

THE IMPORTANCE OF NEOTROPICAL SUBOSCINE BIRDS AS STUDY SYSTEMS IN ECOLOGY AND EVOLUTION

J. A. Tobias¹, J. D. Brawn², R. T. Brumfield³, E. P. Derryberry³, A. N. G. Kirschel^{1,4},
N. Seddon¹

¹Edward Grey Institute, Department of Zoology, University of Oxford, UK

²Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, Illinois 61801 USA

³Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803

⁴Department of Biological Sciences, University of Cyprus, PO Box 20537, Nicosia 1678, Cyprus

Abstract. – Suboscine passerine birds are one of the most prominent components of Neotropical avifaunas, yet they remain relatively poorly studied in comparison with their sister-clade, the oscine passerines. This situation appears to be changing rapidly as more ornithologists realize that suboscine birds offer ideal study systems for investigating a variety of research questions. We summarise a symposium focused on studies of tracheophone suboscines (woodcreepers, ovenbirds, antbirds and allies) and highlight recent advances in our understanding of their history and behavior. We argue that because of their antiquity and high levels of diversity, they make excellent subjects for comparative analyses and phylogenetic models. Moreover, several details of their breeding and signaling systems predispose them to field-based observational and experimental studies of social interactions and signal evolution, as well as automated techniques for vocal recognition. We discuss potential new avenues of research on suboscine passerines, and conclude that they are likely to play an increasingly important role as study systems in tropical ecology and evolutionary biology.

Suboscine birds account for over 10% (~1150 species) of global bird diversity, and around a fifth of passerine diversity. They have radiated to a spectacular extent in the Neotropics, which is home to all but a handful of suboscine species (Ricklefs 2002). Despite this, they have received remarkably little research attention in comparison with their sister-clade, the oscine passerines, which abound in the temperate zone. A preliminary survey of literature reveals that 202 articles published since 1926 contain “suboscine” in the title or abstract (see Fig. 1). This may appear substantial, but it contrasts markedly with the 17,852 papers published in the same period containing the word “passerine” and excluding the word “suboscine”. A small proportion of

this larger total is made up of general studies, which potentially include at least some data from suboscines, but the vast majority is focused specifically on oscines. Indeed, the true research output based on oscine systems is far higher than these calculations imply as much of it is published without noting the word “passerine”, including many thousands of papers on high-profile model systems such as great tits (*Parus major*), red-winged blackbirds (*Agelaius phoeniceus*) and zebra finches (*Taeniopygia guttata*).

Further research biases exist within the subsocines. The infraorder Tyrannides, sometimes referred to as the non-tracheophone (or “bronchophone”) subsocines, a clade primarily consisting of tyrant-flycatchers

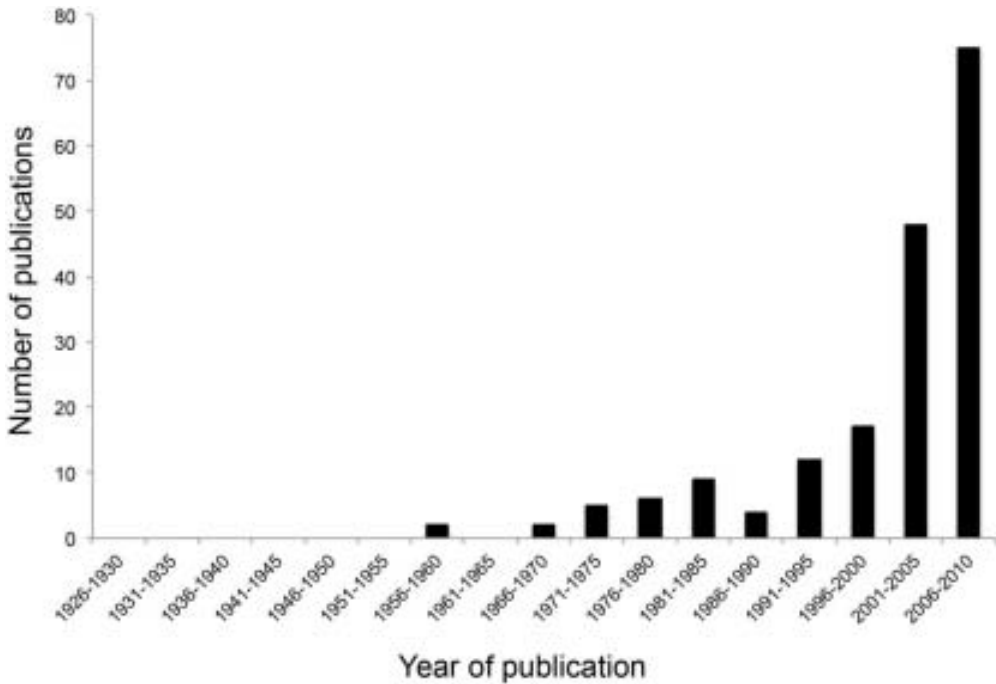


FIG. 1. Increasing rate of publication for papers focused on suboscines, since 1926 (data binned into 5-year periods). Totals are numbers of papers containing the word “suboscine” in title, abstract or keywords extracted from Web of Knowledge. We do not make a direct comparison with oscines because most papers focusing on suboscines tend to highlight the fact, whereas those focusing on oscines do not.

(Tyrannidae), manakins (Pipridae) and cotingas (Cotingidae), has received the most attention. Conversely, the infraorder Furnariides, i.e. tracheophone families such as the antbirds (Thamnophilidae) and ovenbirds (Furnariidae), has traditionally been largely ignored. The historical emphasis on Tyrannides has occurred in part because several lineages colonized the temperate zone, breeding as far north as the United States and Canada. Moreover, tropical forms such as manakins and cotingas are often highly charismatic, with extreme sexual dimorphism and extravagantly ornamented males. In contrast, tracheophone suboscines are absent from the temperate zone, and tend to be overlooked even in the tropics because they are perceived as dull or difficult to study (Remsen 2003).

The situation has changed rapidly over recent years as a growing number of researchers have realized that tracheophone suboscines make ideal research subjects for a number of practical reasons. First, they are ecologically diverse, occurring in all major habitats from humid lowland tropical forests to the snowline. Second, they are socially diverse, spanning a variety of breeding systems from social monogamy to cooperative breeding. Third, they are typically highly responsive to tape playback, making them relatively easy to catch in mistnets, and therefore to measure, color-band, radio-tag, blood-sample and so on (Bard et al. 2002). It also means that they are amenable to playback experiments. Fourth, many species of suboscines are fairly common, loud and conspicuous, even in human-modified

environments. This means that it is relatively easy to find and follow them for the purpose of observational studies, and to record their vocalizations. Thus, it is possible to build up sufficient sample sizes (in terms of numbers of individuals) for statistical tests an important consideration given that many tropical species are found at lower population densities than their temperate-zone counterparts (Tobias et al. 2012b).

The signaling systems of tracheophone suboscines also offer intrinsic practical advantages for biologists. For example, it is well known that their vocalizations are relatively simple and stereotyped (Kroodsmma 1984, Morton 1996, Lindell 1998), thus facilitating acoustic analyses used in tests of evolutionary theory (e.g. Seddon 2005) and speciation (e.g. Seddon and Tobias 2007, Seddon et al. 2008), as well as analyses of geographic variation (Ippi et al. 2011) and criteria for assessing species limits (Isler et al. 1998, Tobias et al. 2010a). This contrasts with many oscine taxa in which song learning is prominent, leading to complex local and regional variation in vocalizations (e.g. individual repertoires, dialects), such that mechanisms of ecological or social selection are difficult to disentangle from cultural evolution (Tobias et al. 2010b).

Similarly, the finding that many oscine groups have high levels of plumage reflectance in ultra-violet (UV) wavelengths, as well as visual sensitivity to such wavelengths, suggests that the use of human vision to assess plumage colors and contrasts is invalid (Eaton 2005). Human vision is insensitive to UV wavelengths and thus numerous previous studies have overlooked cases of signal divergence or cryptic dichromatism in oscine birds (Bleiweiss 2004, Eaton 2006). These problems are negligible in tracheophone suboscines as their plumage generally has very low levels of UV reflectance and the spectral sensitivity of their visual systems is not tuned to UV wavelengths (Seddon et al. 2009). This means that

suboscine clades are amenable to comparative analyses based on simple visual comparison of plumage colours and contrasts, rather than the use of colour spectrophotometry coupled with visual modelling (e.g. Seddon et al. 2008).

Another aspect that has drawn researchers to the tracheophone suboscines is the contrasting perspective they provide on a number of long-standing questions (Ricklefs 2002). In particular, they offer unparalleled systems for studying the evolutionary implications of 'slow' life history strategies. Most members of this clade are characterized by classic tropical social systems involving convergent sex-roles, long-term pair-bonds and year-round territoriality (Greenberg and Gradwohl 1983, Kirschel et al. 2011, Tobias et al. 2011). As a corollary, they also tend to be extremely sedentary (Greenberg & Gradwohl 1997, Woltmann et al. 2012), with delayed natal dispersal and highly stable territorial networks (Greenberg & Gradwohl 1986, Kirschel et al. 2011). Overt evidence of sexual selection such as polygyny and extra-pair fertilizations appears to be rare (Fleischer et al. 1997), although divorce and territory switching may exert more cryptic forms of sexual selection (Morton et al. 2000, Tobias et al. 2009a).

These features contrast with many avian model systems, which tend to have short-term pair-bonds, seasonal territoriality and high-levels of overt sexual selection, particularly in the temperate zone. Even tropical studies often focus on visually attractive species with extreme sexual dichromatism and male-biased ornamentation, such as manakins (Pipridae). Thus, tracheophone suboscines offer useful insight into overlooked questions about the origins and implications of long-term monogamous partnerships and selection on females (Tobias et al. 2012a). Much of the work to date has focused on the evolution of communal displays, such as duets, and their multiple functions in cooperative resource defense, mate defense (Seddon and Tobias

2006) and sexual conflict between partners (Tobias and Seddon 2009c).

Two final reasons why tracheophone suboscines are becoming increasingly popular in studies of evolution and ecology are their enigmatic evolutionary history and sheer diversity. Because their plumage is relatively subdued, they have proved to be a hotbed for the discovery or description of cryptic species (e.g. Zimmer 1997, Isler et al. 2007, 2009, Chaves et al. 2010) and genera (Chesser et al. 2009, Claramunt et al., 2010, Derryberry et al., 2010a, 2010b). Moreover, the challenge of numerous unresolved evolutionary relationships has attracted the attention of molecular biologists, such that extensive phylogenetic trees are now available (e.g. Irestedt et al. 2002, Chesser 2004, Moyle et al. 2009, Derryberry et al. 2011). This combination of high species richness and availability of phylogenetic data has made the tracheophone suboscines an increasingly important system for multi-species studies testing evolutionary and ecological theory, and models of diversification in particular (e.g. Ricklefs 2006, Seddon et al. 2008, Claramunt 2010, Gómez et al. 2010, Claramunt et al. 2011).

These factors help to explain why the output of research focused on suboscines has increased exponentially in recent years (Fig. 1). The goal of this symposium was to summarise advances in our understanding of suboscine birds, to emphasise the insights they provide on life-history evolution, signal evolution and speciation, and to clarify the main avenues for future research.

WHAT DO SUBOSCINES TELL US ABOUT AVIAN LIFE HISTORIES?

Jeff Brawn summarized some of findings of long-term population studies of understory species in the lowland forests of central Panama. These studies include capture-mark-release (CMR) sampling that was initiated in

1979 and continues today, along with a series of single species or comparative studies often involving species from tropical and north temperate latitudes. Suboscine passerines are prominent in the sample, e.g. 25 (71%) of 35 species for which data are sufficient to estimate demographic parameters. Others studies conducted in neotropical forests report similar proportions of suboscines when sampling understory species with mist nets (see Karr et al 1990).

A series of analyses comparing tropical and north temperate species indicates a complex suite of associations among key traits such as survival rate, body mass, stress responses, reproductive effort, energetics, and immune function (see summary in Robinson et al. 2010). The "fast-slow" axis summarizing the pace of life histories is a useful metaphor for comparative studies, but tropical and temperate species do not necessarily ordinate "cleanly" on this gradient. Comparison of species sampled in North America and Panama indicate that for certain traits such as energy expenditure (e.g., field metabolic rate), and constitutive immune function (i.e., the part of immune system that is not induced by the presence of a pathogen), tropical species do seem to have a slow pace of life whereby investment is structured by a comparatively long expected lifespan. Alternatively, parental effort and survival rate do not exhibit an obvious tradeoff. The classic view of avian life histories at tropical latitudes is that they live longer and therefore invest less in any one reproductive cycle.

The characteristically small clutch size of tropical species is typically invoked as evidence of this tradeoff. Yet, a series of recent studies conducted on the Western Slaty Antshrike (*Thamnophilus atrinucha*) reports significant investment with respect post-fledging parental care (Tarwater and Brawn 2010). Tropical species may therefore have a "quality over quantity" strategy that is somewhat independent of expected longevity.

Overall, these studies reveal little “signal” or constraint owing to phylogenetic history (e.g., K. Lee unpublished MS). Nonetheless, Cohen et al. (2008) report that correlations among traits (e.g., between concentrations of circulating antioxidants survival rate), and therefore potential tradeoffs, can vary between suites of oscine and suboscines. It may be that certain traits are somewhat constrained by history while others vary more “freely” within a clade. Clearly, much of what we know about the demography and life histories of tropical species comes from studies of suboscines. The message emerging from these studies is that the life histories of tropical species are not easily categorized and that further studies are required in diverse ecological settings within the Neotropics.

DEVELOPMENT, FUNCTION AND EVOLUTION OF SONG IN NEOTROPICAL SUBOSCINES

Nathalie Seddon discussed the implications of song learning, or lack thereof, for studies of evolution. Oscine song has been used to test numerous evolutionary ideas, but the fact that in many species these songs develop through an imprinting-like process means that conclusions may not be valid. For example, it is often argued that habitat-related differences in oscine song are the result of acoustic adaptation (e.g. Nicholls et al. 2006, Derryberry 2009) but it could just as easily be explained by young individuals learning the songs, or parts of songs, that they perceive most clearly in their natal habitat (Hansen 1979). For this reason, habitat-associated patterns of oscine song variation may lack a genetic basis, reflecting phenotypic plasticity rather than acoustic adaptation (Ripmeester et al. 2010). Similarly, oscine song convergence in contact zones has been attributed to convergent character displacement (Cody 1969) but it could simply be explained by heterospecific copying, where one species accidentally learns the song, or

song types, of another species (Helb et al. 1985). Again, the convergent songs produced by this form of copying lack a genetic basis, and therefore do not qualify as character displacement driven by divergent selection (Tobias & Seddon 2009b).

Because of these issues, the nature of song development in suboscine birds takes on greater importance. Suboscine songs are often proposed to develop without learning (Kroodsma 1984, Isler et al. 1998, Zimmer & Isler 2003), potentially offering a useful contrasting system for studies of signal evolution. However, this paradigm has been challenged over recent years, suggesting that further work is required to validate assumptions. To address this question, spotted antbirds (*Hylophylax naevioides*) were reared by hand from the egg in soundproofed aviaries at the Smithsonian Tropical Research Institute in Panama. Developing chicks were raised either in silence or were exclusively exposed to the song of a related species with a distinctly different song (*Hylophylax naevius*). All of the five individuals that survived to maturity produced normal adult song, which is consistent with the hypothesis that tracheophone suboscines develop songs without learning.

In the light of these findings it is useful to weigh up the evidence that song learning may be widespread in suboscines. Looking broadly across all suboscine species, rudimentary song learning has been suspected in only three species, all of which have lekking or polygamous reproductive strategies. Trainer et al. (2001) proposed that male *Chiroxiphia linearis* adjust song frequency by copying lek-mates, yet Trainer & Parsons (2002) found no microgeographic variation in song structure, suggesting that learning is minor or absent. Similarly, lek-specificity of songs in *Lipaugus vociferans* may indicate learning (Fitzsimmons et al. 2008), but the evidence is weak (Kroodsma 2011). Finally, the finding that geographic variation in male songs of *Procnias tricarunculata*

was not explained by genetic variation is again suggestive of learning (Saranathan et al. 2007), as this tends to produce a mismatch between vocal and genetic variation (Nicholls et al. 2006). However, the subtle mismatch detected in *Procnias tricarunculata* could potentially be explained by phenotypic plasticity unrelated to learning. Thus, the evidence for song learning in suboscines remains weak, and entirely restricted to lineages with lek-breeding reproductive strategies (i.e. strong sexual selection).

Balanced against these largely inconclusive cases, we note that experimental studies in socially monogamous non-tracheophones found no evidence of learning (Kroodsma 1984), nor the forebrain cell clusters that control song acquisition in oscines (Kroodsma and Konishi 1981). Switching attention to tracheophone suboscines, several studies suggest that their songs are innate: (1) individual variation in song structure is low, with no indication of mimicry, repertoires and dialects (Lindell 1998; Bard et al. 2002; Seddon and Tobias 2006); (2) geographical variation in songs and genes is typically concordant (Isler et al. 2005; Chavez et al. 2010); (3) in one species (*Thamnophilus doliatus*), captive individuals produced normal songs as adults after being reared in silence or exposed to heterospecific tutors during the nestling phase (Kroodsma 1984); (4) unlike hybrid oscines in which songs are typically copied from the parental male, hybrid tracheophone suboscines produce structurally intermediate songs (Cadena et al. 2007). We also note that there are no cases of lekking or polygamous reproductive strategies in this clade (Marantz et al. 2003; Remsen 2003; Zimmer and Isler 2003). These facts, in conjunction with the evidence from captive-rearing experiments, are consistent with the idea that song learning is minimal, or even nonexistent, in all tracheophone suboscines.

Minimal learning in suboscines adds weight to recent studies showing that acoustic structure of suboscine songs is predicted by

sound transmission properties of Amazonian habitats, and therefore subject to diversifying selection in heterogeneous environments (Tobias et al. 2010). It also helps to explain high levels of stereotypy and individual distinctiveness, features which have been shown to facilitate individual (mate) and species recognition in antbirds, even when overall differences in signal design are very small (Seddon and Tobias 2010). These findings fit with the results of other mate removal and playback experiments in Amazonia confirming that male and female songs in antbirds have dual functions in mate attraction and territory defense (Tobias et al. 2011). Taken together, these findings suggest that song divergence, mediated by ecological adaptation and social selection, could play a key role in the diversification of suboscine birds.

USING SONG RECORDINGS AND PLAYBACK EXPERIMENTS TO MAP TERRITORIES AND INFER SONG FUNCTION

The simplicity and stereotypy of suboscine songs suggests that they are amenable to automated song feature extraction procedures used to identify songs to species (Trifa et al. 2008), or even individuals (Bard et al. 2002, Kirschel et al. 2009, 2011), with potential applications to improving our understanding of the ecology of poorly known species. Early attempts to apply automated algorithms to the vocal identification of 5 antbird species occurring in a Mexican rainforest worked reasonably well, with 98% successful classification achieved (Trifa et al. 2008). Alex Kirschel presented work exploring this further at the individual level in the Mexican antthrush (*Formicarius moniliger*), a monomorphic species where female song appears indistinguishable from male song. Like many Ground Antbirds (Formicariidae), Mexican antthrush are very difficult to see in the field, so identifying individuals or their

sex is very challenging. Using song recordings and statistical classifications, however, it was possible to identify over 30 individuals in a 50 hectare study area in Chiapas, Mexico, and to map territory occupancy over a 5-year period. Songs were found to be largely invariant from year to year and individuals' songs could thus be recognized with accuracies over 80% among different years. Territory locations were determined by mapping where identified birds were recorded singing, including where possible, with the use of a wireless sensor network (Collier et al. 2010, Kirschel et al. 2011). Based on the distribution of songs it was possible to determine that shapes and sizes of territories can vary over time when individuals are replaced from their territories, and territory dynamics varied between males and females (Kirschel et al. 2011). Moreover, by identifying the song of each individual, it was possible to determine when males and females sang. The song similarity between the sexes – a method to distinguish song to sex has still not been found – suggests convergence between the sexes in territory defense. Intrasexual territory defense appears commonplace in suboscines (Seddon and Tobias 2006, Tobias et al. 2011), but song convergence among the sexes might facilitate intersexual competition in ground antbirds.

MORPHOLOGICAL ADAPTATION SHAPES VOCAL EVOLUTION IN A MORPHOLOGICALLY DIVERSE RADIATION OF SUBOSCINE BIRDS

Divergence of signals used in mate choice and male-male competition can promote the process of speciation (Coyne and Orr, 2004). Thus, understanding the evolutionary forces that shape signal divergence is fundamental to our understanding of phenotypic evolution and diversification. One important route of signal divergence is via ecological selection on traits related to signal production. There are often biomechanical limitations on the production

of signals, such as limits on movements of the vocal tract during song production in birds (Nowicki et al. 1992). Signals may therefore diverge as a by-product of morphological adaptation to different foraging niches and habitats (Podos and Hendry, 2006). Such morphological traits have been referred to as 'magic traits' (Gavrieltis 2004) when they affect the production of mating signals because divergent ecological selection can give rise indirectly to non-random mating.

Much of the evidence for an indirect effect of ecological selection on signals comes from studies of oscine song (Badyaev et al. 2008, Ballentine, 2006; Huber and Podos, 2006; Podos, 2001). The link between ecological selection and signal evolution is particularly clear in birds (Podos, 2001), as the organ used to forage the beak can also be used to modulate the resonance properties of the vocal tract during sound production (Westneat et al. 1993). For example, beak size and shape in Darwin's finches is often forwarded as one of the best examples of a 'magic trait' linking ecological divergence to reproductive isolation (Pfennig and Pfennig, 2010; Servedio et al. 2011). Because most work on the indirect effects of ecological selection have been conducted on oscines, it is difficult to tease apart the influence of cultural processes on vocal evolution from the potential impact of morphological and ecological adaptation (Seddon, 2005), and suggests that the conclusions of previous studies may only apply to song-learning birds (~ 40% of all avian species). A few studies outside of oscines (Anatidae: Hausberger et al. 1991; Furnariidae: Palacios and Tubaro, 2000; Thamnophilidae: Seddon, 2009) suggest that the mechanistic link between beaks and songs may be more widespread but its generality remains unclear. Here, we explore the interface between morphological and vocal evolution in a major radiation of suboscine birds, the woodcreepers (Dendrocolaptinae). Unlike oscine passerines (the focus of previous studies), suboscines make ideal subjects because they develop their songs

with minimal learning, and hence patterns of vocal divergence are not complicated by cultural evolution.

Using a well-resolved molecular phylogeny of the woodcreepers (Derryberry et al., 2011), we tested the vocal tract constraint hypothesis (Podos, 1997). This taxonomically widespread constraint is a tradeoff between the rate at which sounds are produced and the frequency bandwidth of those sounds, as described in more than 40 species of oscines (Passeri; reviewed in Podos et al., 2009) including a large number of wood warblers (Parulidae: Cardoso and Hu, 2011) and one species of seabird (Stercorariidae: Janicke et al. 2008). If this constraint is an important factor in song diversification and evolution in suboscines, then woodcreeper songs should occupy a bounded acoustic space of frequency bandwidth as a function of the rate of note production. We also tested the hypothesis that there is a biomechanical limit on performance of this motor constraint related to beak size (Podos, 2001). This hypothesis has been examined most intensively in Darwin's finches (Herrel, et al. 2008; Huber and Podos, 2006; Podos, 2001). As found in Darwin's finches, we predicted a negative relationship between beak size and ability to perform the trade-off between frequency bandwidth and pace.

Our results suggest that the proximate features of signal production influence the evolution and diversification of woodcreeper songs (Derryberry et al. 2012). We found evidence that woodcreeper songs have diversified within a bounded acoustic space such that slow songs are produced at a range of frequency bandwidths but as song pace increases, maximal values of frequency bandwidth decrease. We also found a positive relationship between beak size and ability to perform the trade-off between frequency bandwidth and pace: species with large beaks tend to produce low performance songs, whereas species with small beaks

tend to produce high performance songs. The evolution of performance is associated closely with the evolution of beak size over time. Altogether, our findings suggest that limitations on signal production may play an important role not only in the evolution of oscine songs but also in the evolution of vocal signals in woodcreepers. Our results add weight to previous studies proposing a link between beak size and song structure in suboscines (Palacios and Tubaro, 2000, Seddon, 2005), suggesting that correlated evolution via biomechanical constraints may be widespread in birds.

Because divergence in woodcreeper vocal signals is in part a by-product of ecological selection on beak morphology, our results have important implications for the role of ecology in suboscine diversification. We hypothesize that strong ecological selection during the adaptation of woodcreepers to different habitats and foraging niches promotes divergence in beak morphology among species, and that this leads, indirectly, to acoustic divergence in songs. Because vocalizations mediate species recognition in this clade, our results are also consistent with the idea that beak morphology serves as a 'magic trait' not only in some oscine clades but across the entire passerine radiation (>5000 species), and that 'magic traits' themselves are relatively widespread (Servedio et al. 2011). Nonetheless, we still have much to learn about the extent to which ecological selection on beak morphology has had a pleiotropic effect on the diversification of song, and the extent to which song divergence in turn influences reproductive isolation in suboscine clades.

THE ROLE OF SPECIES INTERACTIONS IN PHENOTYPIC EVOLUTION

Classical evolutionary theory predicts that phenotypes of closely related species diverge

in sympatry by character displacement, i.e. selection acting to minimize costs of ecological and reproductive interference (Grant 1972, Losos 2000, Pfennig & Pfennig 2009). However, direct evidence of divergent character displacement is largely restricted to young taxa, and much remains to be learnt about how species interactions shape phenotypic evolution over the longer timeframes of evolutionary radiations. Joe Tobias reported an extensive comparative analysis designed to explore this question, using Neotropical ovenbirds as model systems. Data on ecological traits (beak shape and tarsus length) and signaling traits (song structure) were collected from specimens and field recordings of 350 lineages (including intraspecific lineages). The results showed that occurrence in sympatry did not predict trait divergence, contrary to the predictions of character displacement theory. The only significant pattern detected was greater similarity of songs in sympatric lineages versus allopatric lineages. This apparent convergence in songs can either be attributed to acoustic adaptation to shared environments, or to convergent character displacement driven by interspecific territoriality (Cody 1969). It was noted that several old furnariid lineages with interspecific territoriality coexist with remarkably similar songs, raising the possibility that character convergence has been driven by competitive interactions. This fits with evidence from *Hypocnemis* antbirds that competing species use convergent male songs to defend territories against heterospecifics (Tobias and Seddon 2009b). Moreover, even though such songs also function in mate attraction (Tobias et al. 2011), their convergent design does not lead to hybridization because females are adept at discriminating between species and even individuals on the basis of subtly different vocalisations (Seddon and Tobias 2010). These lines of evidence suggest that

divergent character displacement may apply to the recognition mechanism rather than to the acoustic trait itself.

Future steps

Genetics underlying song design

Fleshing out the genetic sampling required at the species level, particularly across tyrant-flycatchers etc

True impression of biological diversity which seems to be greatly underestimated

Further exploration of use of song in automated identification of species and individuals.

Studies should be very cautious pooling samples of oscine and suboscine species together.

These factors make many suboscines ideal for field studies of behavior and life history, and for testing broader hypotheses about the role of social and ecological selection on evolution and diversification.

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