CHAPTER FOUR

# Integrating Museum and Media Collections to Study Vocal Ecology and Evolution*

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*Abstract.* Studies of animal vocalizations have generated key insights into the evolutionary and ecological forces that shape behavioral diversity in birds and other animals. Natural history collections and media archives provide a wealth of data that are being incorporated into studies of vocal evolution with increasing frequency and sophistication. Here, we review recent advances regarding the integration of museum and media collections to study vocal evolution and ecology of animals with a special emphasis on birds. We consider how digital archives of bioacoustic data combined with vouchered specimens and other biological collections have improved our understanding of geographic variation in vocalizations, longitudinal studies of cultural evolution, and comparative studies of vocal evolution and diversification, among other topics. We highlight case studies that exemplify the novel approaches and insights gained from studies of animal vocalizations that leverage biological collections. In providing this overview, we encourage the scientific community to further consider how natural history collections can address longstanding questions in ecology and evolutionary biology.

*Key Words*: archives, bird song, specimen.

Animals vocalize to exchange information with other individuals for tasks essential to reproduction and survival, such as attracting mates and defending territories (Bradbury and Vehrencamp 1998). Bioacoustics and the study of avian vocalizations have deep roots in ornithology, and studies therein have provided important advances that contribute to our broader understanding of animal behavior (e.g., Marler and Slabbekkoorn 2004, Dugatkin 2009). Traditionally, studies of animal vocalizations have relied on behavioral observations of live organisms rather than museum specimens from natural history collections; ongoing and recent studies, however, increasingly leverage natural history and technological innovations to enable large-scale investigations of animal vocalizations—both within and among populations and species. Here, by reviewing recent studies that combine bioacoustics and museum specimens, we identify emergent trends in how natural history collections have advanced our understanding of the evolutionary and ecological

processes that shape the remarkable diversity of animal vocal signals that occur in nature.

Although the field of bioacoustics and the practice of recording birds for scientific purposes have existed since the early 1900s (Gaunt et al. 2005), recent technological innovations have induced a paradigm shift in how natural sounds are collected, archived, and distributed to scientific researchers, educators, and the general public (Ranft 2004, Betancourt and McLinn 2012). The advent of digital audio has transformed large rooms filled with reels upon reels of analog recordings into terabytes—or even petabytes—of digital audio files, which can be accessed by anyone with an Internet connection (Budney et al. 2014, Marques et al. 2014). Large-scale digital archiving initiatives, such as efforts spearheaded by the Macaulay Library (http://macaulaylibrary.org/), the Borror Laboratory of Bioacoustics (https://blb.osu.edu/), and Xeno-Canto (http://www.xeno-canto.org/), among others, have made millions of recordings readily available. This massive amount of bioacoustic data has enabled diverse research initiatives at an unprecedented scale across geographic space, taxonomy, and time.

In this chapter, we review recent developments in how data from ornithological collections—such as audio recordings and physical specimens—have advanced our understanding of the evolution and ecology of bird song, including geographic variation, selective constraints, and rates of vocal evolution and diversification (Figure 4.1). Birds produce a wide variety of sounds, including nonmating calls and mechanical sounds; we focus on songs, which serve as courtship and territorial displays and are typically conspicuous behaviors (Catchpole and Slater 2008). One prominent way in which songs differ among avian lineages is whether vocal displays are learned through cultural transmission or are inherited genetically (Slater 1986, Kroodsma 2005). Learning can have profound effects on the evolution of characters involved in sexual selection
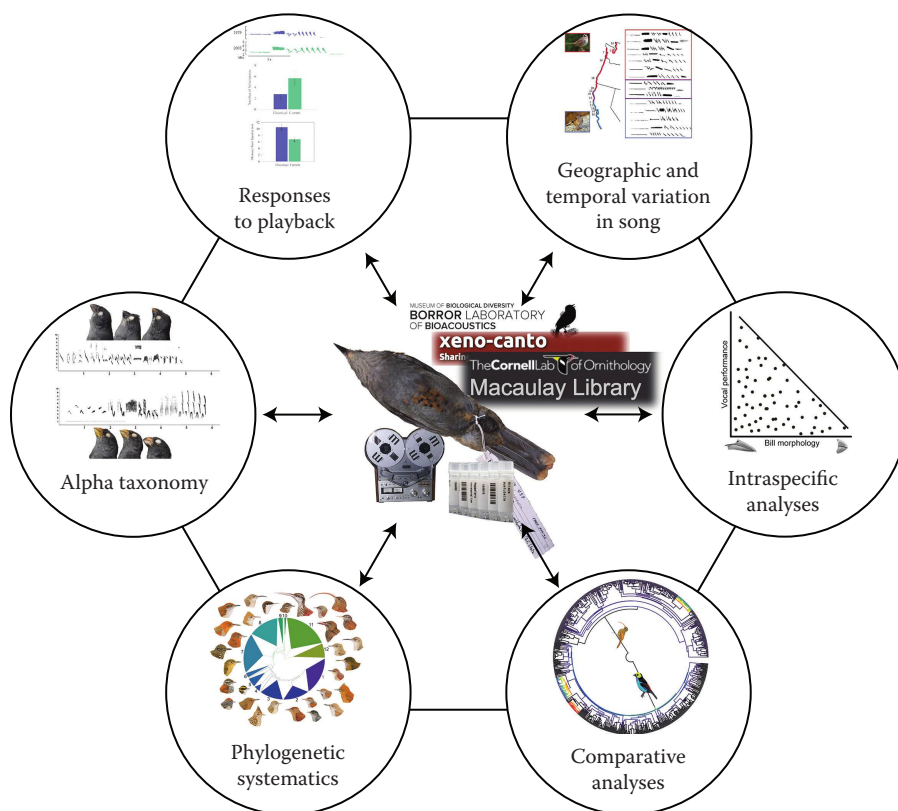


Figure 4.1. Conceptual advances enabled by combining media archives and natural history collections. Each circle on the perimeter represents a research topic that has been advanced by combining data from physical museum specimens and digital bioacoustic archives.

and speciation (Verzijden et al. 2012). In allopatry, learning can accelerate vocal evolution and speciation (Lachlan and Servedio 2004). When distributions overlap, however, learning can diminish the role of songs as premating barriers to gene flow (Seddon and Tobias 2007, Olofsson et al. 2011). Thus, the impacts of learning on vocal evolution and diversification are complex and context dependent (Wilkins et al. 2013). Although we emphasize birds throughout the chapter, we also include a brief section on parallel advances in nonavian taxa. Finally, we consider future directions and goals of the field in leveraging natural history collections to further the study of animal vocalizations.

## SPECIES LIMITS AND GEOGRAPHIC VARIATION IN BIRD SONG

Many species exhibit geographic variation in vocalizations (Podos and Warren 2007), and these patterns of vocal variation play an important role in understanding species limits in avian taxonomy (Alström and Ranfft 2003, Tobias et al. 2010). Closely related species are often most differentiated in secondary sexual characteristics (Coyne and Orr 2004), and birds often exhibit stronger premating than postmating reproductive barriers (Grant and Grant 1997, Price 2007). As such, it is not surprising that geographic variation in song can act as a cue and precursor to genetic divergence. Recent studies highlighting the importance of vocalizations in delimiting avian species include the newly described Tropeiro Seedeater (*Sporophila beltoni*; Repenning and Fontana 2013) and Perijá Tapaculo (*Scytalopus perijanus*; Avendaño et al. 2015). Since 1990, more than 25 published species descriptions include analyses of audio recordings that are curated by digital sound archives, such as the Macaulay Library (e.g., Fitzpatrick and Willard 1990, Zimmer et al. 2001, Cuervo et al. 2005, Herzog et al. 2008), and the majority of those publications reference a media specimen as a "vocal type voucher" that can augment the value of traditional museum specimens.

Songs often vary substantially among populations and individuals within a species as well as among species; quantifying geographic variation among populations is another fundamental use of audio recordings of bird song. Until recently, however, most studies exploring geographic variation in bird song have relied on individual efforts to sample vocalizations from different populations

and to characterize variation in songs and vocal repertoires among the sampled individuals and populations. Such early efforts were motivated by attempts to document song learning as well as interspecific and intraspecific patterns in geographic song variation. Early examples include the studies of Luis Baptista from the California Academy of Natural Science. In the 1970s and 1980s, Baptista and colleagues captured individual and geographic measures of song variation across multiple subspecies of White-crowned Sparrows (*Zonotrichia leucophrys*), covering thousands of miles (Baptista 1975, 1977; Orejuela and Morton 1975; Baptista and Morton 1982). Those efforts made possible a series of later studies on geographic and temporal variation in White-crowned Sparrow song (Chilton and Lein 1996a; Harbison et al. 1999; Derryberry et al. 2007; Derryberry 2009, 2011). Many examples exist of similarly impressive early efforts to document geographic variation in the song of birds (see Mundinger 1982 for overview). Unfortunately, many of these early efforts survive only as spectrograms printed in journal articles: the original recordings no longer exist. Baptista's archival efforts reflected his position as a museum curator. Most other early recordists—many of whom were not associated with museums—did not archive their analog materials, and these recordings are often lost or are now too degraded for scientific use (Van Bogart 1995). Historically, gathering recordings to study avian vocalizations was largely an individual endeavor requiring extensive time and effort in the field by the primary investigators rather than a community-based initiative.

In sharp contrast, recent studies of geographic variation in bird song leverage preexisting recordings that are made available by digitized bioacoustics libraries, which has enabled large-scale studies of geographic variation in vocalizations that were previously unfeasible. Direct collection of digital audio recordings, in contrast to analog recordings, which required heavier equipment and digitization time, has facilitated more individuals making recordings (including "citizen science" approaches) and wider dissemination of those recordings (August et al. 2015). This recent boom in material has necessitated new conversations regarding best practices for annotating and vouchering recorded materials (Ranft 2004).

Among songbirds, recent studies on Common Yellowthroat (*Geothlypis trichas*; Bolus 2014), Alder

Flycatcher (*Empidonax alnorum*; Lovell and Lein 2013), Yellowhammer (*Emberiza citronella*; Petrusková et al. 2014), and Ruddy-capped Nightingale-thrush (*Catharus frantzii*; Ortiz-Ramírez et al. 2016) demonstrate how researchers can draw from multiple sources of audio recordings to characterize geographic variation in song. Nonetheless, many studies continue to rely on individual efforts, particularly in geographic regions that have few birders or ornithologists actively collecting animal sounds. Petrusková et al. (2010), for instance, categorized individual and geographic variation from over 2,000 songs of Tree Pipit (*Anthus trivialis*) at multiple spatial scales in eastern Europe. Other examples include Cicero and Benowitz-Fredericks (2000), who recorded over 4,500 songs from more than 50 male Lincoln's Sparrow (*Melospiza lincolnii*) to characterize variation in repertoire size and song types. While the availability of bioacoustics data through media archives and the digitization of analog recordings have enabled large-scale geographic studies, continued individual and collective recording efforts are still required to expand both the breadth and depth of available data for many species and regions.

The studies summarized here do not cover exhaustively the extensive work done by contemporary ornithologists to characterize geographic variation in bird song. Nevertheless, these studies do illustrate general trends in how audio data are collected, digitized, and widely disseminated for modern studies of animal communication. In addition to increased access to bioacoustics data, recent advances in analytical methods, including improved software and algorithms for detailed and automated analyses, have enabled high-throughput processing of numerous recordings (Aide et al. 2013). Together, these approaches have facilitated large-scale studies of avian vocalizations and cultural evolution among many taxa and across impressive geographic and temporal axes.

## CULTURAL EVOLUTION AND TEMPORAL VARIATION IN AVIAN VOCAL DISPLAYS

Our understanding of the tempo and mode of song evolution is largely limited to studies of *current* variation in vocal displays. Whereas contemporary geographic variation in song provides one snapshot of song variation representing the results of different selective pressures acting on song over time, longitudinal studies can provide a more

direct assessment of how sexual and natural selection shape bird song. Nonhistorical approaches to temporal processes are problematic in the study of cultural traits (Payne 1996) as well as genetic traits (e.g., Gillespie 1991). Some common assumptions made by only considering current geographic variation in phenotypes—many of which are probably not met by song—are that traits evolve at a constant rate, that traits diverge gradually over time, and that local dispersal explains the geographic distribution of traits (Lynch et al. 1989, Lynch and Baker 1993). For example, in one of the few studies to carefully follow changes in song over time, changes in song did not reflect a branching tree among Indigo Bunting (*Passerina cyanea*) populations; instead, patterns of song evolution resembled a reticulated network in which song components were shared among individuals from different lineages rather than following a strict pattern of inheritance (Payne 1996). Measures of temporal variation in song are thus essential to a complete understanding of the tempo and mode of song evolution. Although song can evolve within contemporary timescales and can be documented within an investigator's lifetime, many questions remain about temporal variation at longer, multigenerational timescales. Such questions can only be answered with access to archived, historical song samples.

The earliest studies on temporal variation in song documented patterns of cultural transmission. Changes in songs over time were due to innovations, mistakes, or preferential learning. These studies often represented the efforts of individual scientists recording banded individuals within populations over one or a few generations of birds (e.g., Jenkins 1978; Mundinger 1980; Payne et al. 1981, 1988; Payne and Payne 1993; Payne 1996; Lang and Barlow 1997). Building on this foundation, subsequent studies compared songs recorded within the same locality but across decades, often relying on earlier datasets and recordings collected by a different investigator. These types of studies documented both remarkable stability (e.g., Payne et al. 1981, Baker and Jenkins 1987, Harbison et al. 1999, Derryberry 2009) as well as rapid turnover (e.g., Ince et al. 1980, Chilton and Lein 1996b, Payne 1996, Baker et al. 2003) of song features. Such variation in transmission patterns inspired follow-up work to assess the selective pressures shaping bird song (e.g., Nelson et al. 2004, Derryberry 2009). Only a handful of the

recordings from earlier studies on temporal variation were archived, thereby limiting the number of species that can be currently studied over multiple generations of birds. Yet continued archiving of natural sounds ensures that future generations of scientists can study how vocal signals evolve using longitudinal datasets.

## BEHAVIORAL RESPONSES TO GEOGRAPHIC AND TEMPORAL VARIATION IN SONG

The efficacy of mating signals depends on successful communication, or the transmission and reception of a signal (Searcy and Nowicki 2005). Any breakdown in this process can lead to reduced fitness by suppressing either mate attraction or territoriality (West-Eberhard 1983, Sætre 2000). Less effective signals may reduce an individual's ability to compete successfully against rival males, thereby affecting their ability to obtain a mate (West-Eberhard 1983; Andersson 1994). Interspecific behavioral barriers to gene flow may form if populations diverge in mating signals and/or signal recognition. Grant and Grant (1997) suggest that avian speciation, in particular, is often driven by the evolution of premating barriers, and one source of these barriers may be the diversification of song. Studies of geographic and temporal variation in bird song not only allow determination of the sources of selection driving song diversification, but also permit measurement of the functional consequences of diversification in mating signals. The 60-plus years of work on song indicates that both potential mates and competitors respond differently to geographic and temporal variants of song. Substantial geographic variation in song has been documented in many species (e.g., Baptista and King 1980, Krebs and Kroodsma 1980, Tubaro and Segura 1995, Martens 1996, Chilton et al. 2002). In turn, individuals (both male and female) generally respond more strongly to conspecific rather than heterospecific song (Ratcliffe and Grant 1985, Grant and Grant 1996, Bentley et al. 2000, Soha and Marler 2001, Nelson and Soha 2004; but also see Sætre et al. 1997, Irwin et al. 2001a). Many individuals also prefer songs of their local population over songs of other conspecific populations (reviewed in Andersson 1994, Catchpole and Slater 1995, Searcy and Nowicki 2005). Species often have diverse vocal repertoires that include distinct signals involved in territoriality or mate attraction,

and these different signals frequently evolve under distinct selective pressures among signal producers and receivers (Searcy and Brenowitz 1988, Seddon and Tobias 2010). In certain instances, taxa may converge on similar songs through cultural selection acting on interspecific territorial displays, whereas signals involved in mate attraction may remain diagnostic among species (Podos and Warren 2007, Tobias and Seddon 2009). These behavioral assays of response to heterospecific and geographic song variants demonstrate that the reproductive and territorial efficacy of vocal displays depends on the source population of both the signal producer and the receiver and the ecological context in which signals are produced.

Testing receiver responses to geographic song variants is often used as an approximation of signal evolution over time (e.g., Irwin et al. 2001b). Differences in responses to playbacks of songs from separate populations within a species' range indicate that signal divergence among populations may lead to reproductive isolation (Lachlan and Servedio 2004). Yet patterns of responses to playbacks provide little information on how signal evolution within populations contributes to reproductive isolation. Another approach measures receiver responses to statistical reconstructions of ancestral signals to infer the formation of reproductive barriers between species (Ryan and Rand 1995, Losos 1999).

The most direct test of the effect of signal evolution on signal efficacy within populations is to measure the response of receivers to actual mating signals at different time points within a single population. Measurement of responses to actual mating signals are rarely used because of the obvious difficulty of preserving historical songs in a manner that allows their use in behavioral tests. Stimuli used in behavioral assays must have high signal-to-noise ratios and minimal degradation. In addition, recordings of multiple individuals are needed to avoid pseudoreplication during experiments (Kroodsma 1990). In the 1960s, the use of audio recordings to document bird song became widespread, and recordings that were properly archived are now a primary source of historical songs of sufficient quality to be used in behavioral assays, including territorial playbacks, copulation solicitation, and operant conditioning assays.

Derryberry (2007) used historical recordings of song from a population of White-crowned Sparrows at Tioga Pass, California, to test whether

changes in mating signals over time induced a loss in signal efficacy. Derryberry leveraged historical stimuli recorded by Baptista, archived at the California Academy of Sciences, and later curated by the Borror Laboratory of Bioacoustics. This study demonstrated that song evolution affected the efficacy of songs in this population: females performed more solicitations and males approached a simulated intruder more closely during playback of current songs compared to songs recorded 24 years earlier. Historical songs were less effective signals for receivers in the current population, both in the context of female mate choice and male–male competition. These data represented the first direct demonstration in a single natural population that signal evolution can impact the capacity for historical stimuli to elicit conspecific responses. These findings also suggested that signal evolution contributes to the formation of behavioral barriers to gene flow. However, the mechanisms underlying birds' responses to historical songs may not be the same mechanisms underlying responses to geographic variation in song. In order to understand how song evolution within populations contributes to the formation of behavioral barriers between populations, it is important to understand how response to song evolution within populations compares to response to geographic variation in song.

Derryberry (2011) contrasted male responses to temporal and geographic variation in song. Specifically, males' responses to historical local, current nonlocal, and heterosubspecific songs were compared using a series of playback experiments. Historical local songs were as effective as current nonlocal songs and significantly more effective than the songs of another subspecies in eliciting a response from territorial males. In addition, the songs of the local and nonlocal populations had changed in a roughly parallel direction in acoustic space while distinct song types were maintained during the past 35 years (Harbison et al. 1999). Variation in this acoustic space appeared to explain variation in male response to playback songs, such that the more dissimilar a song stimulus was to current variation in local song, the less strongly a male responded (Derryberry 2011). Altogether, these findings suggest that similar mechanisms may explain male response to song along the axes of both time and space. Additional studies are sorely needed to assess whether similar results hold true in other species. Bioacoustics archives offer a starting point for future studies by curating historical and current recordings for the future.

## MACROEVOLUTIONARY PATTERNS OF AVIAN VOCALIZATIONS

In parallel with recent improvements in the availability of bioacoustics data and analytical techniques, the systematics and museum communities have generated massive amounts of molecular data, enhancing our understanding of evolutionary relationships among birds. Phylogenies generated from these molecular data provide the necessary framework to consider evolutionary patterns of diversification and trait evolution at deep evolutionary timescales. By examining vocal variation among species in conjunction with additional phenotypic and genetic data gathered from museum specimens, many investigators are answering long-standing questions about how bird song coevolves with other aspects of avian biology. Here, we provide an overview of two research programs as case studies of how phenotypic and genetic data from museum specimens are being combined with vocal data to further our understanding of avian communication and evolution. We focus on recent work on tanagers (Thraupidae) and ovenbirds and woodcreepers (Furnariidae), but note that important advancements regarding interspecific patterns of avian vocal evolution are also being made in other lineages, such as wood warblers (Cardoso 2010, Cardoso and Hu 2011), fringilid finches (Cardoso et al. 2012), fairy-wrens (Greig et al. 2013), blackbirds (Odom et al. 2015), and leaf warblers (Tietze et al. 2015), among many others.

Tanagers (Thraupidae) were traditionally limited to include only a group of bright, frugivorous songbirds in Central and South America that typically produced inconspicuous and simple vocalizations (Isler and Isler 1999). However, recent molecular phylogenies have transformed the taxonomic boundaries of tanagers: many species that were previously considered tanagers are actually members of other avian families, and species that were assumed to be distantly related to tanagers form a monophyletic group with the remaining tanagers (Burns et al. 2014, Barker et al. 2015). The recent revisions of the taxonomic grouping of tanagers now include species that span an impressive array of vocal variation that has been the subject of a recent series of studies on vocal evolution (Mason 2012; Figure 4.2). Mason et al. (2014) used
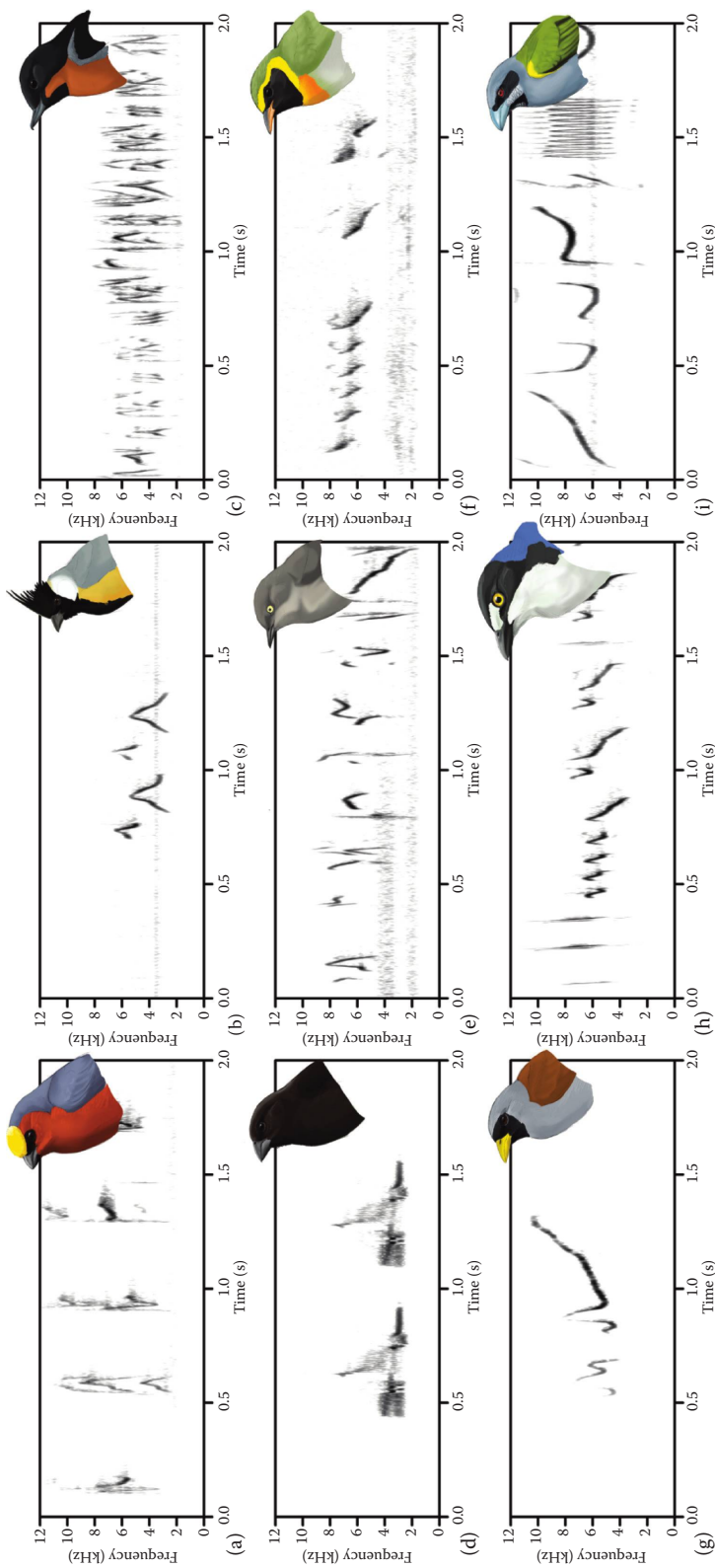
Figure 4.2. Spectrograms illustrating vocal diversity among tanagers. Representative species from 15 different subfamilies of Thraupidae are included. Darker shades of gray in the spectrograms indicate higher decibel levels. Spectrograms are on equal scales for frequency and time, demonstrating the diversity in frequency and temporal aspects of thraupid songs. These vocal data were used in combination with museum specimen data to study vocal evolution in a series of publications. (a) *Catamblyrhynchus diadema*, (b) *Charitospiza euosma*, (c) *Diglossa brunneiventris*, (d) *Geospiza fuliginosa*, (e) *Hemispingus xanthophthalmus*, (f) *Hemithraupis guira*, (g) *Incaspiza personata*, (h) *Nemosia pileata*, and (i) *Parkerthraustes humeralis*. (Portraits are courtesy of Mary Margaret Ferraro. Adapted from Figure 1 of Mason and Burns 2015 with permission from *Biological Journal of the Linnean Society*.)
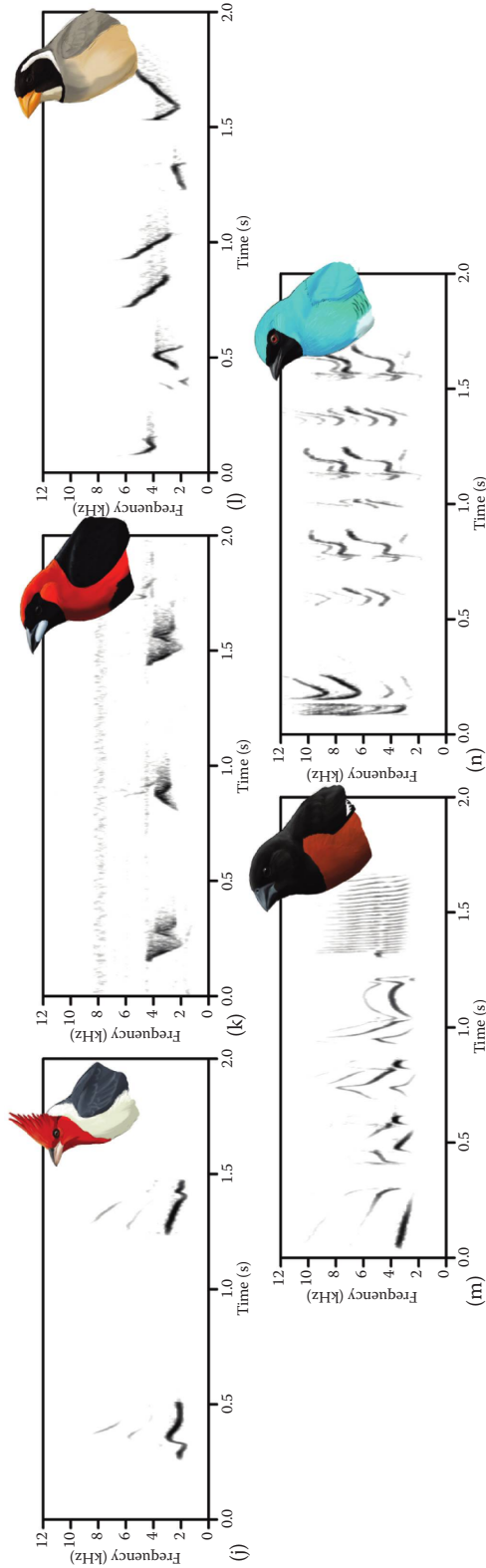
(Continued)

Figure 4.2. (Continued) Spectrograms illustrating vocal diversity among tanagers. Representative species from 15 different subfamilies of Thraupidae are included. Darker shades of gray in the spectrograms indicate higher decibel levels. Spectrograms are on equal scales for frequency and time, demonstrating the diversity in frequency and temporal aspects of thraupid songs. These vocal data were used in combination with museum specimen data to study vocal evolution in a series of publications. (j) *Paroaria coronata*, (k) *Ramphocelus nigrogularis*, (l) *Saltator aurantiirostris*, (m) *Sporophila angolensis*, and (n) *Tersina viridis*. (Portraits are courtesy of Mary Margaret Ferraro. Adapted from Figure 1 of Mason and Burns 2015 with permission from *Biological Journal of the Linnean Society*.)

a dataset of over 300 species of tanagers with archived recordings in natural sounds collections and spectrophotometry data from museum specimens. This study tested whether there is an evolutionary trade-off between song and plumage elaboration, which has been coined the "transfer hypothesis" (Darwin 1871, Gilliard 1956). The transfer hypothesis posits that elaborate plumage and song are both costly to produce and maintain in males, and that female-driven sexual selection acts on just a single trait such as song or plumage, but not both (Iwasa and Pomiankowski 1994). Despite the extensive variation in both song and plumage complexity among tanagers, there was no generalized relationship between song and plumage complexity, suggesting that elaborate vocal displays and complex plumage evolve independently in tanagers (Mason et al. 2014). Using the same dataset of tanager vocalizations, Mason and Burns (2015) found that body mass data, which were also collected from museum specimens, were strongly correlated with multiple aspects of tanager song, whereas broad categorizations of habitat type were not. These studies illustrate the capacity for contemporary studies to quantify macroevolutionary patterns across many hundreds of species and deep evolutionary timescales. Studies of this nature are not possible without digital sound archives, the availability of decades of bioacoustics recordings, and the ongoing recording efforts of the ornithological community. Moreover, comparisons among vocalization, coloration, and body mass data, as well as molecular phylogenies, all depend heavily on museum specimens, recapitulating the importance of museum specimens in modern, comparative studies of avian vocalizations.

Parallel studies in other avian lineages have similarly leveraged museum collections to produce new insights into avian vocal evolution. Among suboscines, the Neotropical radiation of woodcreepers and ovenbirds (Furnariidae) has provided an important system for understanding signal evolution in taxa with innate, or unlearned, vocalizations (Tobias et al. 2012). Derryberry et al. (2012) examined the tempo and mode of song evolution within woodcreepers and evaluated morphological constraints on song diversification. Dendrocolaptinae exhibit remarkable diversity in bill morphology, in which species with larger bills are limited in their ability to produce rapid trills over large frequency ranges, which emphasizes the role of indirect selection on song via morphological adaptation (Derryberry et al. 2012).

Currently, Derryberry and colleagues are using 276 Furnariid taxa to test the relative roles of sensory drive and "magic traits" in the evolution of innate song (unpubl. data). Sensory drive is the process by which acoustic differences among signaling environments influence the evolutionary divergence of mating signals by optimizing signal transmission (Wilkins et al. 2013). So-called magic traits are phenotypes that are under natural selection and also function in mate choice, such that ecological divergence can influence sexual selection and possibly speciation (Servedio et al. 2011). Sensory drive is often assumed to be more pervasive than magic traits, yet our understanding of how these direct and indirect processes interact during signal evolution is limited. Derryberry et al. (unpubl. data) compared the extent to which vocal evolution was related to the direct influence of habitat characteristics and the indirect effect of beak size, a well-established magic trait in birds. They found that sensory drive is an important factor explaining the structure of acoustic signals across this diverse radiation, but when the effects of beak size were included, it became clear that a balance between these processes drives signal evolution. These results confirm that two independent mechanisms shape bird songs over evolutionary time, and also suggest that the primary origin of signal diversification is ecological selection on magic traits (beaks) driving correlated evolution of mating signals (songs).

Similar to the series of tanager studies, this research on Furnariids relied heavily on museum collections for access to vouchered DNA samples, study skins to take accurate and detailed morphological measurements, and song samples with detailed and accurate metadata from various bioacoustics archives, including the Macaulay Library and Xeno-Canto. In many cases, morphological data could be taken from the same study skin used to voucher a DNA sample, creating a powerful link between morphological and genetic data. Such a link exists between some song and museum specimens as occurs when the audio recording is of the same bird that was subsequently collected, but these links are rare (see next section). Comparative analyses on the tempo and mode of vocal evolution will be most powerful

when information linking museum vouchers to song data are readily available.

## LINKING MUSEUM VOUCHERS AND AUDIO RECORDINGS

Curated links between physical specimens and behavioral data, such as bird song, strengthen studies on the tempo and mode of signal evolution and recognition. For example, if a recording is associated with a specific physical specimen, then any question as to the species or population identity of that vocalization can be addressed by returning to the physical specimen of interest (Winker et al. 2010). This is similar to the traditional use of a physical specimen as a permanent record with potentially unforeseen utility, but the vouchered data extended to include curated vocalizations linked to the specimen (Palmer et al. 2013). The ability to make links between physical specimens and curated data is especially important when experts disagree over the identity of a song or simply when behavioral data are needed by someone other than the original collector. Population-level vouchers or curated links between song data and specimens collected from the same population at the same time (but not the same individual) can also facilitate the correct association of genetic and behavioral data (see Chapter 13, this volume).

Curating behavioral data in association with physical specimens should provide an important means of (1) validating behavioral data, (2) facilitating studies comparing behavior to other phenotypic traits (e.g., bill morphology), and (3) lowering the expense and time associated with studies on signal evolution. For example, incorrectly associating a song phenotype with a terminal taxon of a molecular phylogeny may yield false estimates of the rate of behavioral change. Further, building cross-referenced molecular, morphological, and behavioral datasets, given the separate collection of those data, is extremely difficult and time consuming. These issues are avoided when analyzing genetic or morphological data by restricting sampling to tissues associated with a physical specimen or by taking morphological data only from physical specimens. Similarly, issues of validation and building cross-referenced datasets can be minimized by the curation and use of song data associated with physical specimens.

Research on song evolution in the Neotropical radiation of woodcreepers and ovenbirds (see earlier) is a case study that illustrates the time involved in building cross-referenced datasets due to a lack of vouchered behavioral data. Several datasets were required for this research project: morphological data on bill size, molecular data for phylogenetic analysis, and behavioral song data. The morphological dataset was assembled by taking measurements from study skins archived in natural history museum collections around the world. The molecular dataset was assembled by sequencing DNA extracted from tissues frozen at the time of specimen collection and stored in cryo facilities at various institutions. These "vouchered tissues" were linked in the field to specific physical specimens later identified and curated into a collection. If, at any time, a question arose regarding results associated with the molecular or morphological dataset, sequences and traits could be traced directly back to a physical specimen to verify its identity. Although representative songs for most of the 290-plus species in Furnariidae could be found in existing scientific or online song databases (Figure 4.3), no means existed to link these recordings directly to specimens used in the molecular dataset. Although a population-level voucher would suffice in this comparative study, there also were no curated links between acoustic and physical collections at the population level. Instead, it took more than 2 years to associate the geographic origin of the song data with the geographic origin of the physical specimens and then to validate that one was representative of the other. Such efforts would be streamlined by curated song data, particularly when associated with physical specimens.

The best method to align behavioral and molecular data for comparative analyses of trait evolution is to associate both sources of data based on collection locality. However, many collections of acoustic and physical specimens do not provide full locality information in their databases. For physical vouchers, it is often necessary to look at the actual specimen tags attached to the study skin to identify exact location. For acoustic data, it is necessary to return to the notes associated with the song or to contact the recordist directly to determine the exact location of a particular recording. Once locality data are obtained for both datasets for each taxon, it is then necessary to determine whether the two locations for each
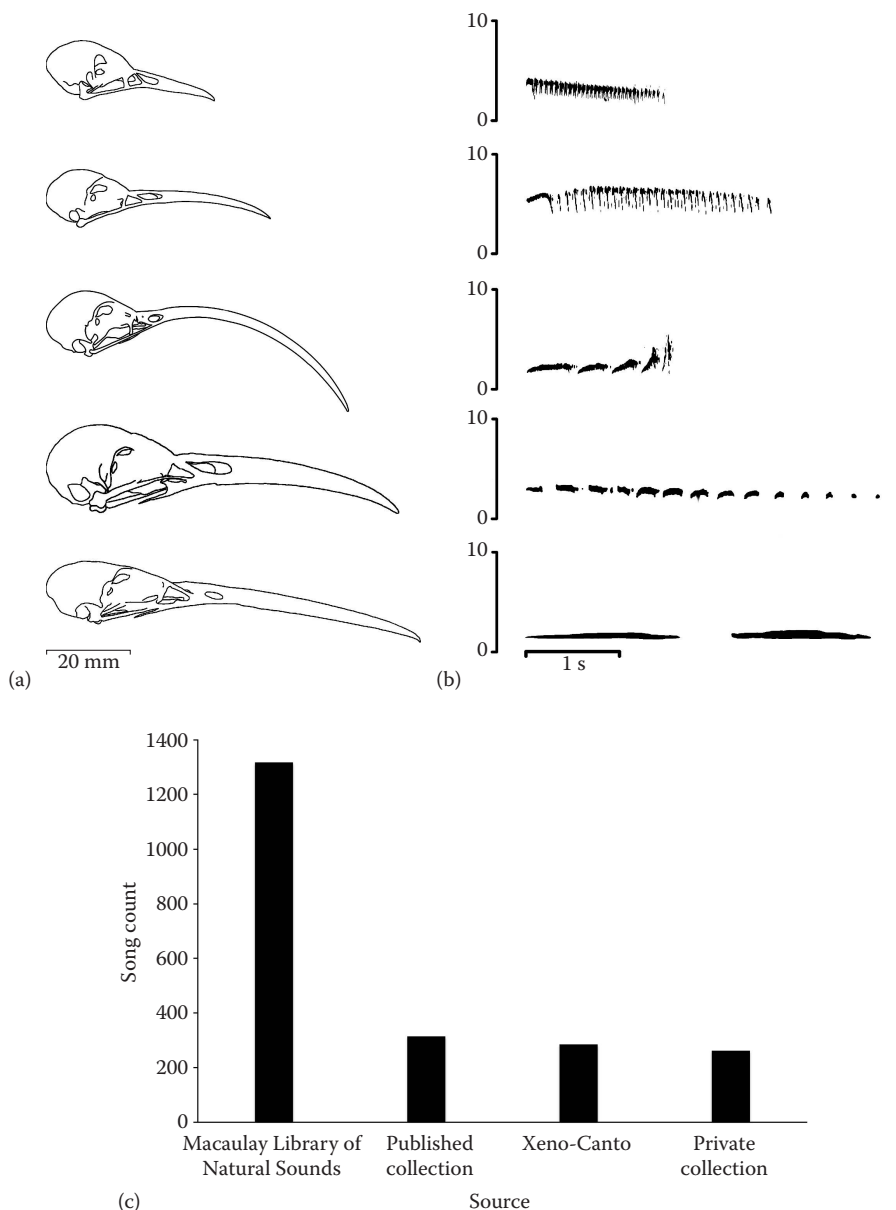
Figure 4.3. Illustration of datasets linked by specimens (morphological and genetic data) and not linked by specimens (song) used in analysis of the evolution of ecological and social traits in the Furnariidae. (a) Outlines of bill profiles and (b) sound spectrograms of typical loud songs produced by five species representing variation in bill and song structure in Dendrocolaptinae (Aves: Furnariidae): (top to bottom) *Certhiasomus stictolaemus*, *Lepidocolaptes albolineatus*, *Campylorhamphus trochilirostris*, *Xiphocolaptes promeropirhynchus*, and *Nasica longirostris*. (Adapted from Figure 1 in Derryberry et al. 2012 with permission from *Evolution*.) (c) Histogram of the sources for songs used in the study, including the Macaulay Library of Natural Sounds, collections published on CDs, Xeno-Canto, and individual private collections. (Details on sources and data can be found in Tobias et al. 2014.)

taxon are representative of one another. To do this requires extensive knowledge about the scale at which species vary in their song phenotype as well as the degree to which populations within species are genetically differentiated. Often, both of these types of information are not known or are held by different experts. For example, are *Asthenes dorbignyi* songs recorded in Peru in the Departamento de Tacna representative of the genetic population of *A. dorbignyi* sampled in the Departamento

de Arequipa? As songs are not available from the Departamento de Arequipa, it is necessary to find an expert who can identify the song of *A. dorbignyi* and has been to both locations. Failing that, we have to assume that the variation between songs from these two locations is less than the variation found between songs of *A. dorbignyi* and its sister species, *A. baeri*. Although working assumptions are valid, noise is added to the dataset, which might obscure important patterns of signal evolution.

Building curated links between natural history collections and collections of behavioral data will facilitate many important research studies on the tempo and mode of signal evolution. A number of museums with active natural history collections often make a vocal recording of an individual prior to collecting the voucher, including the Louisiana State University Museum of Natural Science and the Kansas University Biodiversity Institute and Natural History Museum among others. As more major natural history collections actively collect behavioral data in the field, the need for standard acquisition and curation of these ancillary data is pressing. Use of a standard approach to curate behavioral data improves the long-term quality of these data, consistency in these data across collections, and relevance to scientists over time. Similar approaches could be applied to banding stations, in which banders could prioritize audio recordings from the birds that they band, measure, and take blood or feather samples. The studies summarized here, and discussion of the challenges associated with linking behavioral and genetic data, indicate that the labor involved in collecting and curating these recordings is commendable and justifiable.

## PARALLEL ADVANCES IN NONAVIAN TAXA

Acoustic signals offer a powerful lens into the evolution of communication in multiple taxa, not just birds. Similarly, physical specimens provide a starting point for studying mechanisms of signal evolution and recognition in nonavian taxa. Here, we briefly highlight a few recent studies linking museum specimens with sound archives to better understand the biology of anurans, insects, and mammals.

Morphology and allometry play important roles in shaping vocal evolution at broad evolutionary scales. Frequently, the physical dimensions and properties of peripheral structures involved in sound production explain the majority of variation in signal form. As illustrated by Mason and Burns (2015), a long-standing inverse relationship between body size and dominant frequency has been documented in other birds (Wallschager 1980, Ryan and Brenowicz 1985), mammals (Hauser 1993, Jones 1999, Fitch and Hauser 2003, García-Navas and Blumstein 2016), and across many distantly related taxa (Gillooly and Ophir 2010). In anurans, similar correlations have been inferred among datasets with less geographic or taxonomic sampling (Cocroft and Ryan 1995, Hoskin et al. 2009). To explore whether such patterns generalize to larger phylogenies, Gingras et al. (2013) examined vocal parameters extracted from sound archives with data on body size based in part on museum specimens from 136 frog species distributed worldwide. The authors confirmed a strong association between body size and call frequency in anurans, and posited that laryngeal allometry and vocal fold dimensions mediate this relationship in most vertebrate taxa (Gingras et al. 2013).

Similar to investigations of putative evolutionary constraints between elaborate plumage and avian song complexity (e.g., Mason et al. 2014), Santos et al. (2014) explored the relationship between aposematic coloration and acoustic diversification in poison frogs (Dendrobatidae). Although some poison frogs advertise their unpalatable skin alkaloids to predators with visually conspicuous colors, most are cryptic and rely on camouflage (Santos et al. 2003). In addition, males of all species produce acoustic advertisement signals to attract mates (Zimmerman 1990). If predators associate mating signals with unpalatability, then release from predation pressure may allow aposematic species to evolve more elaborate mating signals. Santos et al. (2014) combined data on visual conspicuousness from live-caught animals, molecular data from museum specimens, and acoustic data from their own recordings and sound archives to test the hypothesis that aposematism enhances signal diversification. Indeed, changes in spectral and temporal features of acoustic signals were associated with aposematism, suggesting that relaxed predation facilitated the diversification of vocal signals, presumably via sexual selection.

Evolutionary constraints in acoustic parameters may also arise through morphometric and/or energetic trade-offs inherent in sound production

mechanisms. For example, many crickets stridulate by rubbing a scraper on one wing against a file on the opposite wing, and females are sensitive to temporal aspects of male calls (Gerhardt and Huber 2002). Given constant wing closure velocities, longer files produce longer pulse durations, but also increase the time between each stridulation. Until recently, however, empirical evidence for such trade-offs did not exist. Walker and Funk (2014) combined morphological and molecular data from physical specimens with acoustic recordings from sound archives to investigate the evolution of calls in North American brown sword-tailed crickets (*Anaxipha* spp.). As expected, pulse duration was associated with files that were longer and the density of file teeth, but was inversely related to pulse rate. Another recent study verified a similar morphological and energetic trade-off in a closely related subfamily (*Oecanthus*; Symes et al. 2015), reflecting the importance of biomechanical trade-offs in constraining acoustic parameters across insects and disparate taxa, including birds (Podos 2001) and singing mice (Pasch et al. 2011).

Finally, the efficacy of acoustic communication relies on coevolution of senders and receivers, whereby diversification in signal production is complemented by adaptations in perception (Bradbury and Vehrencamp 1998). Thus, understanding receiver anatomy can provide important insight into the evolution of signal structure. In bats, structural modifications of the inner ear are thought to accompany production of high frequency echolocation signals. To explore the origins of ultrasonic hearing and echolocation, Davies et al. (2013) compared microcomputed tomography scans of cochleae from museum specimens of 16 bat families, encompassing echolocating and nonecholocating suborders, with call parameters obtained from the primary literature and sound archives. The researchers found strong correlations between echolocation call frequencies and cochlear morphology, with ancestral reconstructions of basilar membrane length and cochlear coiling suggesting a common ancestor capable of ultrasonic hearing. However, variation in rates of basilar membrane evolution between suborders indicated that laryngeal echolocation evolved independently (Davies et al. 2013). Finer sampling of museum specimens and sound archives, along with functional experiments that determine hearing sensitivities, will help resolve

this complex evolutionary puzzle. Integrating media collections with museum specimens holds great prospects for exploring similar evolutionary and ecological links in birds and other taxa (e.g., Walsh et al. 2009).

## CONCLUSIONS AND FUTURE DIRECTIONS

It is an exciting time to study the ecology and evolution of vocalizations in birds and other taxa. Recent advances in museum science and the technologies used to acquire and disseminate natural sound recordings have enabled new research initiatives. Increasingly, natural history collections are used to study multiple aspects of the biology of avian vocalizations. Yet the wealth and diversity of new sources of bioacoustic data present certain challenges for ornithologists and curators of bioacoustics archives. These challenges include creating efficient platforms for large-scale collection of acoustic recordings (and other media) and powerful search algorithms that allow researchers to locate the recordings needed for a particular project. Looking ahead, another key challenge will be to standardize the content and availability of data associated with bioacoustic recordings, especially those with links to vouchered specimens. By combining traditionally disparate data from bioacoustics archives and museum specimens, ornithologists continue to gain insight into the ecological and evolutionary forces that shape acoustic signals in nature.

## ACKNOWLEDGMENTS

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