Sexually Selected Traits Predict Patterns of Species Richness in a Diverse Clade of Suboscine Birds

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ABSTRACT: Whether sexual selection acts as an "engine of speciation" is controversial. Some studies suggest that it promotes the evolution of reproductive isolation, while others find no relationship between sexual selection and species richness. However, the explanatory power of previous models may have been constrained because they employed coarse-scale, between-family comparisons and used mating systems and morphological cues as surrogates for sexual selection. In birds, an obvious missing predictor is song, a sexually selected trait that functions in mate choice and reproductive isolation. We investigated the extent to which plumage dichromatism and song structure predicted species richness in a diverse family of Neotropical suboscine birds, the antbirds (Thamnophilidae). These analyses revealed a positive relationship between the intensity of sexual selection and diversity: genera with higher levels of dichromatism and lower-pitched, more complex songs contained greater numbers of species. This relationship held when controlling for phylogeny and was strengthened by the inclusion of subspecies, suggesting that sexual selection has played a role in the diversification of antbirds. This is the first study to reveal correlations between song structure and species diversity, emphasizing the importance of acoustic signals, and within-family analyses, in comparative studies of sexual selection.

Keywords: acoustic signals, dichromatism, sexual selection, speciation, suboscine birds.

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Sexual selection has long been considered a powerful driving force of speciation (Darwin 1871; Lande 1981; West-Eberhard 1983; Barraclough et al. 1995; Price 1998; Panhuis et al. 2001). More recently, sexual conflict has also been proposed to stimulate diversification (Rice 1996; Parker and Partridge 1998; Gavrilets 2000). The idea that these processes can generate premating isolation between populations is supported by theory (reviewed in Turelli et al. 2001) and some field studies (e.g., Boul et al. 2006) but remains difficult to test experimentally (Rice and Hostert 1993). Instead, most studies use the comparative method to look for correlations between species diversity and indices of sexual selection. The results are equivocal: studies of lizards and some invertebrates have revealed positive correlations (Arnqvist et al. 2000; Katzourakis et al. 2001; Stuart-Fox and Owens 2003), while studies of mammals, butterflies, and spiders have not (Gage et al. 2002; Isaac et al. 2005).

This lack of consensus might reflect inconsistencies between higher taxa, but the evidence is equally mixed if we focus on studies within a single class of vertebrates. In birds, early sister-taxon analyses revealed a relationship between species diversity and indices of sexual selection, including mating system (Mitra et al. 1996), sexual dimorphism (Barraclough et al. 1995; Owens et al. 1999), and plumage ornamentation (Møller and Cuervo 1998). However, the recent application of comparative techniques to larger data sets has detected no such correlation. One analysis showed avian species richness to be unrelated to three measures of sexual selection (Morrow et al. 2003); others found no relationship between plumage dichromatism and diversity and instead revealed that variance in diversity could largely be explained by behavioral flexibility (e.g., brain size; Sol et al. 2005) and intrinsic ecology (e.g., feeding generalization and dispersal; Phillimore et al. 2006).

The contradictory results of previous studies may derive from two factors. First, a coarse taxonomic scale may overemphasize the role of intrinsic biology as avian families typically differ in biogeography, ecology, and other factors shaping morphology (Harvey and Pagel 1991; Bennett and

Owens 2002). Second, models may be weakened by incomplete sets of predictors. In all previous analyses, indices of sexual selection were based on mating systems or morphological traits, such as testes size and sexual dichromatism. The reliance on morphological cues is perhaps misleading because breeding decisions are often mediated by multiple interacting signals (Iwasa and Pomiankowski 1994), some of which are not biometrically measurable. Birdsong, in particular, is a species-specific signal with a central role in mate choice and reproductive isolation (Lanyon 1969; McCracken and Sheldon 1997; Kroodsma 2004). Indeed, song structure is subject to strong sexual selection in many avian clades (Catchpole and Slater 1995; Collins 2004), thereby providing a metric by which sexual selection can be assessed. It is also thought that song and plumage may evolve synergistically (de Repentigny et al. 2000) or else be traded off against one another (Darwin 1871; Iwasa and Pomiankowski 1994; Badyaev et al. 2002). Either way, by omitting acoustic signals and their interaction with morphology, previous comparative studies may have misjudged the strength of sexual selection.

To reexamine the role of sexual selection in speciation, we investigated the relationship between plumage dichromatism, male song structure, and species richness in a single clade of suboscine passerines, the antbirds (Thamnophilidae). This family is unequivocally monophyletic and species rich, with more than 45 genera and 200 species (Zimmer and Isler 2003; Irestedt et al. 2004). Interspecific variation is high in terms of sexual dichromatism and song structure but low in terms of mating system, clutch size, and migratory behavior (Zimmer and Isler 2003).

With plumage dichromatism and male song structure as indices, we explored the relationship between sexual selection and diversity at two taxonomic levels: species and subspecies. The subspecies concept was developed as a device to classify geographical variation within species, and thus subspecific designation does not necessarily relate to genetic differentiation (Mayr 1982*a*; Mayr and Ashlock 1991; Zink 2004). However, approximately 36% of currently recognized avian subspecies for which genetic data are available were found to be phylogenetically distinct (Phillimore and Owens 2006), and it is generally posited that patterns of subspecific diversification yield insights into recent evolutionary events and incipient speciation (Miller 1956; Møller and Cuervo 1998; Belliure et al. 2000; Mayr and Diamond 2001; Newton 2003; Sol et al. 2005). We therefore use subspecies richness as a proxy for intraspecific genetic diversity, which we assume to be correlated with contemporary and future speciation events. Focusing on subspecies richness is likely to yield useful insights because it partially controls for the role of drift and natural selection. Small, long-isolated populations may give rise to monotypic species via drift (Mayr 1982*b*), whereas widespread populations are more likely to form polytypic species via deterministic processes such as sexual selection (Coyne and Orr 2004). In effect, the signal from widespread, polytypic, speciation-prone species is strengthened by conducting analyses at the level of subspecies.

We use the relationships between plumage dichromatism, song structure, and patterns of species and subspecies richness to test the hypothesis that sexual selection plays a role in the evolutionary diversification of antbirds. One prediction of this hypothesis is that indices of sexual selection will be positively correlated with species richness. Further, if sexual selection drives contemporary or future speciation events, our indices of sexual selection should be more strongly correlated with subspecies than species richness.

Methods

Study Species

Thamnophilid antbirds are small to medium-sized (6.5–155 g) Neotropical passerines (Zimmer and Isler 2003). Males and, in many species, females produce stereotyped songs that function in intrasexual territorial aggression (Willis 1967; Bard et al. 2002; Zimmer and Isler 2003; Seddon and Tobias 2006) and mate attraction (N. Seddon and J. A. Tobias, unpublished data). These vocalizations are thought to play an important role in maintaining species limits (Isler et al. 1998; Seddon 2005). Therefore, although some taxa with distinct geographical songs intergrade clinally (Isler et al. 2005), most antbird taxa with distinctive songs are cryptic species and will qualify as such in forthcoming revisions (Kroodsma et al. 1996; Isler et al. 1998; Remsen 2005).

As a framework for the designation of species, we followed Remsen et al. (2006), with genera and subspecies assigned according to Zimmer and Isler (2003). However, the systematics of Thamnophilidae is in rapid flux as a result of ongoing genetic and vocal analyses. It is impossible to predict all future revisions, but we minimized the inaccuracy of our classification by incorporating recent modifications (Braun et al. 2005; Brumfield and Edwards 2007; Isler et al. 2007*a*, 2007*b*, 2007*c*) and by assigning species status to all taxa identified as vocally distinct by Isler and Whitney (2002). Accordingly, the published total of 209 species, 46 genera, and 503 subspecies (Zimmer and Isler 2003; Remsen et al. 2006) is increased in our sample to 233 species, 53 genera, and 503 subspecies. For the classification and assignment of species, and a full description of decisions and sources, see table A1 in the online edition of the *American Naturalist*.

Plumage Dichromatism

Sexual dichromatism has long been thought to arise from female choice or male competition (Darwin 1871; Andersson 1994), thus providing a metric by which sexual selection can be assessed (Barraclough et al. 1995; Owens et al. 1999). Positive relationships have been found between plumage dichromatism and degree of polygyny, frequency of extrapair paternity, and testes size (Møller and Birkhead 1994; Owens and Hartley 1998; Dunn et al. 2001), strongly supporting the use of dichromatism as an indicator of sexual selection in birds.

Plumage dichromatism was scored by a naive observer on a scale of 0 (monomorphic) to 10 (maximum dichromatism) from color illustrations of all known antbird species and well-marked subspecies (Zimmer and Isler 2003), following Owens and Bennett (1994), Dunn et al. (2001), and Morrow et al. (2003). We recognized five body regions: head (forecrown, crown, and nape), back (mantle and rump), front (throat, breast, and belly), tail, and wings, and each was allocated a score of 0 ($=$no difference between the sexes), 1 ($=$difference in shade or intensity), or 2 ($=$difference in color or pattern). The mean of subspecies values was taken to produce a composite plumage dichromatism score for each species, and the mean dichromatism for each genus was calculated from these species values. Because most birds are able to see ultraviolet (UV) light (Cuthill et al. 2000), these methods will overlook dichromatism restricted to UV wavelengths. However, UV reflectance is thought to be minor in birds of the dimly lit forest understory, including antbirds (Gomez and Théry 2007), and we found that cryptic dichromatism was correlated with visible dichromatism across 75 antbird species from 43 (79%) of the genera recognized in this study (N. Seddon and A. J. Tobias, unpublished data). Thus, while greater precision could be achieved by measuring and modeling irradiance spectra, human vision provides a reasonable proxy for assessing antbird dichromatism (Badyaev and Hill 2003).

Song Structure

The assumption that vocal traits are sexually selected in birds is buttressed by robust evidence. Song pitch is negatively related to body mass in many avian clades, including antbirds (Seddon 2005), while increases in song pitch, song duration, note number, and note diversity likely involve energetic, physiological, and neurological costs (Gil and Gahr 2002; Collins 2004; Podos et al. 2004). These factors suggest that song structure (i.e., pitch and complexity) may function as an honest signal of male quality used in female choice and/or male competition, as

demonstrated in numerous field studies (Collins 2004; Kroodsma 2004).

We quantified song structure by analyzing spectrograms of high-quality recordings of the songs of male antbirds obtained from commercially available CDs (Isler and Whitney 2002) and private archives (see Seddon 2005 for details). For species with sexually dimorphic songs, only those of the male were analyzed because of the scarcity of recordings of definite female vocalizations. Similarly, although male and female antbirds give calls that may also be targeted by sexual selection, there were too few recordings available to include these calls in our analyses. Songs were digitized at 44.1 kHz using Avisoft SASLabPro, version 4.1c (Specht 2002), and spectrograms were produced using broadband filter settings (bandwidth $=$ 323 Hz, fast Fourier transform $=$ 1,024, frame $=$ 50%, window $=$ FlatTop, overlap $=$ 88%). We recorded eight song variables thought to be targeted by sexual selection owing to their energetic and/or neurophysiological costs (Gil and Gahr 2002; Collins 2004): number of different note types, song duration, maximum and minimum frequency, bandwidth, peak frequency, number of notes, and pace (i.e., number of notes per second). Different notes were distinguished on the basis of unique shapes, where shape is determined by the way in which frequency changes with time. All variables were measured using on-screen cursors moving in increments of 2.9 ms and 43 Hz, except for peak frequency, which was automatically measured from amplitude spectra (fig. A2 in the online edition of the *American Naturalist*). For a detailed description of acoustic procedures and vocal definitions, see Seddon (2005). Because our analyses were focused on among-taxa variation, we averaged data for each taxon across all individuals and locations (mean $\pm$ SD songs per species: 3.4 $\pm$ 2.4, range: 2–11; individuals per species: 1.65 $\pm$ 1.17, range: 1–5). These samples are adequate for the calculation of genus means, especially as antbird songs are more or less genetically determined and characterized by high stereotypy and low geographic variation (Isler et al. 1998, 2001, 2005; Zimmer and Isler 2003).

Song measures were highly correlated within and across species. To enable comparisons across taxa, we generated two principal components of original transformed song measures. The first principal component (PC1) accounted for 37.8% of total variation in the song variables (eigenvalue $=$ 3.02), and an increase in PC1 scores was associated with an increase in maximum frequency (factor loading: .98), minimum frequency (.76), peak frequency (.94), and bandwidth (.68). The second principal component (PC2) accounted for 22.0% of total variation (eigenvalue $=$ 1.76), and an increase in PC2 scores was associated with an increase in note types (factor loading: .57), pace (.74), and note number (.75). Thus, an increase

in PC1 score was associated with an increase in song pitch and bandwidth, while an increase in PC2 score was associated with an increase in number of note types, pace, and note number.

Additional Variables

In birds, species richness has been shown to co-vary with body mass, range size, and clade age (Hutchinson and MacArthur 1959; Rosenzweig 1995; McPeek and Brown 2007). We therefore examined the effects of these variables on species and subspecies richness. Body mass data were obtained from Dunning (1993) and Zimmer and Isler (2003); Geographic information system range sizes (in km^2) were provided by BirdLife International (S. H. M. Butchart, personal correspondence, 2006) for a total of 203 species. These were estimated by superimposing NatureServe shape files (http://www.natureserve.org; Ridgely et al. 2005) onto a Behrmann global equal-area projection using ArcView GIS 3.2 (ESRI 1999). Finally, following McPeek and Brown (2007), and focusing on the 45 antbird genera for which sequence data were available, we measured time-scaled branch lengths from the root to the tips of a published phylogeny (Irestedt et al. 2004) and used these branch lengths as proxies for genus age. Where a genus was represented by more than one taxon, we measured the oldest (i.e., the one with the longest branch).

Phylogeny and Phylogenetic Signal

Our phylogenetic tree comprised 53 genera (fig. A1 in the online edition of the *American Naturalist*). Of these, 45 were positioned according to the molecular phylogeny published by Irestedt et al. (2004), and eight were positioned within this framework on the basis of morphology and vocalizations (Zimmer and Isler 2003; Braun et al. 2005; Isler et al. 2007*c*), as well as additional molecular information (Brumfield et al. 2007). See figure A1 and table A1 for details.

To assess the phylogenetic signal of species and subspecies richness, and of five predictor variables, we used a generalized least squares (GLS) analysis (Grafen 1989; Martins and Hansen 1997; Pagel 1999; Freckleton et al. 2002). A simple multiplier, λ (Pagel 1999), measures the degree to which traits vary/co-vary across a tree in line with the Brownian process (Freckleton et al. 2002). Applied to internal branches, λ adjusts the strength of a signal from phylogenetically independent (0) to phylogenetically conserved (1); a value of $\lambda = 0$ indicates that traits are distributed randomly, while a value of $\lambda = 1$ indicates that traits are distributed nonrandomly, with respect to phylogeny. Thus, with respect to analyzing patterns of species richness, $\lambda = 1$ implies that closely related groups have

more similar numbers of living species than would be expected by chance. We calculated confidence intervals for λ using likelihood ratio tests, with values obtained from the likelihood surface (following Freckleton et al. 2002; Phillimore et al. 2006, 2007).

Comparative Analyses and Statistics

Comparative studies of the relationship between sexual selection and diversification have been criticized on the grounds that species are more likely to be described in lineages with more elaborate secondary sexual characters (Ritchie et al. 2005). This criticism is justified, to some extent, because species limits have traditionally been assigned by museum taxonomists on the basis of morphological characters, while the recent proliferation of vocal and genetic analyses has revealed unexpected cryptic diversity in birds (Alström and Ranft 2003; Remsen 2005). We controlled for taxonomic effects and circularity by adding song structure as an index of sexual selection and including radiations identified through vocal and genetic variation (Braun et al. 2005; Isler et al. 2007*b*, 2007*c*). We assume that all antbird species, regardless of the strength of sexual selection, are divergent in either morphology or song structure.

Our comparative analyses incorporated mean values of dichromatism, song structure, body mass, and range size, calculated for each genus from species values. These mean values were positively skewed and were therefore log transformed before analysis (table A2 in the online edition of the *American Naturalist*). In the absence of a comprehensive phylogeny, we were unable to accurately assess the relationship between our five predictors and the rate of speciation (Freckleton et al. 2002; Phillimore et al. 2006). Instead, following most previous comparative studies (Barraclough et al. 1998; Owens et al. 1999; Arnqvist et al. 2000; Gage et al. 2002; Morrow et al. 2003; Stuart-Fox and Owens 2003), we examined the extent to which a range of predictors (including sexually selected characters) explained variation in the diversity of living species and subspecies among genera.

We first used generalized linear models (GLMs) to investigate the effects of dichromatism, song structure (PC1 and PC2), body mass, and range size on antbird diversity. Strong associations between dichromatism and song structure in antbirds were found in a parallel study (N. Seddon and J. A. Tobias, unpublished data), so we included the interaction between dichromatism and song in our models. Species and subspecies richness were strongly negatively skewed and hence were best modeled using negative binomial errors and log link (Crawley 1993). To counter the influence of one very diverse genus (*Thamnophilus*; 30 species and 90 subspecies), we reran the GLMs excluding

this genus. To explore the influence of vocally distinct taxa not yet described as species, we also reran the GLMs using current taxonomy (i.e., $n = 209$ species).

The phylogenetic signal (λ) of antbird diversity was low (table 1), in agreement with recent studies in birds (Sol et al. 2005; Phillimore et al. 2006, 2007). However, for both species and subspecies richness, the confidence intervals of λ spanned almost the entire range of possible values. Similarly, although λ was low for all five predictors, the confidence intervals of λ for dichromatism, PC2, and range size were broad. This suggests that species diversity, and the evolution of some candidate traits, may have been influenced by shared ancestry.

As a precaution, and so as to make our results comparable with previous studies, we use two complementary techniques to control for phylogenetic inertia: (1) sister-taxa analysis (following Barraclough et al. 1998; Owens et al. 1999) and (2) independent contrasts analysis (following Morrow et al. 2003). In method 1 we systematically searched down the antbird phylogeny (fig. A1) and selected pairs of sister genera that differed in the five independent variables. Wilcoxon signed-rank tests were then used to assess the strength of association between these traits and species/subspecies richness. In method 2 we used MacroCAIC (Agapow and Isaac 2002) to generate independent contrasts for the five predictors. Species and subspecies differences were measured using the proportional dominance index (PDI; length $n_i/[n_i + n_j]$, where n_i is the number of species [or subspecies] in the clade with the larger value of the predictor trait and n_j is the number of species [or subspecies] in the clade with the smaller value of the predictor trait). Although PDI is recommended for equal branch length analyses by Isaac et al. (2003), we repeated the analyses using relative rate difference (RRD; $\ln[n_i/n_j]$) so that we could directly compare our results to those produced by Morrow et al. (2003). We analyzed PDI and RRD by using one-sample t-tests to measure the qualitative strength of association and then carrying out multiple linear regression forced through the origin (Garland et al. 1992). We regressed absolute values of PDI and RRD against number of species and subspecies at each node to check that there were no significant relationships, and we regressed absolute residuals against predicted values of PDI/RRD to check for constant error variance. To test the robustness of our conclusions, we reran these analyses excluding contrasts with large residuals (i.e., >1.96 or <-1.96).

We used the small-sample version of the Akaike Information Criterion (AIC), AIC_c, to identify the simplest models with the best explanatory power (Burnham and Anderson 2004). We estimated the phylogenetic signal of traits in the R environment (R Development Core Team 2004), using the APE package (Paradis et al. 2004) and

Table 1: Phylogenetic signal of species and subspecies richness and for the five predictors

Trait	Phylogenetic signal
Species richness	.35 (.00–.98)
Subspecies richness	.00 (.00–.97)
Dichromatism	.00 (.00–.63)
PC1	.00 (.00–.38)
PC2	.00 (.00–.92)
Body mass	.00 (.00–.52)
Range size	.00 (.00–1.00)

Note: The maximum likelihood values of λ are given with 95% confidence intervals in parentheses.

code provided by R. P. Freckleton. All other analyses were carried out using GenStat (2006) and SPSS (2007).

Results

Nonphylogenetic analyses revealed that dichromatism was positively associated, and body mass negatively associated, with species and subspecies richness (table 2). Song pitch (PC1) and the interaction between PC1 and dichromatism were retained in the AIC_c best models of species and subspecies richness, although the correlations were significant in the subspecies model only. Song complexity (PC2) and range size were unrelated to diversity at both taxonomic levels (table 2). The exclusion of *Thamnophilus* did not qualitatively change these associations (table A4 in the online edition), nor did the exclusion of vocally distinct taxa not yet described as species (table A5 in the online edition).

Using sister-taxa analyses, we found that dichromatism and PC2 were associated with increases in diversity; that is, genera with higher levels of dichromatism and more complex songs contained significantly higher numbers of species and subspecies (table 3). Body mass was marginally significantly associated with species richness, but range size was unrelated to both measures of diversity. Using independent contrasts, we found strong significant differences from 0 in species and subspecies richness (calculated as PDI) over all nodes for contrasts in dichromatism ($P < .0001$; table 4). Positive associations were also found for contrasts in song complexity (PC2) and range size ($P < .05$; table 4). The AIC_c best models explained 14% of the total variation in species richness and 34% of the total variation in subspecies richness. Dichromatism was the only significant term in the species models, while dichromatism and the interaction between dichromatism and PC1 made significant contributions to the subspecies models (table 4; fig. 1). Rerunning analyses using RRD produced nearly identical results (table A7 in the online edi-

Table 2: Multivariate models of species and subspecies richness across 53 antbird genera

	Species richness			Subspecies richness		
Trait	Slope $\pm$ SE	t	P	Slope $\pm$ SE	t	P
Dichromatism	1.48 $\pm$ .58	2.58	**.013**	2.07 $\pm$ .62	3.33	**.002**
PC1	.63 $\pm$ .47	1.33	**.191**	1.29 $\pm$ .51	2.51	**.016**
PC2	.08 $\pm$ .13	.610	.543	.18 $\pm$ .14	1.27	.209
Dichromatism $\times$ PC1	$-$.97 $\pm$ .56	-1.73	**.090**	$-1.78 \pm$ .61	-2.94	**.005**
Dichromatism $\times$ PC2	.32 $\pm$ .42	.77	.448	.25 $\pm$ .44	.56	.578
Body mass	$-2.04 \pm$ .48	-4.23	**<.001**	$-1.79 \pm$ .52	-3.47	**.001**
Range size	$-$.04 $\pm$ .21	$-$.20	.841	.31 $\pm$ .23	1.37	.178

Note: Values refer to final output from a generalized linear model with negative binomial errors and log link. Each character is tested when included with all other significant traits. Bold denotes traits and interactions that were included in the AIC_c best species ($F = 6.90$, df $= 4, 45$, $P < .001$) and subspecies ($F = 7.0$, df $= 4, 45$, $P < .001$) models. Parameter estimates for full models are given in table A3 in the online edition of the *American Naturalist*.

tion). Similarly, rerunning analyses excluding high standardized residuals generated qualitatively similar results (table A8 in the online edition), which further corroborated the robustness of our findings.

In all foregoing analyses, dichromatism was more strongly positively associated with subspecies richness than with species richness. Similar relationships were found for song structure in all tests except sister-taxa analyses. Finally, there was no significant relationship between the time-scaled branch length of a genus and the log-transformed number of species and subspecies it contained (species: $F = .057$, df $= 1, 44$, $r^2 = .001$, $P = .812$; subspecies: $F = .389$, df $= 1, 44$, $r^2 = .009$, $P = .536$), suggesting that differences in species and subspecies diversity were not simply related to the age of respective clades.

Discussion

Sexually Selected Traits and Species Richness

Two predictions of the hypothesis that sexual selection plays a role in avian diversification are met in this study.

Table 3: Correlates of species and subspecies richness across antbird genera using sister-taxa comparisons

	Species		Subspecies	
Trait	Supportive nodes	P	Supportive nodes	P
Dichromatism	11/16	**.033**	14/16	**.004**
PC1	4/17	.184	9/17	.386
PC2	9/17	**.023**	10/17	**.048**
Male mass	10/17	**.049**	9/17	.179
Range size	9/18	.100	10/18	.251

Note: Supportive nodes refer to the number of sister genera in which an increase in the trait is associated with the predicted direction of change in relation to the total number of available comparisons. P values are from Wilcoxon signed-rank tests; bold denotes exact one-tailed probabilities significant at $\alpha = .05$.

First, antbird genera with higher levels of plumage dichromatism and lower-pitched and more complex songs contained more species and subspecies. Second, plumage dichromatism and song structure were better predictors of subspecies richness than species richness. These relationships held after controlling for shared ancestry and removing the most species-rich genus, suggesting that the number of taxa within lineages is positively related to the intensity of sexual selection.

Of our two indices of sexual selection, plumage dichromatism was the strongest predictor of diversity. While this may reflect the greater importance of plumage in mediating mate choice and reproductive isolation, field studies demonstrate that the songs of antbirds also function in mate attraction (N. Seddon and J. Tobias, unpublished data). One possibility is that, by restricting our analysis to male vocalizations, we have generated an imprecise surrogate for sexual selection. Females sing in many antbird species (Zimmer and Isler 2003), and the intensity of sexual selection may therefore be more accurately reflected by sex differences in song structure. In other words, the inclusion of sexual dimorphism in song may improve the explanatory power of models of species richness in suboscine birds, a possibility that should be explored when comprehensive samples of female songs become available.

Although birdsong is widely viewed as carrying a strong phylogenetic signal (Lanyon 1969; Kroodsma et al. 1996; McCracken and Sheldon 1997; Isler et al. 1998; Remsen 2005), we found that λ for song structure was close to 0, suggesting that this trait is phylogenetically labile across antbird genera. This may partly explain why the relationship between song and diversity was weakened after correcting for phylogeny using the independent contrasts method, which assumes a Brownian model of trait evolution. Nonetheless, even after correction using this technique, our models were strengthened by the inclusion of song structure and its interaction with plumage. This find-

Table 4: Multivariate models for species richness produced using phylogenetically independent contrasts with regression through the origin of proportional dominance index (PDI) on character contrasts

Trait	t[a]	Species model[b] Slope $\pm$ SE	t	P	Subspecies model[b] Slope $\pm$ SE	t	P
Dichromatism	7.57**	.07 $\pm$ .03	2.51	**.016**	.14 $\pm$ .03	4.21	**.000**
PC1	−.75	.11 $\pm$ .08	1.33	.190	−.04 $\pm$ .12	−.33	**.750**
PC2	2.29*	−.03 $\pm$ .07	−.45	.660	.02 $\pm$ .07	.25	.810
Dichromatism × PC1	−1.03	.08 $\pm$ .06	1.42	.170	.18 $\pm$ .08	2.2	**.033**
Dichromatism × PC2	1.85	−.01 $\pm$ .05	−.16	.871	.01 $\pm$ .06	.24	.812
Body mass	.37	−.15 $\pm$ .36	−.42	.680	.19 $\pm$ .44	.43	.670
Range size	2.26*	.00 $\pm$ .01	−.06	.950	.01 $\pm$ .01	1.20	.240

[a] t-tests examining whether species richness (PDI) at all nodes differed from 0 for all traits of interest.

[b] Values refer to final output from a multiple regression model. Each trait is tested when included with all other significant traits. Bold denotes traits and interactions that were included in the AIC$_c$ best species ($F = 6.30$, df = 4, 45, $P = .016$, $r^2 = .14$) and subspecies ($F = 6.36$, df = 4, 45, $P < .001$, $r^2 = .34$) models. Parameter estimates for full model are given in table A6 in the online edition of the *American Naturalist*.

* $P < .05$.

** $P < .0001$.

ing implies that song plays a role in avian diversification and emphasizes the importance of including acoustic characters in comparative studies of sexual selection.

Dichromatism and song pitch (PC1) were better predictors of subspecies than species richness in antbirds, suggesting that taxa with more intense sexual selection are more likely to produce geographical variants below the species level. This can be interpreted in three ways. First, if subspecies are viewed as incipient species, we might conclude that sexual selection plays an important role in the early stages of speciation (as predicted by theory; Darwin 1871; West-Eberhard 1983; Price 1998) but that its signature fades with time. Second, tropical taxonomy lags behind temperate taxonomy. Thus, many geographically isolated antbird subspecies probably represent true species, or at least incipient species (Zimmer and Isler 2003), a view supported by recent taxonomic revisions (Braun et al. 2005; Brumfield and Edwards 2007; Isler et al. 2007*a*, 2007*b*, 2007*c*). Third, many antbirds, particularly among the 133 monotypic species in our sample, may have achieved species status through natural selection and drift during long isolation, whereas subspecies diversity in widespread taxa is more likely to arise through deterministic processes such as sexual selection. Each, and perhaps all, of these interrelated factors may contribute to our finding that indices of sexual selection were better explained by subspecies richness than species richness.

In revealing a positive correlation between indices of sexual selection and species richness, our results corroborate those of early studies using sister-taxa analyses (Barraclough et al. 1995; Mitra et al. 1996; Møller and Cuervo 1998; Owens et al. 1999; Arnqvist et al. 2000) but challenge those of more recent research using mixed models and independent contrasts (Morrow et al. 2003; Sol et al. 2005;

Phillimore et al. 2006; Phillimore et al. 2007). Why does our study identify correlations where others using similar methodologies find none?

The Role of Song and Taxonomy

There is growing support for the idea that antbirds, and all other tracheophone suboscine passerines, develop their songs without learning (Isler et al. 1998, 2005; Zimmer and Isler 2003; Remsen 2005). Even if some evidence of learning is eventually demonstrated, the structural simplicity of antbird songs, coupled with low levels of geographic variation and absence of dialects (Isler et al. 1999, 2001, 2005), indicates that its influence on song structure is minor. If suboscine birds are less able to copy or recognize divergent songs, the absence of learning may directly limit hybridization (Graves 1992; Grant and Grant 1996; Seddon and Tobias 2007), and sexual selection acting on acoustic signals in allopatric populations may lead to premating isolation. Thus, not only do the simple, stereotypic songs of antbirds make them unusually amenable to the compilation of indices based on vocal characters, but they may also partly explain why those indices are related to patterns of diversification.

Another explanation may be found in the subtleties of taxonomic scale and evolutionary age. Previous studies in birds made comparisons across families differing in multiple attributes, including migratory behavior, dispersal distance, altitudinal distribution, insular/continental distribution, geographical range size, latitude, life-history traits, body mass, and ecological specialism. These intrinsic properties have all been shown to influence diversification rates and to co-vary with species richness (Hutchinson and MacArthur 1959; Rosenzweig 1995; Belliure et al.
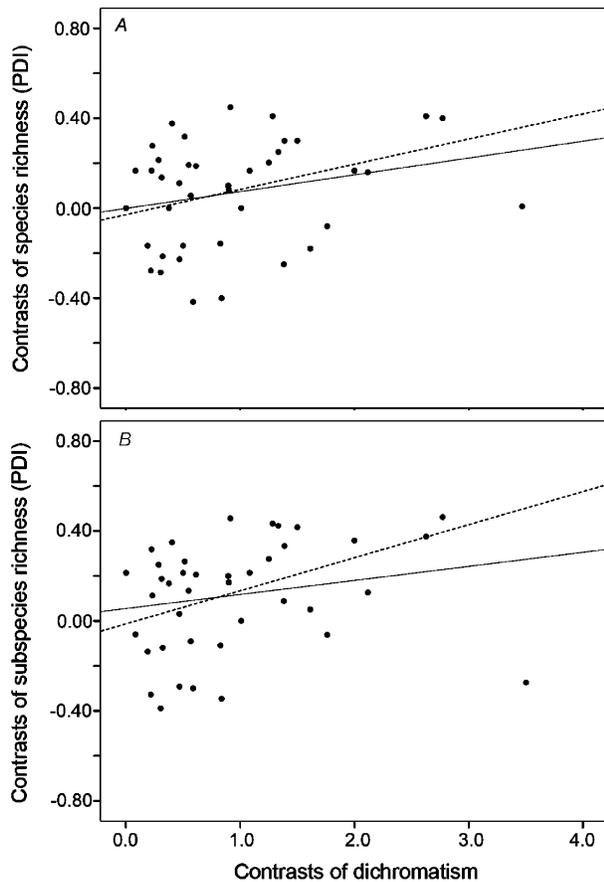
Figure 1: Relationship between dichromatism and number of species (*A*) and subspecies (*B*) in antbird genera, controlling for phylogeny using independent contrasts. Dashed lines exclude outliers.

2000; Phillimore et al. 2006, 2007). Variation in clade age is another important consideration, not only because it correlates with species richness at higher taxonomic levels (McPeek and Brown 2007) but also because current patterns of diversity are determined by the balance between speciation and extinction, and this tends to be skewed toward extinction in older clades (Gaston and Blackburn 1997).

We control for most of these variables by restricting our analysis to within-genus diversity in a single monophyletic family. The antbird clade contains a high diversity of genera and species, all of which are nonmigratory, continental, Neotropical insectivores, with year-round territories, essentially lowland distributions, and small clutches of one or two eggs (Zimmer and Isler 2003). Although most antbird species (>95%) are thought to be socially monogamous, they vary widely in population density (Terborgh et al. 1990; Zimmer and Isler 2003) and presumably therefore in competition for mates and in opportunity for ex-

trapair fertilizations. This clade is also one of few avian families diverse enough to permit an internal comparative analysis (Seddon 2005). Broader analyses, operating at the level of family, are more likely to be influenced by diverse evolutionary histories and therefore less likely to detect the signature of sexual selection. They may also be relatively insensitive because calculating indices for large families, rather than smaller genera, leads to oversimplification. Restricting comparative analyses to single families can overcome some of these problems, but this needs to be balanced against costs, namely, a reduction in statistical power and, perhaps, in external validity. Once robust vocal and phylogenetic data become available for other large avian families, particularly in the suboscine clade, further comparative analyses should test the generality of our findings.

Additional Hypotheses

Previous studies have shown that body size and range size are important predictors of species and subspecies richness in birds (Belliure et al. 2000; Sol et al. 2005; Phillimore et al. 2006, 2007). Body size is thought to play a role in speciation on the basis that small-bodied lineages tend to be more species rich than large-bodied ones (Hutchinson and MacArthur 1959; van Valen 1973; May 1986; Dial and Marzluff 1998). Our nonphylogenetic analyses support this view: antbirds with small bodies (e.g., *Myrmotherula* antwrens) are more diverse than those with large bodies (e.g., *Batara* antshrikes), perhaps because smaller-bodied birds can more finely divide their environment (Hutchinson and MacArthur 1959; Purvis et al. 2003). However, the relationship disappeared after controlling for phylogeny, suggesting a strong influence of shared ancestry (Nee et al. 1992; Owens et al. 1999). In addition, we note that body mass appears to have a low phylogenetic signal across antbird genera, indicating that it does not adhere to the Brownian motion model assumed by independent contrasts analysis.

Increased range size is predicted to promote speciation because larger ranges offer greater opportunity for range fragmentation and thereby geographical isolation (Rosenzweig 1995; Gaston and Blackburn 1997). Larger ranges may also contain a broader variety of environments facilitating divergence (Jablonski and Roy 2003). Accordingly, previous studies found positive relationships between the total range size of a clade (sum of constituent taxa) and the number of species or subspecies it contains (Owens et al. 1999; Belliure et al. 2000; Phillimore et al. 2007). Conversely, if speciation events are associated with range division, there should be a negative relationship between mean range size of a clade (average of constituent taxa) and species richness, as has been shown in mollusks

(Jablonski and Roy 2003) and birds (Phillimore et al. 2006). We found no such relationship in antbirds.

Despite our results, antbird speciation is likely to have been strongly influenced by range fragmentation. Neotropical forests are separated by mountain ranges and arid regions, while low-stature forests and dry forests are isolated by tall, humid forests. Historical vicariance events have apparently produced ideal conditions for allopatric speciation, even within Amazonia (Haffer 1997; Hall and Harvey 2002; Aleixo 2004; Isler et al. 2007*b*). Here, up to 50 resident antbird species can occur in sympatry, including multiple congeneric species (Terborgh et al. 1990). This alpha diversity, perhaps unique in bird families, may be at least partly explained by physical properties of Amazonian forests such as high structural complexity (MacArthur and MacArthur 1961) and habitat heterogeneity (Tuomisto et al. 1995). On the other hand, it may also arise from intrinsic properties of the antbird clade that facilitate species diversification and coexistence. High alpha diversity also suggests that speciation in antbirds has been repeatedly followed by range expansion, making it difficult to detect correlations between range size and species richness.

From Pattern to Process

Our finding that plumage dichromatism and song structure are associated with species and subspecies diversity is consistent with the hypothesis that sexual selection has played a role in speciation in a diverse suboscine assemblage. However, the mechanisms behind these correlations remain unclear. Divergence in traits and associated preferences is key to the speciation process (West-Eberhard 1983; Price 1998; Coyne and Orr 2004) and may evolve as a by-product of ecological adaptation (Schluter 2001; Price 2007). In birds, for example, plumage evolution is shaped by habitat, light, and predation (Marchetti 1993; Endler and Théry 1996; Badyaev and Hill 2003), while vocal evolution is shaped by the constraints imposed by morphology and environment (Ryan and Brenowitz 1985; Podos et al. 2004; Seddon 2005). On the other hand, sexual traits can diverge in the absence of ecological divergence in invertebrates (Gray and Cade 2000; Masta and Maddison 2002), cichlid fish (Seehausen et al. 1997), and amphibians (Boul et al. 2006), and the same may be true in birds.

The relationships found in this study add weight to the argument that sexual selection can generate or accelerate reproductive isolation between diverging populations, but they cannot disentangle the relative roles of ecological and sexual selection. This question should be addressed in suboscine and oscine passerine birds by detailed field studies and further comparative analyses, making use of more highly resolved phylogenies as they become available. This approach would improve our understanding of how the evolution of ecologically and sexually selected traits, especially acoustic signals, influences patterns of diversity in birds.

Acknowledgments

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