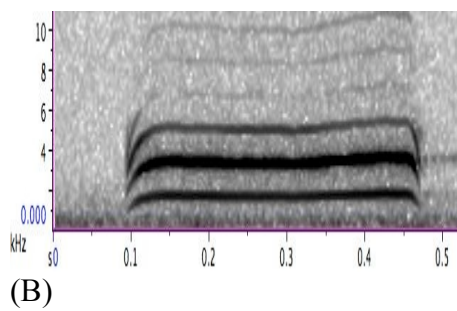
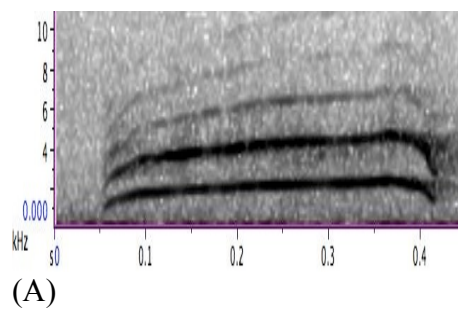
(D)

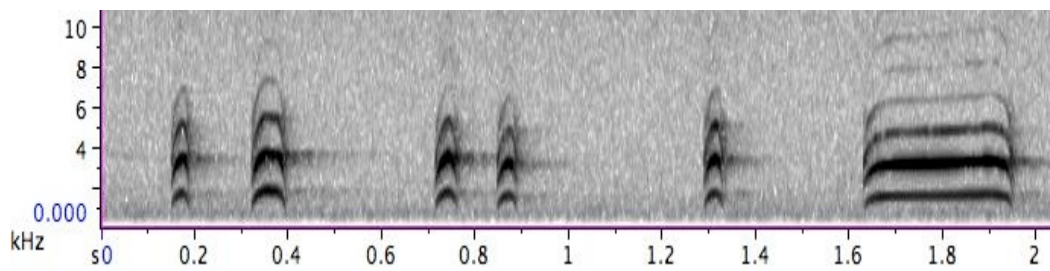
- A. Song of *S. tithys*, Prov. Loja, Ecuador. (M. B. Robbins; MLNS 57087)
- B. Song of *S. tithys*, Prov. Guayas, Ecuador. (P. Coopmans; MLNS 68097)
- C. Aberrant song, Prov. Guayas, Ecuador. This was given once within a series of normal songs. (L. R. Macaulay; MLNS 122723)
- D. Harsh call note, Depto. Tumbes, Peru. (F. Angulo; XC 9634)

### *Synallaxis unirufa*

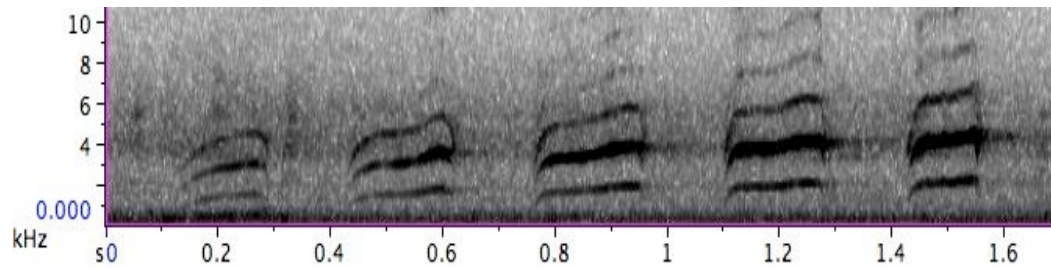
The song of *S. unirufa* shows considerable individual and geographic variation. The song of most Andean populations is a single long, ascending note with a variable amount of inflection (A, B). An introductory note (C) or a trilled phrase (D) may precede this note; it may be doubled (E), or interspersed among irregular series of shorter notes (K). Individuals typically sing at least two variants of the song during a singing bout, especially after playback. The song of *S. u. meridana* consists of two or three shorter notes (F, G); after playback, the third note may be lower-pitched and longer (H). A rising series of inflected notes, which appears to be an alternate song, has been recorded from Venezuela (J) and Peru (L). A dawn song has been recorded from *S. u. meridana* (I). Calls include a harsh note typically given in an irregular series (M). High-pitched notes have been recorded from a juvenile in the presence of an adult (N).



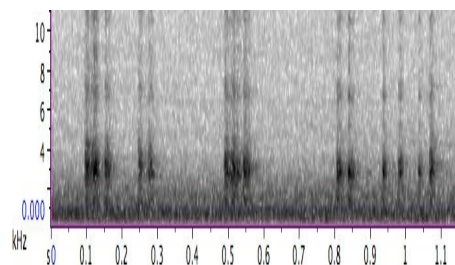




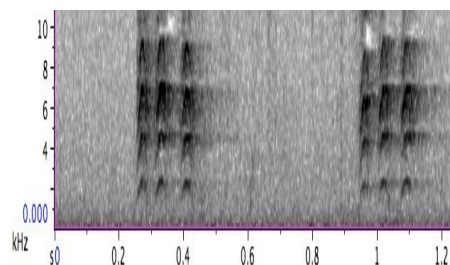
(K)



(L)



(M)



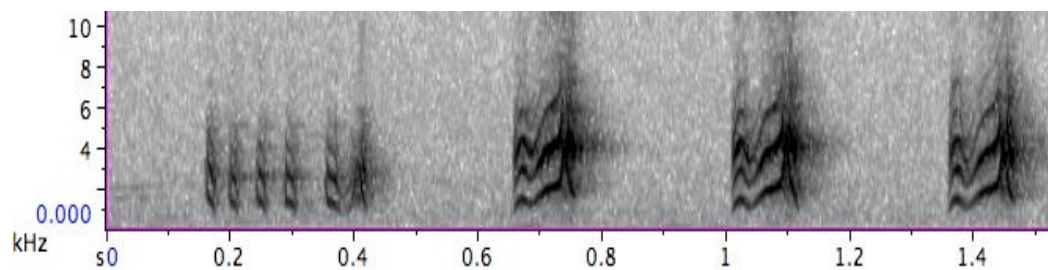
(N)

- A. Song of *S. u. unirufa*, Depto. Antioquia, Colombia. (R. Gaviria; BSA 30831)
- B. Song of *S. u. ochrogaster*, Depto. La Libertad, Peru. (T. A. Parker III; MLNS 17293)
- C. Song of *S. u. unirufa* with introductory note, Depto. Cundinamarca, Colombia. (M. Álvarez; BSA 22546)
- D. Song of *S. u. unirufa* with trebled introductory phrase, Ecuador. (L. R. Macaulay; MLNS 58855)
- E. Song of *S. u. unirufa* featuring doubled long note, Depto. Caldas, Colombia. (A. M. López; MLNS 11469)
- F. Song of *S. u. meridana*, Edo. Mérida, Venezuela. (P. A. Schwartz; MLNS 66132)
- G. Three-noted song of *S. u. meridana*, Edo. Táchira, Venezuela. (P. A. Schwartz; MLNS 66135)

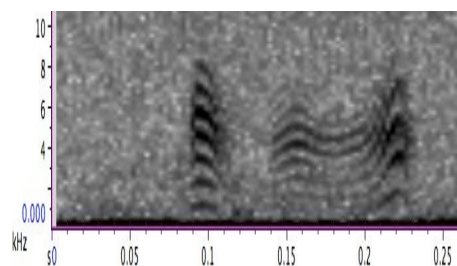
- H. Three-noted song in response to playback, *S. u. meridana*, Edo. Táchira, Venezuela. (P. A. Schwartz; MLNS 66135)
- I. Alternate song of *S. u. meridana*, Edo. Trujillo, Venezuela. (P. A. Schwartz; MLNS 66139)
- J. Alternate song of *S. u. meridana*, Edo. Táchira, Venezuela. (P. A. Schwartz; MLNS 66142)
- K. Disjointed introductory notes preceding song, *S. u. unirufa*, Depto. Cundinamarca, Colombia. (M. Álvarez; BSA 22546)
- L. Alternate song of *S. u. ochrogaster*, Depto. San Martín, Peru. (J. P. O'Neill; MLNS 18073)
- M. Harsh scold notes of *S. u. ochrogaster*, Depto. Cusco, Peru. (W. ten Have; XC 3770)
- N. Calls of juvenile *S. u. meridana*, Edo. Táchira, Venezuela. (A. Renaudier; XC 22884)

### *Synallaxis zimmeri*

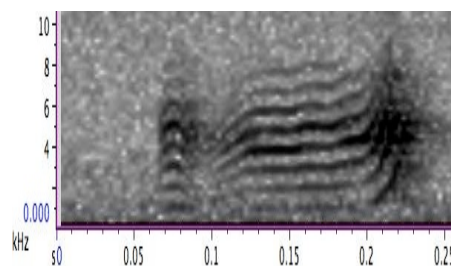
The song of *S. zimmeri* is a series of rapid notes followed by two or three incisive, sharply inflected notes. It is similar to the song of *S. stictothorax*. Calls include a soft contact call (B) and a similar but more forceful rising note (C).



(A)



(B)



(C)

- A. Song of *S. zimmeri*, Depto. La Libertad, Peru. (D. Edwards; XC 27824)
- B. Contact call. (D. F. Lane; from personal archives)
- C. Rising note. (D. F. Lane; from personal archives)

## **Appendix B. Recordings Used in Chapter 3**



Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
MLNS66110	<i>azarae</i>	<i>elegantior</i>	Venezuela: Edo. Mérida; La Mucuy	2100	P. A. Schwartz
MLNS66111	<i>azarae</i>	<i>elegantior</i>	Venezuela: Edo. Mérida; La Mucuy	2100	P. A. Schwartz
MLNS66112	<i>azarae</i>	<i>elegantior</i>	Venezuela: Edo. Mérida; La Cuchilla	2300	P. A. Schwartz
MLNS66114	<i>azarae</i>	<i>elegantior</i>	Venezuela: Edo. Mérida; above La Azulita	1800	P. A. Schwartz
MLNS66113	<i>azarae</i>	<i>elegantior</i>	Venezuela: Edo. Táchira; above Queniquea	1700	P. A. Schwartz
BSA19519	<i>azarae</i>	<i>media</i>	Colombia: Depto. Valle del Cauca; El Cairo, Cerro Inglés	2165	A. M. Cuervo
BSA19618	<i>azarae</i>	<i>media</i>	Colombia: Depto. Antioquia; Amalfi, Bosque Guayabito, Finca Costa Rica	1830	A. M. Cuervo
BSA30424	<i>azarae</i>	<i>media</i>	Colombia: Depto. Antioquia; Sabaneta, La Romera	1700	A. M. Cuervo
BSA30605	<i>azarae</i>	<i>media</i>	Colombia: Depto. Antioquia; Envigado, Alto de San Sebastián	2700	A. M. Cuervo
BSA30696	<i>azarae</i>	<i>media</i>	Colombia: Depto. Antioquia; Envigado, Alto de San Sebastián	2640	A. M. Cuervo
XC7993	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa Valley	1860	N. Athanas
XC10020	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa Valley	2200	A. T. Chartier
XC10021	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa Valley	2200	A. T. Chartier
XC10023	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa Valley	2200	A. T. Chartier
XC16093	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa Valley, Tandayapa Bird Lodge	1700	K. Allaire
MLNS28611	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Old Pipeline Road, Chiriboga		A. B. Van den Berg
MLNS36054	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; near Chiriboga	2000	T. S. Schulenberg
MLNS56994	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Azuay; W bank Rio Leon, ca 6 km N Ona	2000	M. B. Robbins
MLNS57280	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; new road from Tandayapa Pass to Mindo	2040	L. R. Macaulay

Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
MLNS84072	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Tandayapa-Old Mindo Hwy, Nanegalito	2200	D. L. Ross, Jr
MLNS84077	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Pichincha; Nono Mindo Rd	2700	P. Coopmans
MLNS84465	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Napo; Rio Napo at La Horesta	1920	R. A. Rowlett
MLNS85024	<i>azarae</i>	<i>media</i>	Ecuador: Depto. Napo; 10 km S Baeza, Hacienda San Isidro	2000	P. K. Donahue
XC3674	<i>azarae</i>	<i>ochracea</i>	Ecuador: Depto. El Oro; upper road, near Pinas	900	D. Jones
MLNS21881	<i>azarae</i>	<i>ochracea</i>	Peru: Depto. Piura; 33 km SW Huancabamba	3050	T. A. Parker III
MLNS47330	<i>azarae</i>	<i>ochracea</i>	Ecuador: Depto. Loja		B. M. Whitney
MLNS68263	<i>azarae</i>	<i>ochracea</i>	Ecuador: Depto. Loja; Utuana	2500	P. Coopmans
MLNS124470	<i>azarae</i>	<i>ochracea</i>	Ecuador: Depto. El Oro; Buenaventura	800	L. R. Macaulay
MLNS129483	<i>azarae</i>	<i>ochracea</i>	Ecuador: Depto. El Oro; Buenaventura	900	P. A. Hosner
MLNS18058	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Amazonas; 33 km NE Ingenio	2135	J. P. O'Neill
MLNS18066	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Amazonas; 33 km NE Ingenio	2135	J. P. O'Neill
MLNS21583	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Piura; Huancabamba	2135	T. A. Parker III
MLNS21632	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Piura; 5 km NE Huancabamba	2285	T. A. Parker III
MLNS21674	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Cajamarca; E slope Cerro Chinguela	2135	T. A. Parker III
MLNS21735	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Cajamarca; E slope Cerro Chinguela	2135	T. A. Parker III
MLNS21844	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Piura; 2 km NE Huancabamba	2135	T. A. Parker III
MLNS68195	<i>azarae</i>	<i>fruticicola</i>	Ecuador: Depto. Zamora-Chinchipec; Zumba	1250	P. Coopmans
DFL0318-1	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Amazonas/San Martín; Abra Patricia, ca 22 km NE Florida	2400	D. F. Lane
DFL0418-013	<i>azarae</i>	<i>fruticicola</i>	Peru: Depto. Amazonas; above Leimebamba, ca 37 km NE Celendin	3200	D. F. Lane

Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
MLNS35756	<i>azarae</i>	<i>infumata</i>	Peru: Depto. Pasco; Santa Cruz, ca. 9 km SE Oxapampa	2050	T. S. Schulenberg
MLNS92194	<i>azarae</i>	<i>infumata</i>	Peru: Depto. Junín; Cordillera Vilcabamba, "Camp 2"	2050	T. S. Schulenberg
MLNS92239	<i>azarae</i>	<i>infumata</i>	Peru: Depto. Junín; Cordillera Vilcabamba, "Camp 2"	2050	T. S. Schulenberg
DFL uncat.	<i>azarae</i>	<i>infumata</i> <sup>3</sup>	Peru: Depto. Junín; Lampa, ca 39 km ENE Huancayo, 11°58'S, 74° 53'W	2850	D. F. Lane
XC15040	<i>azarae</i>	<i>infumata</i> *	Peru: Depto. Junín; Andamarca	3340	R. Ahlman
MLNS28872	<i>azarae</i>	<i>infumata</i> ** <sup>4</sup>	Peru: Depto. Huánuco; Carpish Mountains, Paty Trail	2075	A. B. Van den Berg
MLNS17614	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; Huyro, Bosque Aputinye	1675	T. A. Parker III
MLNS24077	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; Macchu Picchu	2300	T. A. Parker III
MLNS24079	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; Macchu Picchu	2300	T. A. Parker III
MLNS26513	<i>azarae</i>	<i>urubambae</i>	Peru; Depto. Cusco; ca. 30 km N Abra Málaga	2740	P. R. Isler
MLNS35469	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; Abra Málaga, Canchailloc, San Luis	2680	T. A. Parker III
MLNS135305	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; near La Esperanza on Manu Road	3000	B. J. O'Shea
DFL0024-1	<i>azarae</i>	<i>urubambae</i>	Peru: Depto. Cusco; near Pillahuata on Manu Road	2650	D. F. Lane
XC1596	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. Cochabamba; Corani Low	2500	S. Mayer
XC1961	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Cotapata Trail (behind the petrol station)	3000	S. Mayer
XC2079	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Chojña Khota, second lower camp, near Inquisivi	2900	S. Mayer

<sup>3</sup> \* denotes divergent song type from Mantaro Valley, Depto. Junín, Peru.

<sup>4</sup> \*\* denotes second divergent song type from near type locality of *S. a. infumata*. See Appendix A for spectrographs.

Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
MLNS13821	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Serranía Bellavista, ca. 35 km N Caranavi		T. A. Parker III
MLNS17102	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Serranía Bellavista, ca. 35 km N Caranavi		T. A. Parker III
MLNS120809	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Madidi National Park, Apolo Madidi Savanna	1900	A. B. Hennessey
MLNS132713	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Bosque Apa Apa	2000	P. A. Hosner
MLNS85607	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. La Paz; Sacramento Alto Trail	2440	R. A. Rowlett
DFL0710-2	<i>azarae</i>	<i>azarae</i>	Peru: Depto. Puno; Abra de Maruncunca	2100	D. F. Lane
DFL0021-1	<i>azarae</i>	<i>azarae</i>	Bolivia: Depto. Cochabamba; Miguelito Pipeline Rd, ca 110 km NE Cochabamba	1600	D. F. Lane
XC1540	<i>azarae</i>	<i>samaipatae</i>	Bolivia: Depto. Chuquisaca; Río Yahuayhua	1000	S. Mayer
XC1562	<i>azarae</i>	<i>samaipatae</i>	Bolivia: Depto. Chuquisaca; southwest slope Cerro Campamentito	2700	S. Mayer
XC4559	<i>azarae</i>	<i>samaipatae</i>	Bolivia: Depto. Tarija; Tariquia, El Cajón	670	A. MacCormick
DFL0022-1	<i>azarae</i>	<i>samaipatae</i>	Bolivia: Depto. Santa Cruz; Chuchial, ca 10 km S Bermejo	1100	D. F. Lane
DFL9909-1	<i>azarae</i>	<i>samaipatae</i>	Bolivia: Depto. Santa Cruz; La Pajcha, ca 28 km S Samaipata	1750	D. F. Lane
XC8973	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Salta; Abra Santa Laura	1400	N. Athanas
MLNS116039	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Salta	1475	L. R. Macaulay
MLNS116108	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Salta; Calilegua National Park	1700	L. R. Macaulay
MLNS129300	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Jujuy; E slope Sierra Santa Barbara	1975	M. J. Andersen
MLNS129336	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Jujuy; E slope Sierra Santa Barbara	1700	M. J. Andersen
MLNS129389	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Jujuy; E slope Sierra Santa Barbara	1975	M. J. Andersen
MLNS132575	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Jujuy; Caleligua National Park	1650	P. A. Hosner
NKK uncat.	<i>azarae</i>	<i>superciliosa</i>	Argentina: Prov. Jujuy; Caleligua National Park	1700	N. Krabbe

Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
XC10300	<i>frontalis</i>	Eastern group	Brasil: Edo. Mato Grosso; São José da Barra	920	L. F. Figueiredo
XC11592	<i>frontalis</i>	Eastern group	Brasil: Edo. Ceará: Barbalha, Chapado do Araripe	920	N. Athanas
MLNS35690	<i>frontalis</i>	Eastern group	Brasil: Edo. Bahía, 2 km NW Boa Nova		T. A. Parker III
MLNS35707	<i>frontalis</i>	Eastern group	Brasil: Edo. Bahía, 12 km NW Boa Nova		T. A. Parker III
MLNS108261	<i>frontalis</i>	Eastern group	Brasil: Edo. Minas Gerais		B. M. Whitney
MLNS43687	<i>frontalis</i>	Chaco group	Argentina		B. M. Whitney
MLNS83843	<i>frontalis</i>	Chaco group	Argentina: Prov. Chaco; 20 km NW Resistencia	200	S. L. Hilty
KZ1995-2B-64	<i>frontalis</i>	Chaco group	Paraguay: Prov. Presidente Hayes; Fortin Zalazar		K. Zyskowski
KZ1995-3A-32	<i>frontalis</i>	Chaco group	Paraguay: Prov. Alto Paraguay; Cerro Leon		K. Zyskowski
KZ2000-3-76	<i>frontalis</i>	Chaco group	Paraguay: Prov. Alto Paraná; Puerto Bertoni		K. Zyskowski
PS uncat.	<i>frontalis</i>	Chaco group	Paraguay: Prov. Presidente Hayes; Laguna Capitan, ca 70 km E Loma Plata		P. Smith
MLNS19228	<i>frontalis</i>	Southern group	Brasil: Edo. Rio Grande do Sul; Banhado São Donato, 35 km NE Itaqui	100	W. Belton
MLNS19259	<i>frontalis</i>	Southern group	Brasil: Edo. Rio Grande do Sul; Arroio Quarai-chico; 64 km NE Uruguaiana		W. Belton
MLNS132402	<i>frontalis</i>	Southern group	Argentina: Prov. Corrientes; 2 km E Estancia Rincón El Socorro	75	M. J. Andersen
MLNS132449	<i>frontalis</i>	Southern group	Argentina: Prov. Corrientes; 30 km SW Estancia Rincón El Socorro	65	M. J. Andersen
MLNS132867	<i>frontalis</i>	Southern group	Argentina: Prov. Corrientes; Estancia Rincón El Socorro	65	P. A. Hosner
XC14988	<i>frontalis</i>	Southern group	Argentina: Prov. Entre Rios; Gualayachú, Puerto Boca		R. Ahlman
XC2100	<i>frontalis</i>	Bolivian group	Bolivia: Depto. La Paz; Inquisivi	2350	S. Mayer

Recording #	Species	Subspecies	Locality	Elevation (m)	Recordist
XC2104	<i>frontalis</i>	Bolivian group	Bolivia: Depto. La Paz; Inquisivi	2350	S. Mayer
MLNS30584	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz	1830	T. A. Parker III
MLNS33630	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; San Isidro, Tambo School		T. A. Parker III
MLNS33659	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; San Isidro, Tambo School		T. A. Parker III
MLNS52488	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; Isla Verde		T. A. Parker III
MLNS52496	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; Isla Verde		T. A. Parker III
MLNS84497	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; below Tambo		R. A. Rowlett
MLNS85652	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; Siberia	2600	R. A. Rowlett
MLNS132774	<i>frontalis</i>	Bolivian group	Bolivia: Depto. La Paz, below Inquisivi	2400	P. A. Hosner
DFL0018-1	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz; Samaipata	1700	D. F. Lane
NKK uncat.	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Chuquisaca; Cerro Palmarcito	2450	N. Krabbe
RH uncat.	<i>frontalis</i>	Bolivian group	Bolivia: Depto. Santa Cruz		R. Hoyer
MLNS46132	<i>frontalis</i>	S. Andean group	Argentina		B. M. Whitney
MLNS129754	<i>frontalis</i>	S. Andean group	Argentina: Prov. Jujuy; E slope Sierra Santa Barbara, near El Fuerte	1000	M. J. Andersen
NKK uncat.	<i>frontalis</i>	S. Andean group	Argentina: Prov. Jujuy; Parque Nacional Calilegua, Bananal	600	N. Krabbe
NKK uncat.	<i>frontalis</i>	S. Andean group	Argentina: Prov. Jujuy; Parque Nacional Calilegua, Bananal	600	N. Krabbe
NKK uncat.	<i>frontalis</i>	S. Andean group	Argentina: Prov. Jujuy; Parque Nacional Calilegua, Bananal	600	N. Krabbe

## Appendix C. Character Matrix for Chapter 4

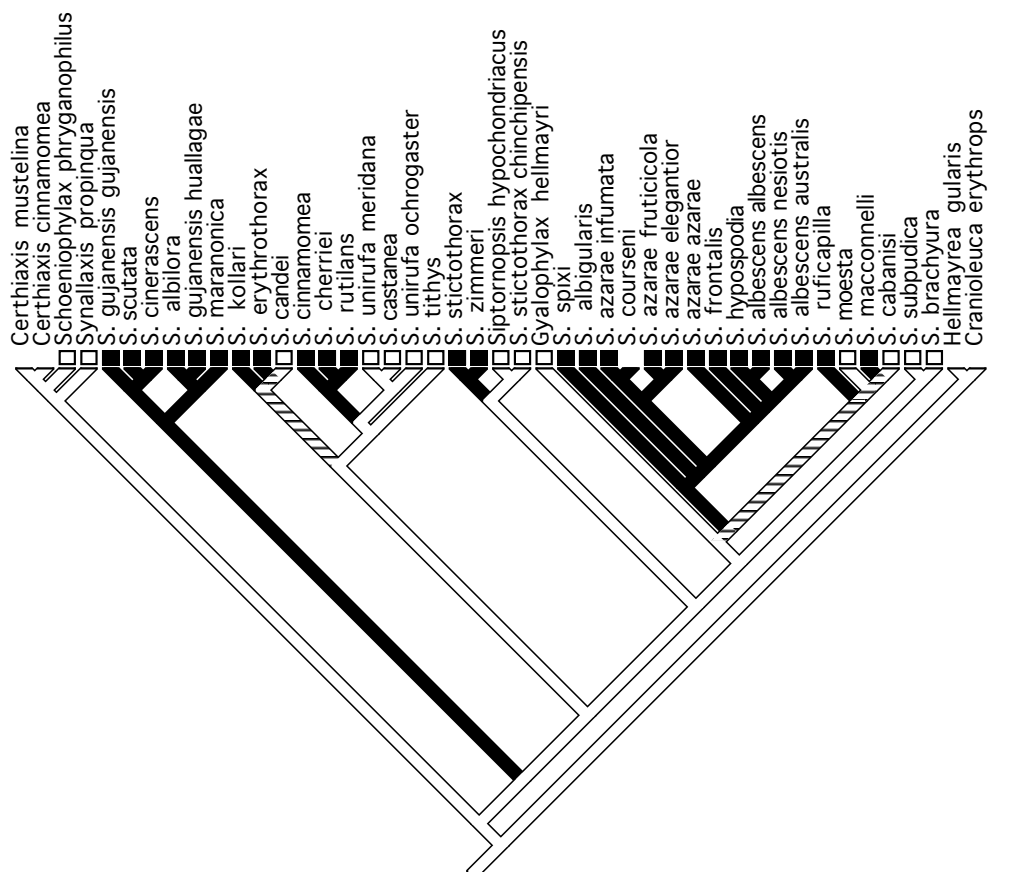
Characters are numbered as in Table 4.1. All genus names are “*Synallaxis*” unless written otherwise.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>S. albescens albescens</i>	1	0	1	1	2	0	1	1	2	0	0	0	0	1	0	1	1	0	1	0	0
<i>S. albescens nesiotis</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	1	0	1	1	0	1	0	0
<i>S. albescens australis</i>	1	0	1	3	2	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	0
<i>S. albigularis</i>	1	0	1	0	2	0	0	2	1	0	2	1	0	0	0	0	0	0	0	0	0
<i>S. albilora</i>	1	1	0	3	3	0	2	0	2	1	0	0	1	0	0	1	1	0	0	1	0
<i>S. azarae elegantior</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. azarae azarae</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. azarae fruticicola</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. azarae infumata</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. brachyura</i>	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0
<i>S. cabanisi</i>	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>S. candei</i>	0	1	0	1	2	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0
<i>S. castanea</i>	0	1	0	1	2	0	1	1	2	1	0	1	0	0	0	0	0	0	0	0	0
<i>S. cinerascens</i>	1	1	0	3	3	0	2	0	1	1	0	0	0	0	0	1	0	0	1	0	1
<i>S. cinnamomea</i>	1	0	1	1	2	0	2	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. cherriei</i>	1	1	0	1	2	0	1	0	2	0	3	1	0	0	0	1	0	0	0	0	0
<i>S. courseni</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. erythrothorax</i>	1	1	1	1	2	0	1	1	2	0	0	1	0	1	0	1	1	0	0	0	0
<i>S. frontalis</i>	1	1	0	1	2	0	1	1	2	0	0	0	0	0	1	1	1	0	1	0	0
<i>S. gujanensis gujanensis</i>	1	0	1	1	3	0	1	1	2	1	0	1	0	0	0	1	0	0	0	0	0
<i>S. gujanensis huallagae</i>	1	1	0	3	3	0	2	0	1	1	0	0	1	0	0	1	1	0	0	0	0
<i>S. hypospodia</i>	1	0	0	2	2	0	1	0	1	1	2	1	0	0	0	1	0	0	0	0	0
<i>S. kollari</i>	1	1	0	2	2	0	1	2	1	0	0	1	0	0	0	0	1	0	1	1	0
<i>S. macconnelli</i>	1	0	0	0	2	0	0	0	2	1	2	1	0	0	0	0	0	0	0	0	0
<i>S. maranonica</i>	1	1	0	1	3	1	2	1	2	1	0	0	0	0	0	0	1	1	0	0	0
<i>S. moesta</i>	0	0	0	0	1	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0
<i>S. ruficapilla</i>	1	0	1	1	2	0	1	0	2	0	2	1	0	0	1	1	0	0	0	0	0
<i>S. rutilans</i>	1	0	1	1	2	0	1	1	2	0	0	1	0	0	1	0	0	0	0	0	0
<i>S. scutata</i>	1	1	0	2	3	0	2	2	1	1	0	0	0	0	0	1	0	0	1	0	1
<i>S. subpudica</i>	0	0	1	2	2	0	1	2	1	1	0	0	0	0	0	0	1	0	0	1	0
<i>S. tithys</i>	0	1	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0

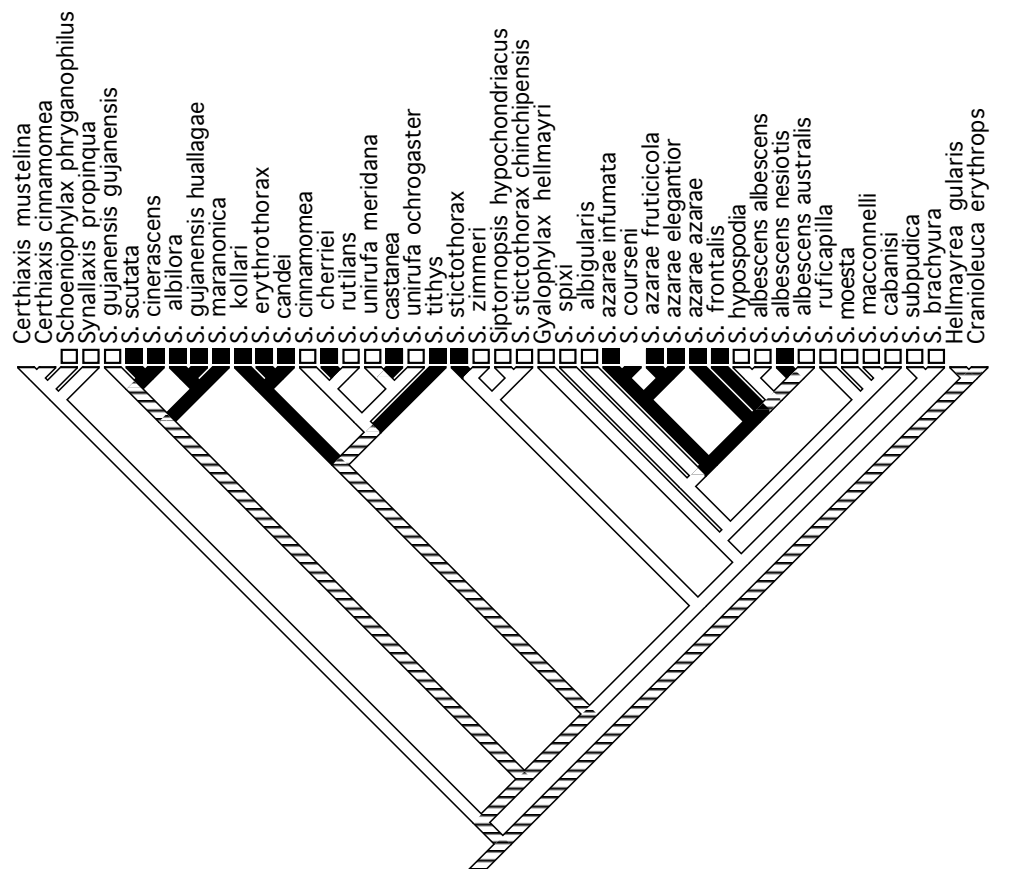


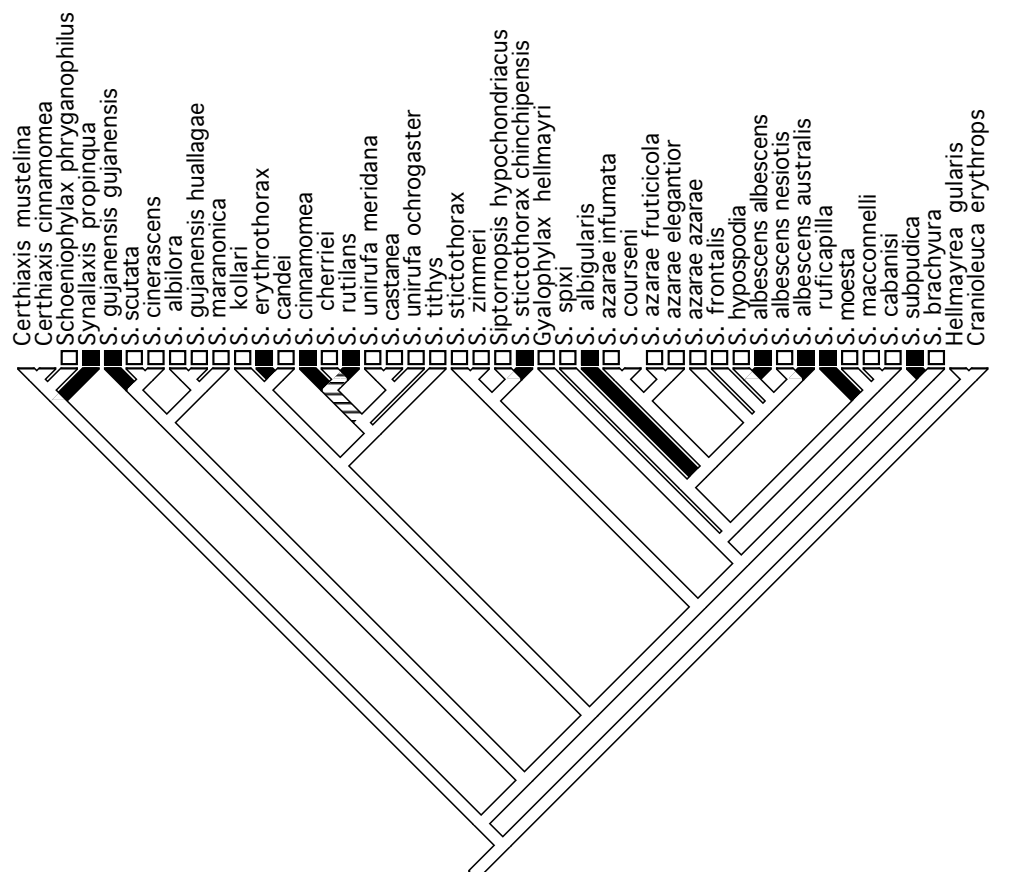
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>S. unirufa ochrogaster</i>	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>S. unirufa meridana</i>	0	0	0	1	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. spixi</i>	1	0	0	2	2	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0
<i>Gyalophylax hellmayri</i>	0	0	0	2	2	0	1	2	1	1	2	1	0	0	0	1	0	0	1	0	0
<i>S. stictothorax</i>	1	1	0	1	2	0	1	1	2	1	2	0	0	0	1	1	1	0	1	1	0
<i>S. zimmeri</i>	1	0	0	1	2	0	1	1	2	1	0	1	0	0	1	1	1	0	1	0	0
<i>Siptornopsis hypochondriacus</i>	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>S. stictothorax chinchipensis</i>	0	0	1	2	1	0	0	2	1	0	3	1	0	0	1	0	1	0	0	0	0
<i>Schoeniophylax phryganophilus</i>	0	0	0	2	2	0	0	2	1	1	3	0	0	0	0	0	1	0	0	1	1
<i>S. propinqua</i>	0	0	1	2	1	0	0	2	0	1	2	1	0	0	0	0	1	0	0	1	0
<i>Certhiaxis mustelina</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Certhiaxis cinnamomea</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hellmayrea gularis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cranioleuca erythrops</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

## **Appendix D. Character Maps**



2-part structure  
 unordered  
 0  
 1  
 equivocal



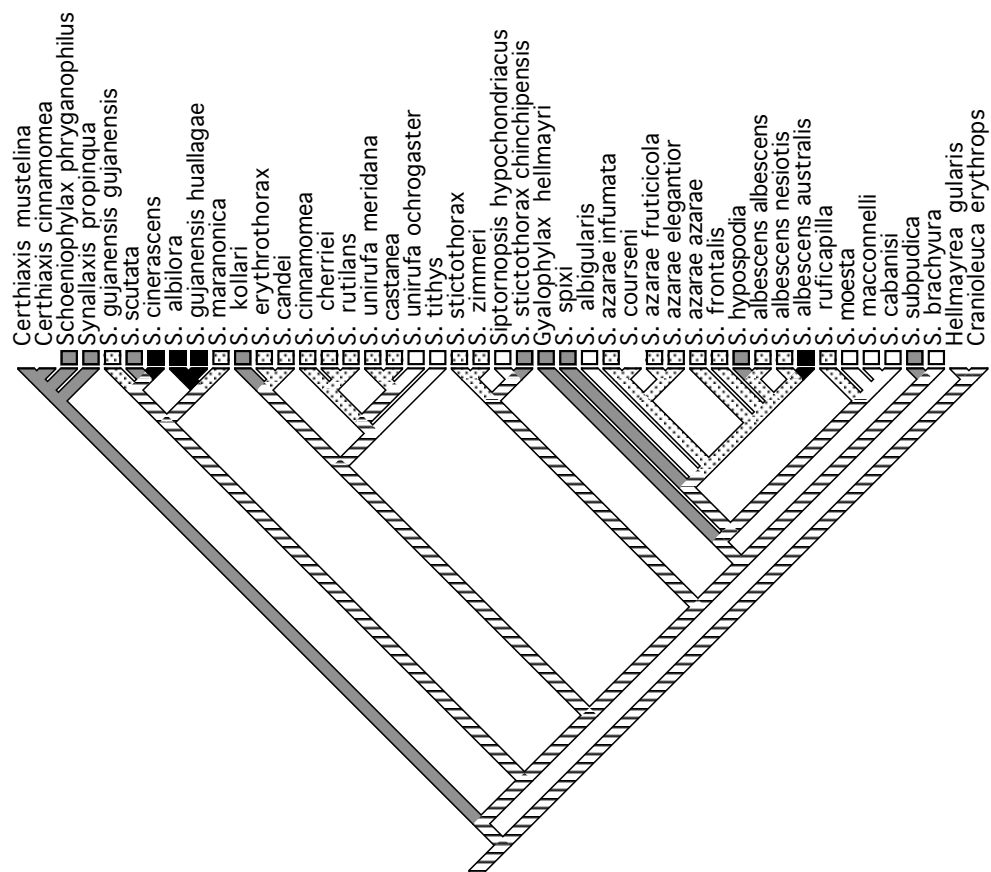


Frequency drop  
unordered

0

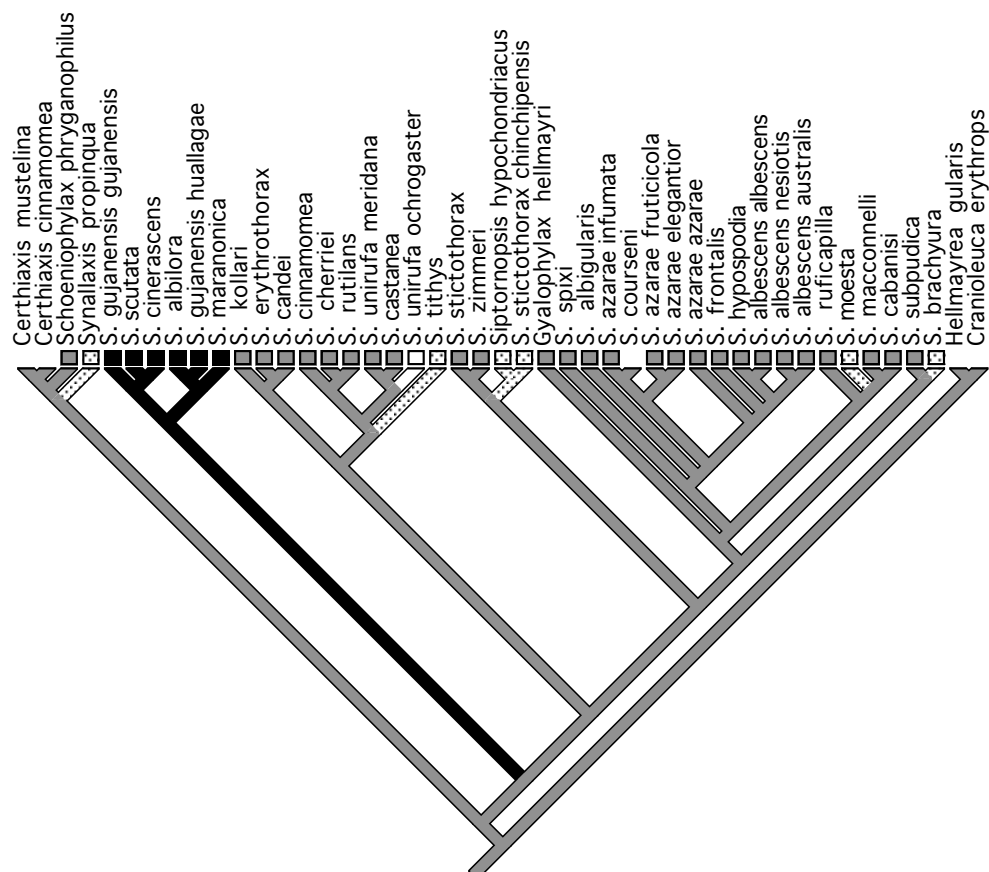
1

equivocal



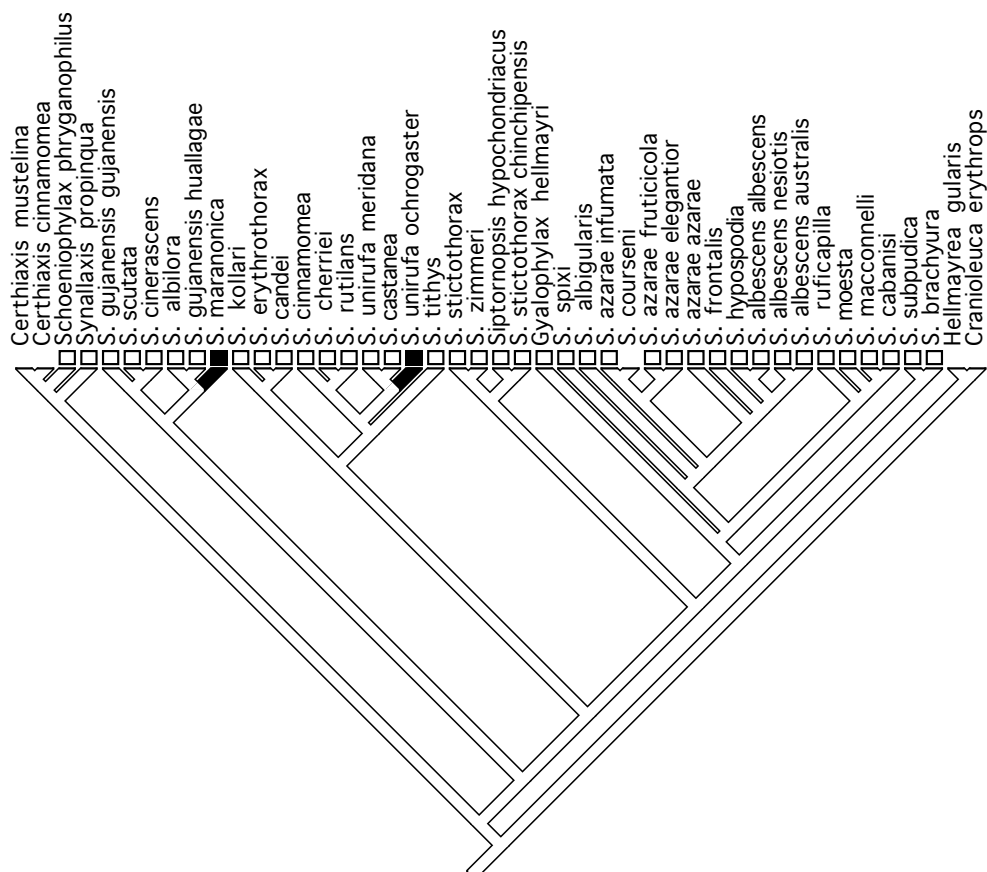
Temporal pattern  
unordered

0
1
2
3
equivocal



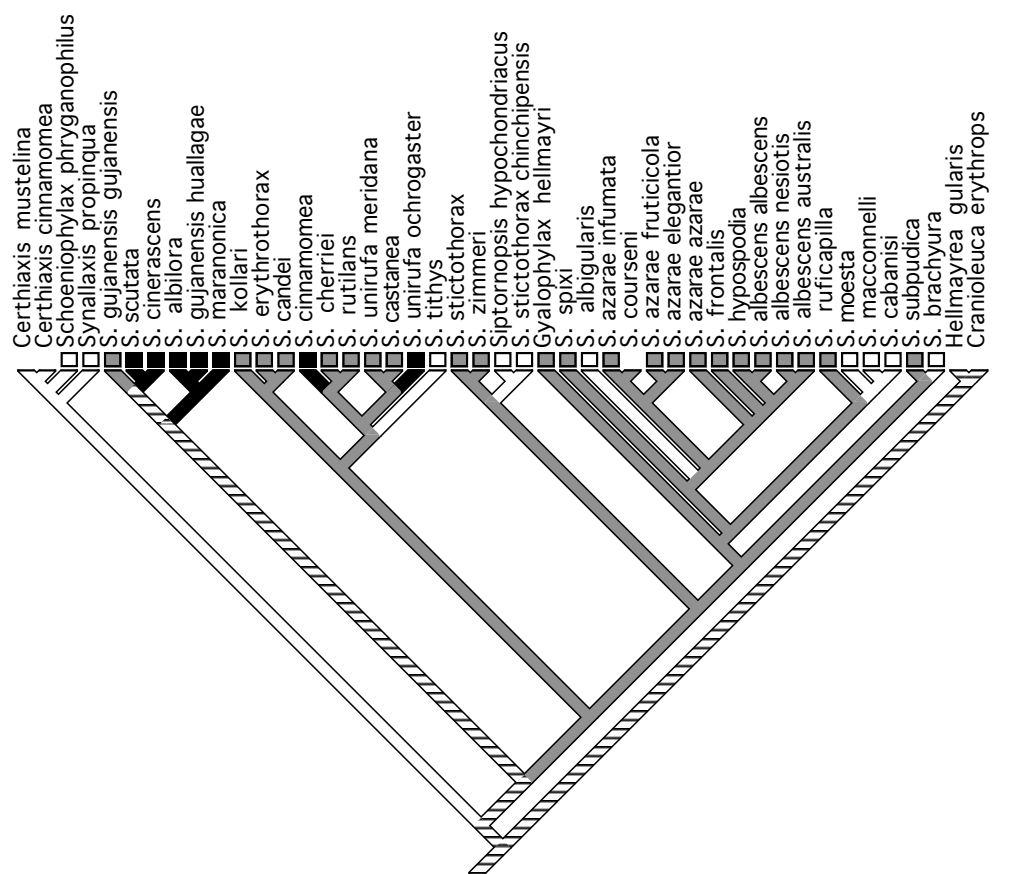
Longest pause  
unordered

0
1
2
3

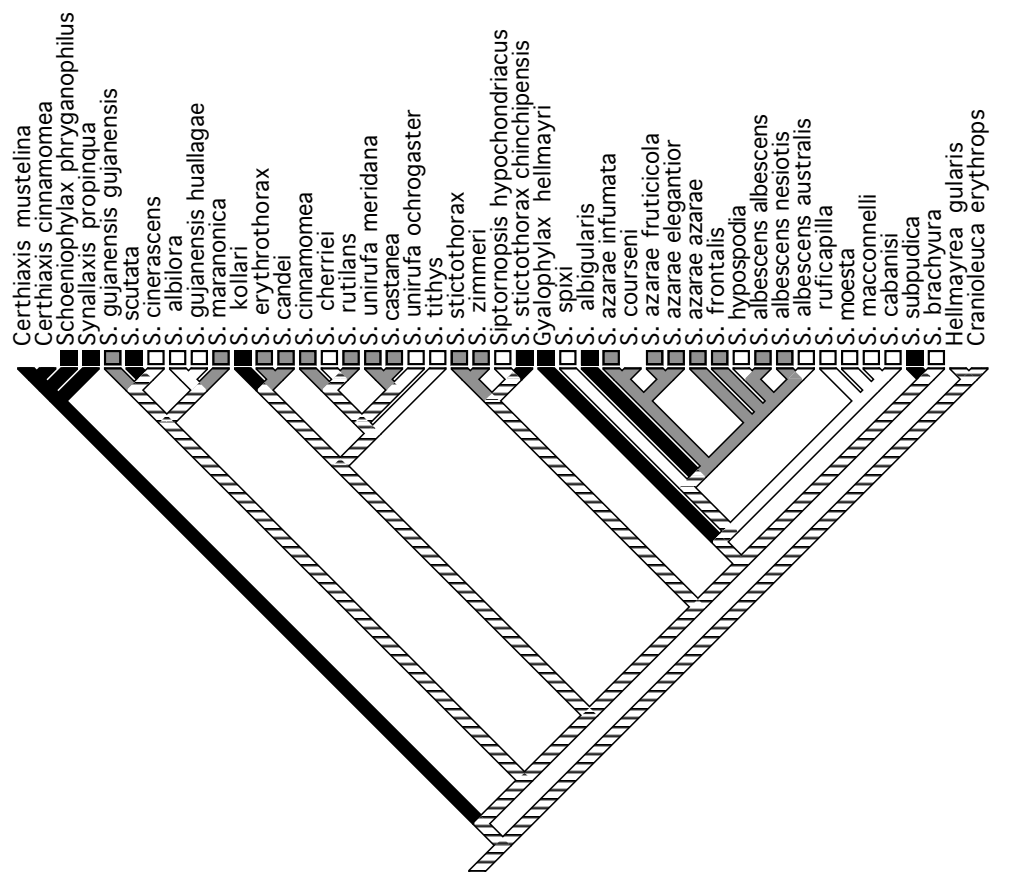


Shortest note  
unordered  
0  
1





Longest note  
unordered  
0  
1  
2  
equivocal



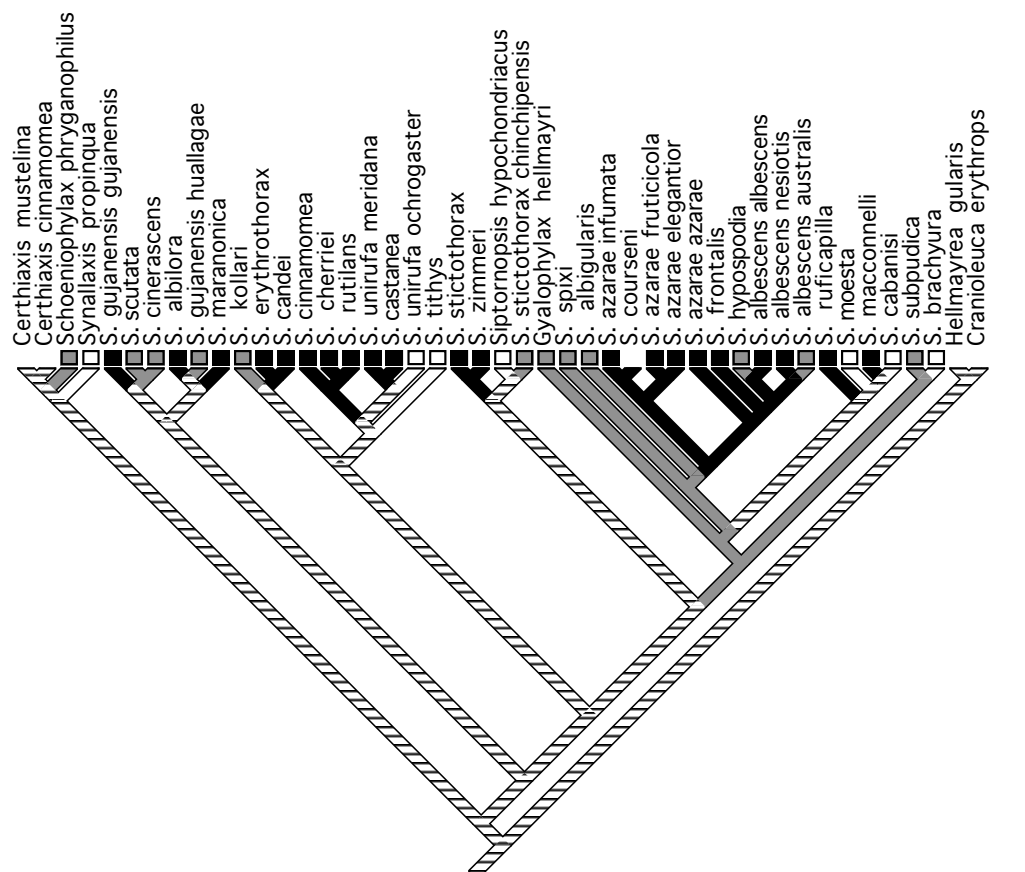
Short position  
unordered

0

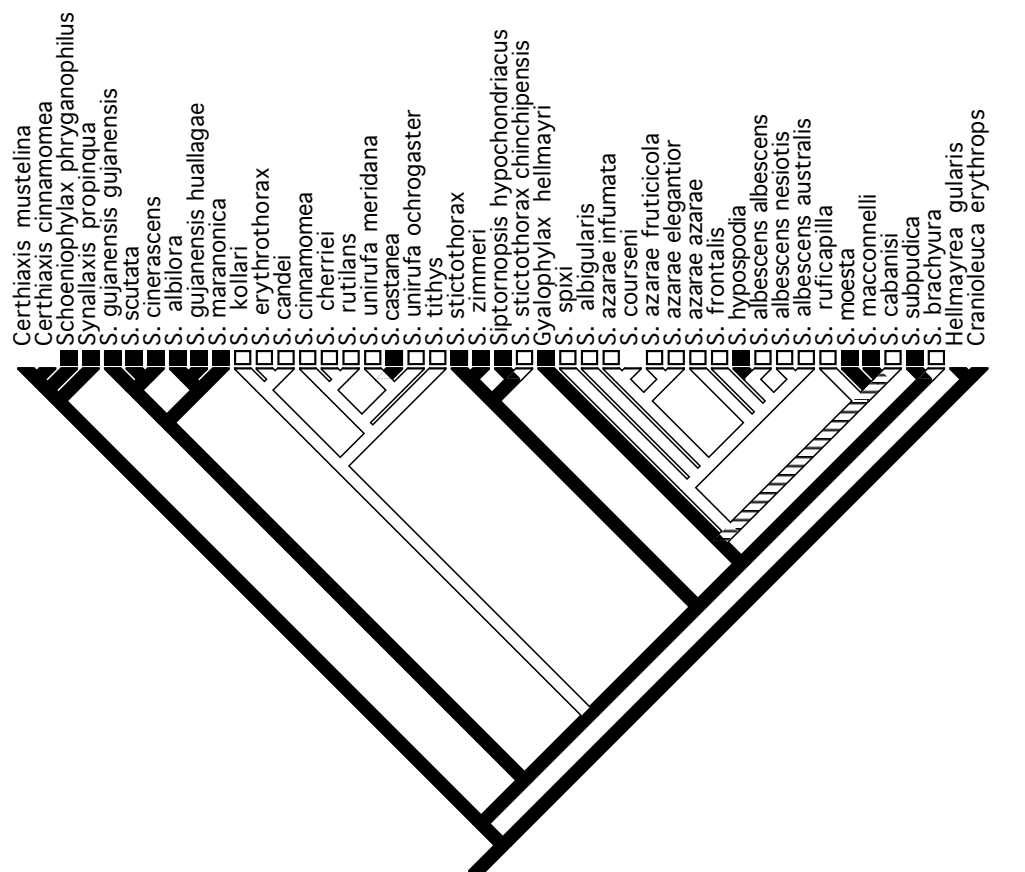
1

2

equivocal



Long position  
 unordered  
 0  
 1  
 2  
 equivocal

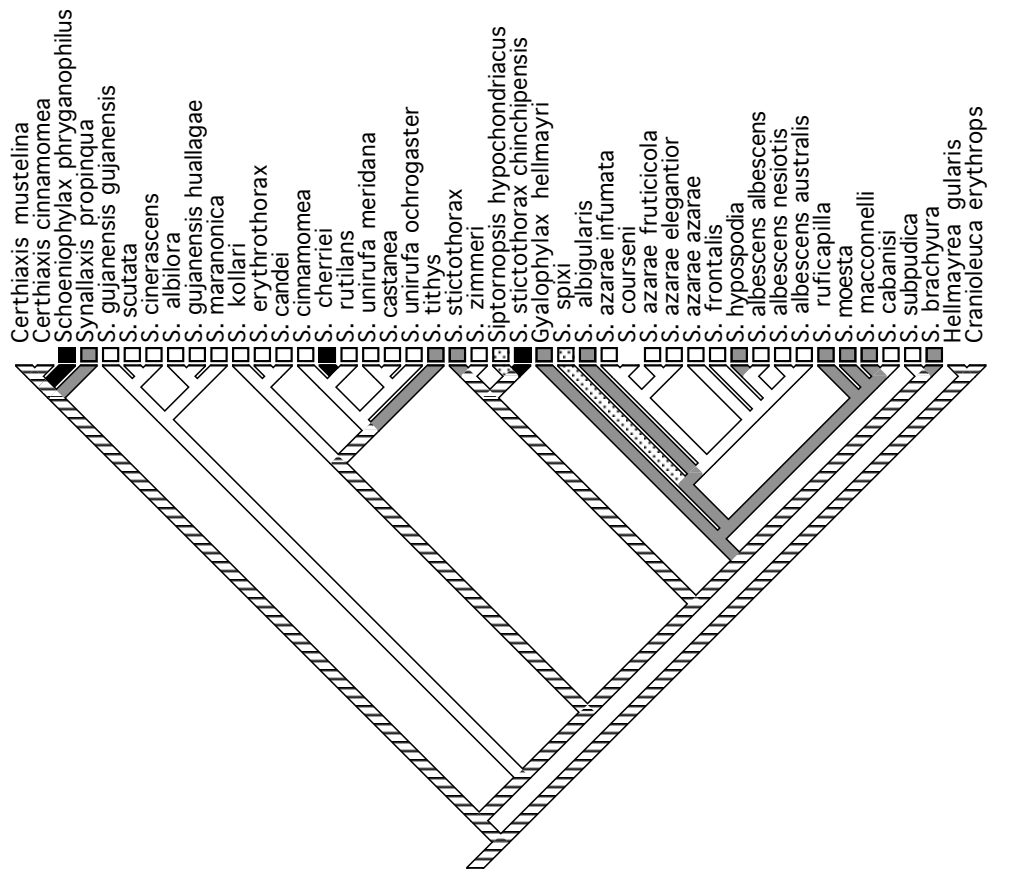


Total length  
unordered

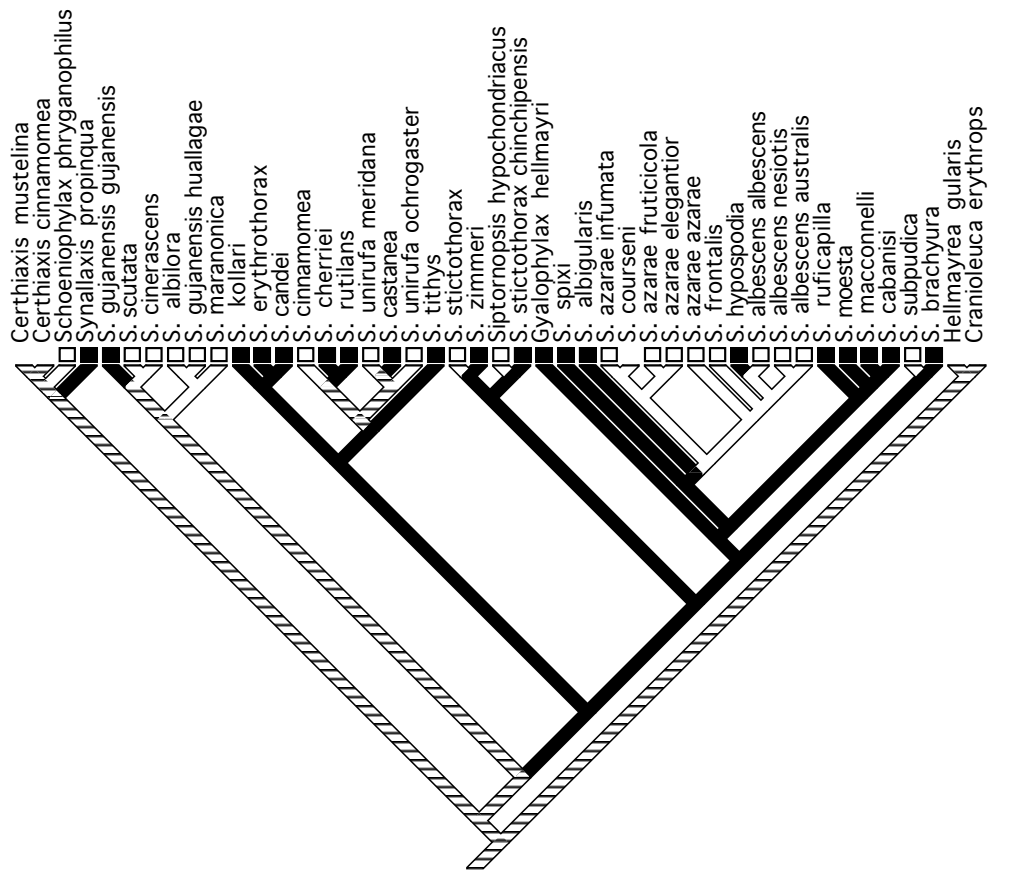
0

1

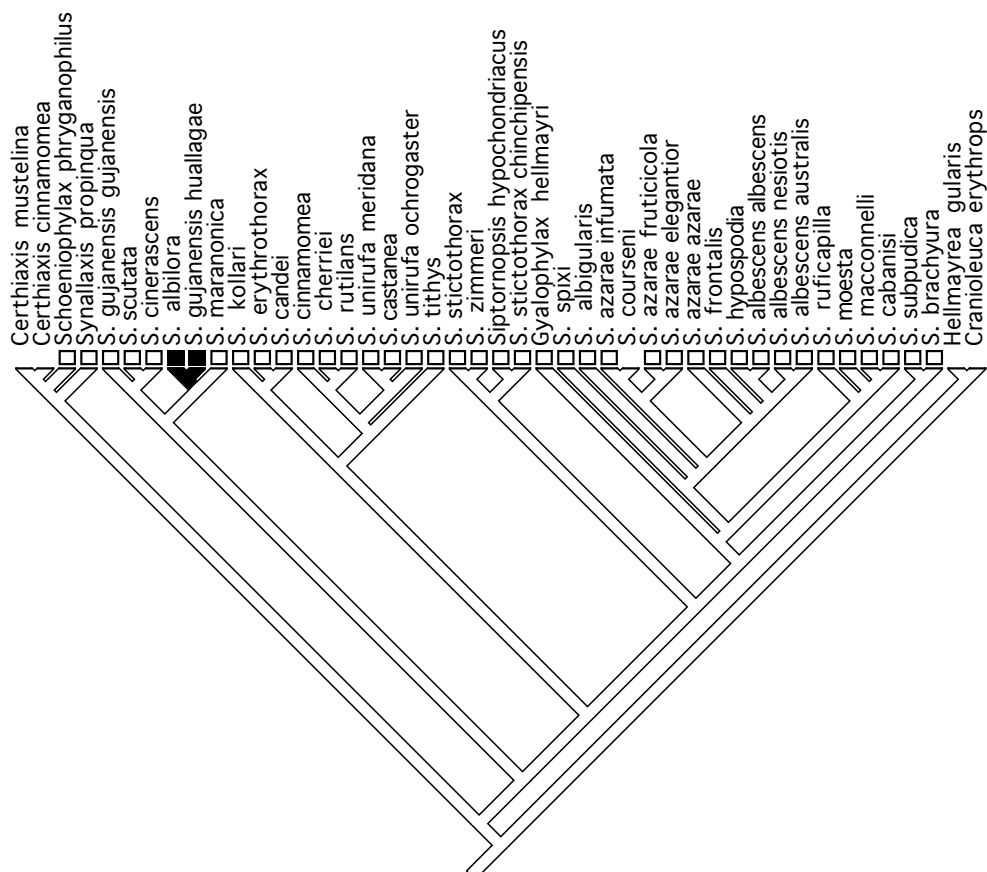
equivocal



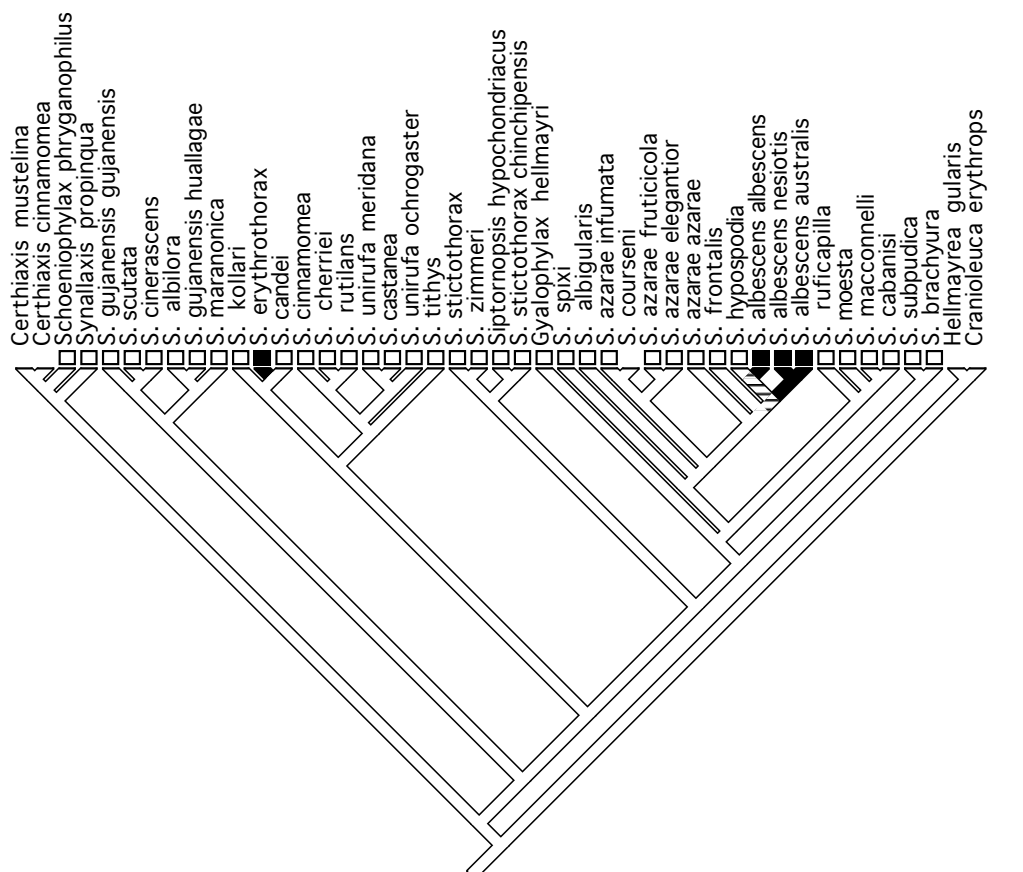
Trill  
 unordered  
 0  
 1  
 2  
 3  
 equivocal



U-note  
 unordered  
 0  
 1  
 equivocal

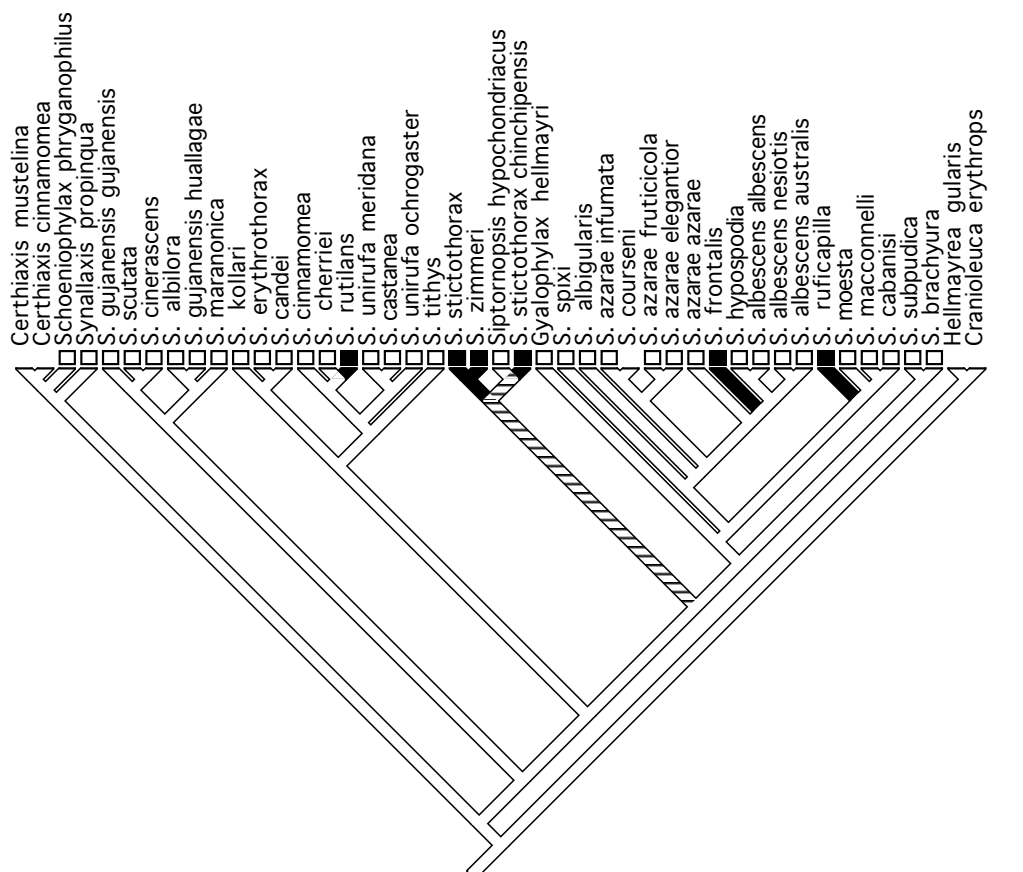


Hiccup  
 unordered  
 0  
 1

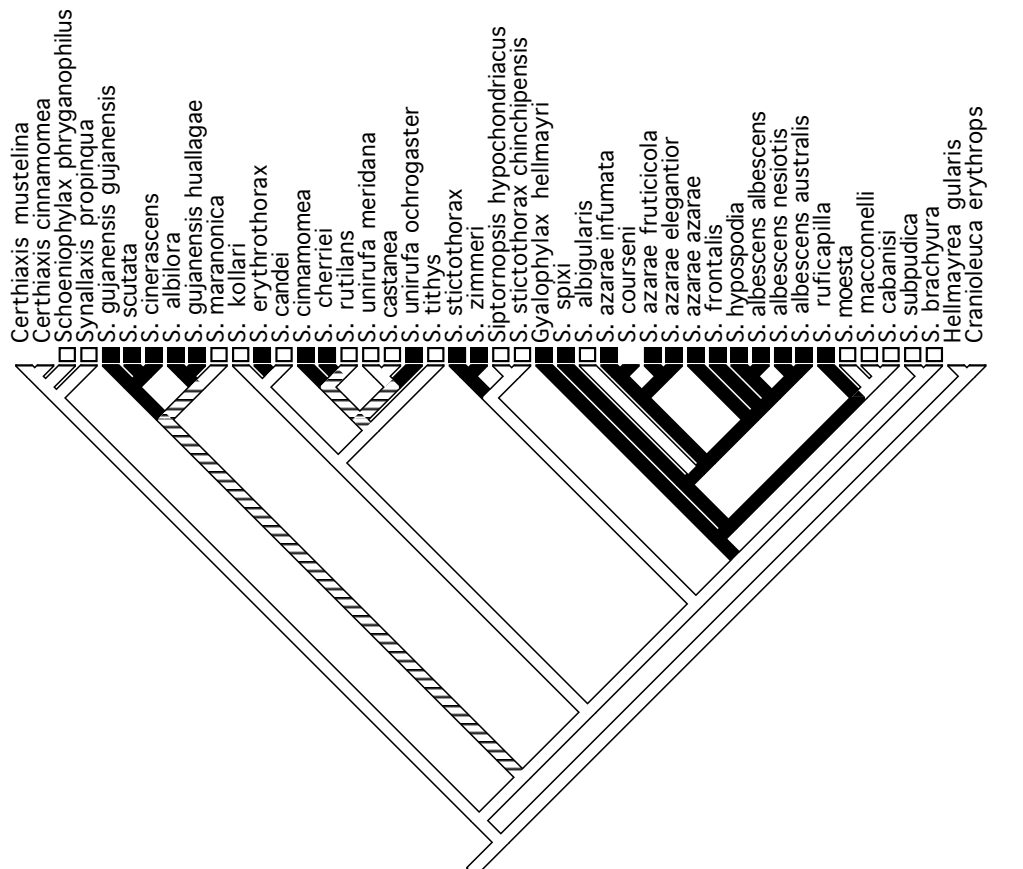


Buzz  
 unordered  
 0  
 1  
 equivocal

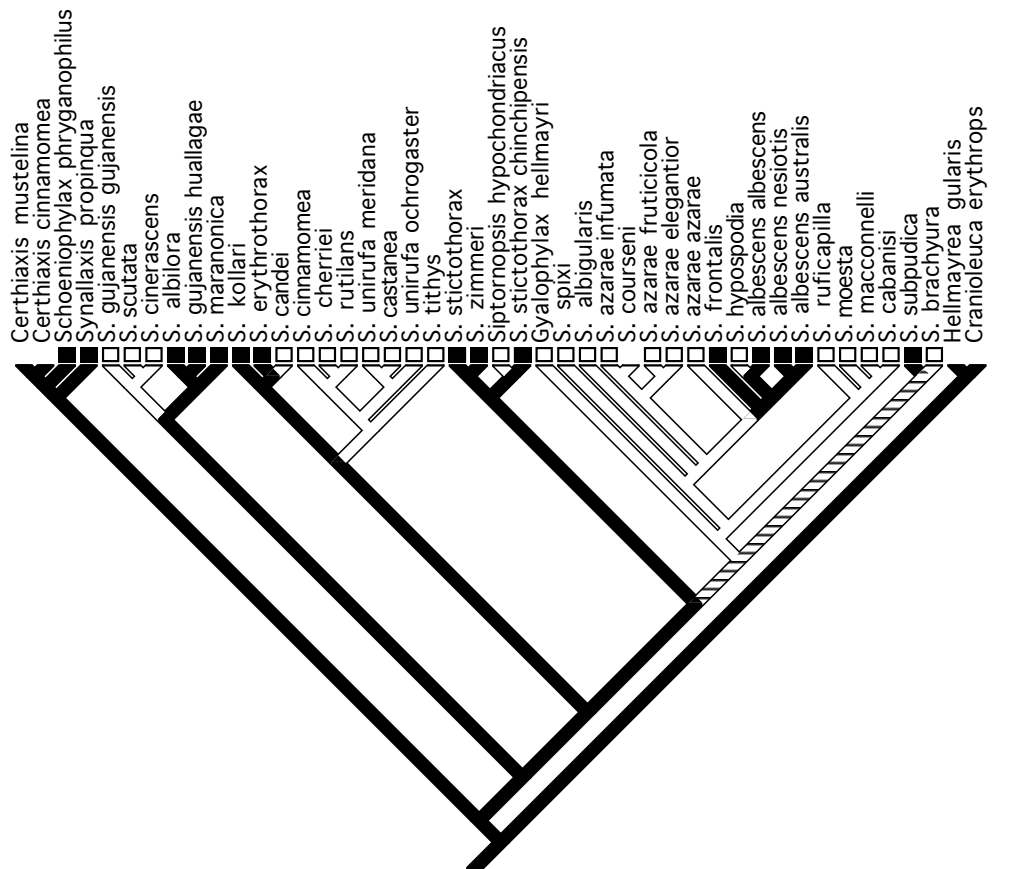




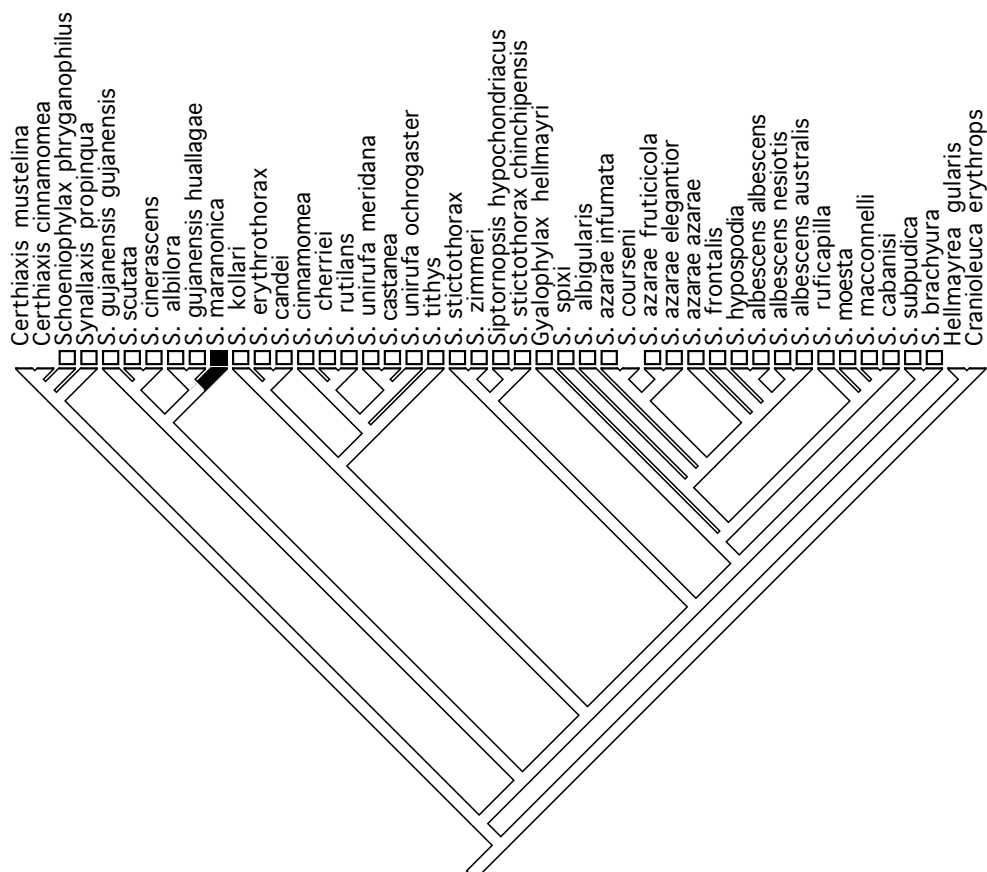
S-note  
unordered  
0  
1  
equivocal



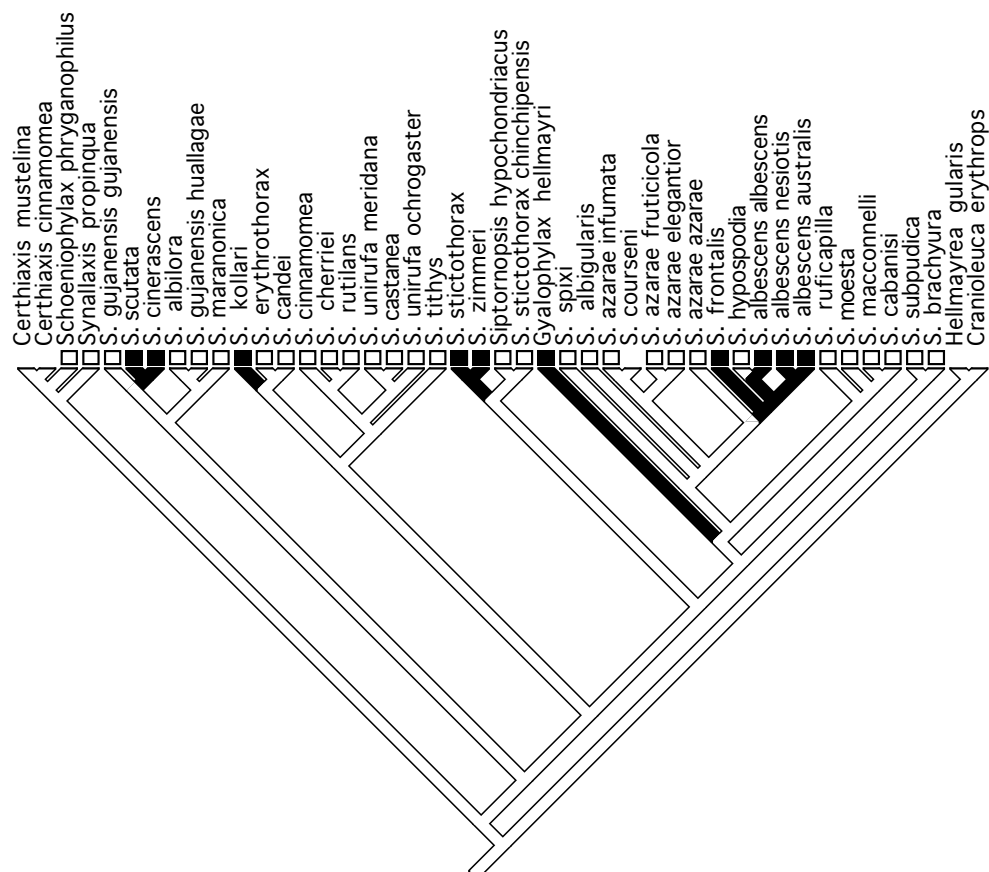
Ascending note  
 unordered  
 0  
 1  
 equivocal



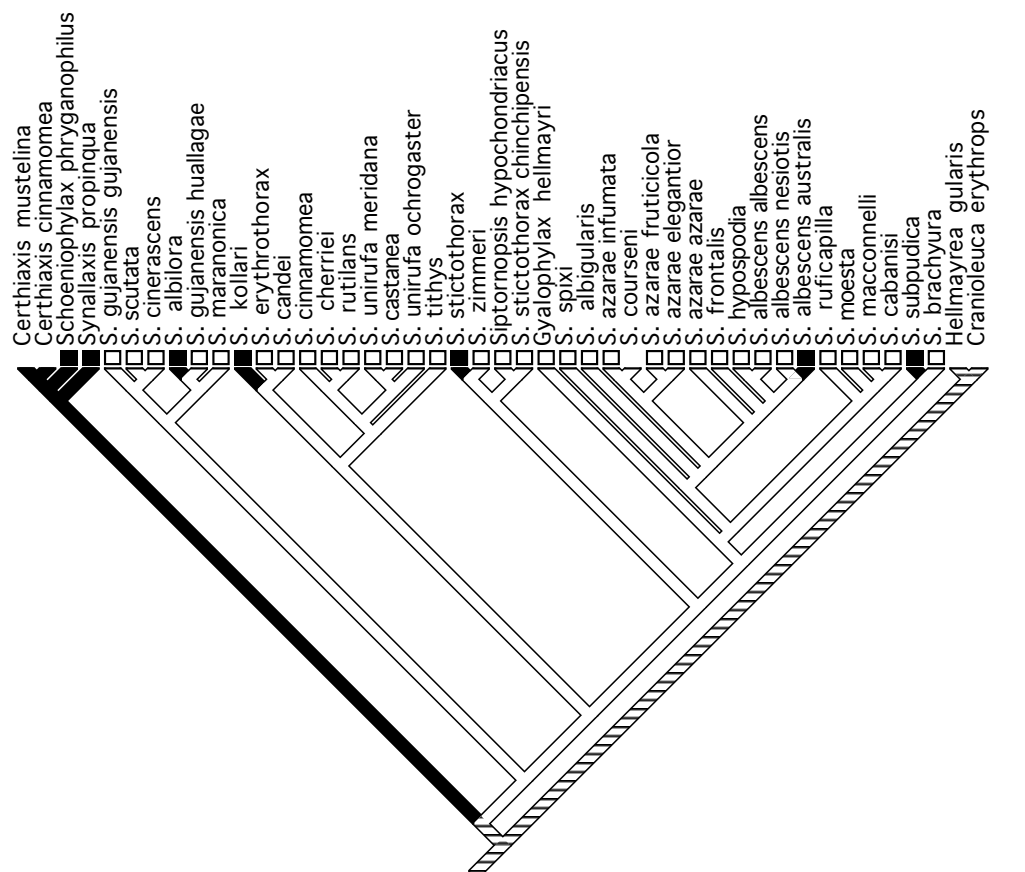
Descending note  
 unordered  
 0  
 1  
 equivocal



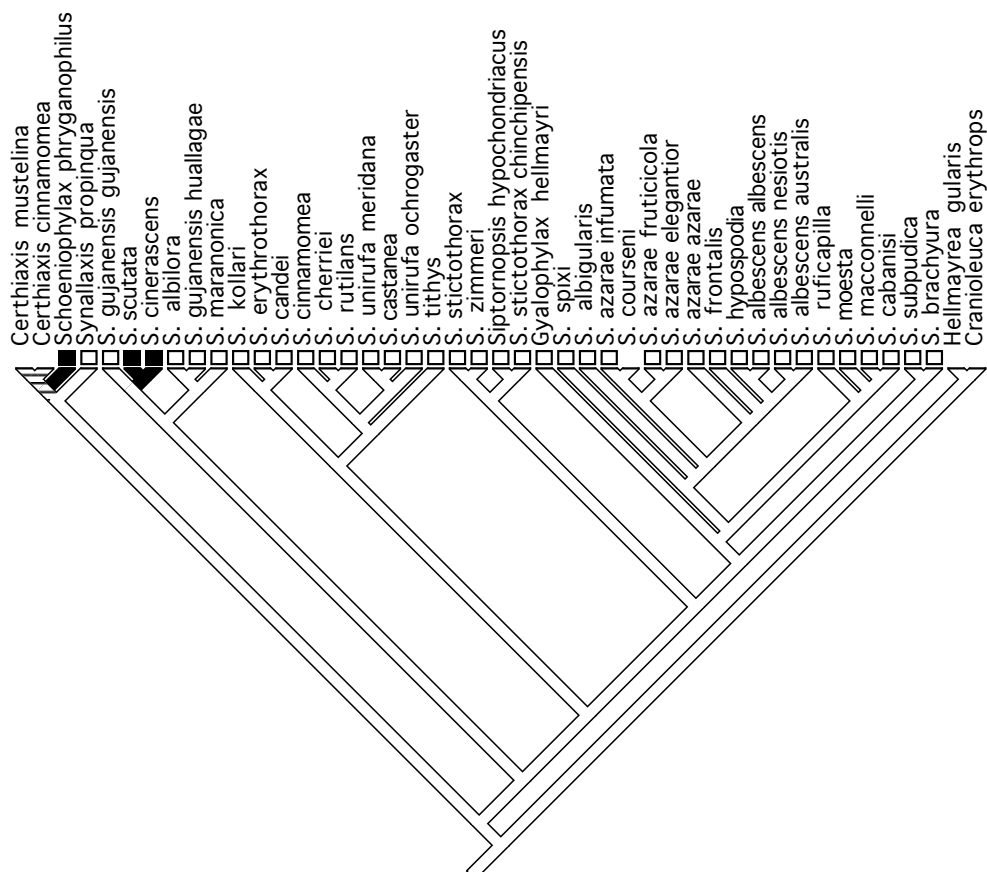
Peak note  
 unordered  
 0  
 1



Terminal spike  
 unordered  
 0  
 1



Initial spike  
 unordered  
 0  
 1  
 equivocal



Fundamental emphasis  
unordered

0

1

equivocal

## **Vita**

Brian John O'Shea was born in July 1975 in Des Moines, Iowa, to James and Nancy O'Shea.

Brian grew up in Washington, D.C., and Chicago, Illinois, and graduated from New Trier

Township High School in 1993. He maintained a keen interest in birds and nature from early

childhood. Brian graduated from Reed College in Portland, Oregon, in 1998, with a Bachelor of

Arts degree in Biology. Upon graduation, he moved to Ithaca, New York, where he first became

acquainted with museum collections under the tutelage of Kevin J. McGowan at the Cornell

University Museum of Vertebrates. Brian held various curatorial and field jobs in ornithology

for the next several years and spent much of this time in the Neotropics. Aside from a stint as

resident collector in Guyana for the Smithsonian Institution's Biological Diversity of the Guianas

Program, he was based primarily at the Field Museum, where he participated in several

expeditions to Peru, Bolivia, and El Salvador. Brian was actively engaged in fieldwork until

shortly before he started his doctoral program under Van Remsen at Louisiana State University

in 2002. During the course of his Ph.D. work, he traveled frequently to Suriname and Guyana,

where he worked as a consultant for the aluminum industry and Conservation International in

addition to collecting birds for the Louisiana State University Museum of Natural Science.

Many of his publications are derived from this fieldwork. Brian is an avid field recordist and has

archived over 1,000 recordings of birds at the Macaulay Library at the Cornell Lab of

Ornithology.